

AN ABSTRACT OF THE DISSERTATION OF

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Earth's atmosphere is unequivocally warming due to CO₂ and other greenhouse gas (GHG) emissions from human activities and this is having widespread impacts on forest ecosystems that provide important services to human societies. Forest ecosystems help regulate atmospheric CO₂ concentrations by sequestering carbon in tree biomass and soils, which is a valuable ecosystem service that is sensitive to climate change and forest management. Rising air temperatures contributed to increased aridity and drought during recent decades among forests in the western United States and projections suggest that many parts of this region could become hotter and drier over the coming century barring significant reductions in GHG emissions. Managing regional forests and GHG emissions in a warming world requires better understanding of how forest carbon cycling is influenced by climate, including climate-mediated disturbance (e.g., fires). The objectives of this dissertation were to assess (1) forest response to water availability and (2) tree mortality from disturbance during recent decades in the western US.

Forest response to water availability was assessed, in part, by quantifying changes in forest productivity and live biomass across sites that varied widely in average water availability. Bioclimatic relationships were developed using (1) field measurements from 12 sites in the eastern Cascade Mountains, (2) inventory and ancillary plot measurements from 1,953 sites in Washington, Oregon, and California (WAORCA), and (3) remote sensing measurements spanning 18 Mha of mature forest in the western US. In each case, forest productivity and live biomass increased markedly across sites as average water availability

increased. For instance, median forest productivity increased from 2.2 to 5.6 Mg C ha⁻¹ yr⁻¹ between the driest and wettest 5% of sites in WAORCA, while live biomass increased from 26 to 281 Mg C ha⁻¹. These bioclimatic relationships illustrate that forests are widely sensitive to changes in water availability, suggesting that continued warming and drying could reduce carbon sequestration over the coming century in parts of the region.

Tree mortality from fires, bark beetles, and timber harvest was quantified from 2003-2012 across the region using remote sensing, federal harvest statistics, and ancillary information. Tree mortality was quantified in terms of carbon storage in aboveground biomass killed by disturbance. Regional tree mortality from these disturbances together averaged 45.8±16.0 Tg C yr⁻¹ (±95% confidence interval), with harvest, beetles, and fires accounting for 50%, 32%, and 18% of mortality, respectively. Tree mortality from timber harvest was concentrated in the high-biomass forests of the Washington and Oregon. Tree mortality from bark beetles occurred largely in Colorado, Wyoming, and Montana, where tree defenses were suppressed by drought and beetle populations bolstered by rising winter temperatures. Tree mortality from fires was highest in California, Idaho, and Montana, which also experienced very dry conditions during this decade. Tree biomass killed by disturbance will gradually decompose and emit CO₂ to the atmosphere over decades to centuries, where it will act as a GHG. This analysis illustrates both opportunities and challenges to managing GHG emissions from forest ecosystems in the region. Swift and significant reductions in GHG emissions are needed to curtail adverse impacts of climate change on forest ecosystems and human societies.

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Forest Response to Water Availability and Disturbance in the Western United States

by
Logan T. Berner

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Logan T. Berner, Author

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CONTRIBUTION OF AUTHORS

Chapter 2: Logan Berner designed and implemented the study, performed the analysis, and drafted the paper. Dr. Beverly Law provided guidance and contributed to drafting the paper.

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Chapter 4: Logan Berner designed and implemented the study, performed the analysis, and drafted the paper. Dr. Beverly Law provided guidance and contributed to drafting the paper. Drs. Jeff Hicke and Arjan Meddens provided data and methods, as well as contributed to drafting the paper.

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Forest Response to Water Availability and Disturbance in the Western United States

by

Logan T. Berner

CHAPTER 1. INTRODUCTION

Earth's atmosphere is unequivocally warming due to human activities, which is having unintentional impacts on forest ecosystems that provide important services to human societies (ACIA, 2004, IPCC, 2013, Melillo *et al.*, 2014). Human fossil fuel consumption and land-use activities (e.g., deforestation) emitted ~600 Pg C into the atmosphere since 1750, causing atmospheric CO₂ concentrations to increase from ~280 ppm to ~400 ppm (Le Quéré *et al.*, 2015). Once in the atmosphere, CO₂ acts as a potent greenhouse gas (GHG) that blocks outgoing infrared radiation. The ongoing buildup of CO₂ and other GHGs (e.g., CH₄, N₂O) is therefore warming the atmosphere and changing global climate (IPCC, 2013, Melillo *et al.*, 2014). Climate change impacts on ecosystems (e.g., forests) and human societies are increasingly evident and concerning (Abatzoglou & Williams, 2016, Allen *et al.*, 2010, Barriopedro *et al.*, 2011, Beck *et al.*, 2011, Ebi, 2010, Melillo *et al.*, 2014). Consequently, there is widespread recognition that swift and significant reductions in GHG emissions are needed to curtail future adverse impacts of climatic change (e.g., The Paris Climate Agreement; UNFCCC, 2015).

Forests play an important role in regulating atmospheric GHG concentrations and global climate (Anderson-Teixeira *et al.*, 2012, Bonan, 2008, Le Quéré *et al.*, 2015), but are also sensitive to ongoing climatic change (Allen *et al.*, 2015, Berner *et al.*, 2013, Nemani *et al.*, 2003). Plant photosynthesis pulls CO₂ from the atmosphere and produces sugars that can be used to synthesize biomass, which is ~50% carbon by dry weight (Campbell & Reece, 2005). Plant photosynthesis in terrestrial ecosystems sequestered ~165 Pg C from the atmosphere since 1750, which was ~28% of the CO₂ released by humans (Le Quéré *et al.*, 2015). Terrestrial ecosystems currently store ~2,000 Pg C (Houghton, 2013), about half of which (~860 Pg C) is sequestered in tree biomass, necromass, and soil organic matter found in forest ecosystems (Pan *et al.*, 2011a). In other words, forest ecosystems store about as much carbon as is currently in the atmosphere (Houghton, 2013), yet climatic change is affecting forest carbon uptake and storage. For instance, rising air temperatures increased productivity in some northern (Berner *et al.*, 2013, Nemani *et al.*, 2003) and high-elevation forests (Salzer *et al.*, 2009) with short, cool growing seasons; however, higher temperatures also suppressed productivity and accelerated tree mortality in other areas due to more severe heat and drought stress (Allen *et al.*, 2010, Beck *et al.*, 2011, van Mantgem *et al.*, 2009, Williams *et al.*, 2012). It is crucial to evaluate forest response to climate given both human

reliance on forest ecosystem services and the potential for forest-climate feedbacks that could accelerate or mitigate ongoing climatic change.

Forests cover ~29% of western United States (US; Hicke *et al.*, 2007) and are strongly influenced by water availability (Gholz, 1982, Littell *et al.*, 2008, Webb *et al.*, 1983, Williams *et al.*, 2010), which varies widely across the region and is changing in many areas with regional warming (Cook *et al.*, 2015, Cook *et al.*, 2004, Mote *et al.*, 2014). Mean annual precipitation (1971-2000) in this region ranged from <10 cm yr⁻¹ among deserts in the Southwest to >500 cm yr⁻¹ along the coast in the Pacific Northwest, with regional variation largely governed by proximity to the ocean and the distribution of mountain ranges (Daly *et al.*, 2008). Pronounced hydrologic gradients play an important role in shaping regional variation in forest composition, productivity, and biomass (Gholz, 1982, Jin & Goulden, 2014, Kang *et al.*, 2014, Webb *et al.*, 1983, Whittaker & Niering, 1975). For instance, forests range from dry woodlands with slow-growing, drought-adapted tree species (e.g., *Juniperus* spp.) to coastal temperate rainforests where tree biomass attains levels among the highest found anywhere in the world (Hudiburg *et al.*, 2009, Keith *et al.*, 2009, Waring & Franklin, 1979). Forests in this region are also sensitive to temporal variation in water availability (Littell *et al.*, 2008, Williams *et al.*, 2010) and in the last several decades parts of the region experienced exceptionally hot and dry conditions that affected forest productivity and tree mortality (Diffenbaugh *et al.*, 2015, van Mantgem *et al.*, 2009, Williams *et al.*, 2012).

Rising air temperatures are exacerbating drought and corresponding drought-stress on forests in parts of the western US. Mean annual air temperatures in this region increased 0.8-1.1°C from 1895 to 2011, though most areas experienced no long-term change in precipitation (Kunkel *et al.*, 2013, Mote *et al.*, 2014). Higher air temperatures increase both potential evapotranspiration from the land surface (Droogers & Allen, 2002) and the likelihood that anomalously high air temperatures will coincide with periods of low precipitation (Diffenbaugh *et al.*, 2015). Consequently, rising temperatures contributed to increases in the extent, frequency, and severity of drought over the past century (Cook *et al.*, 2004, Diffenbaugh *et al.*, 2015, McCabe *et al.*, 2004) and from 2000-2004 the region experienced the most severe drought in the past 800 years (Schwalm *et al.*, 2012). This drought event suppressed regional forest productivity and contributed to extensive tree mortality from fires and bark beetles in some areas (Creeden *et al.*, 2014, Schwalm *et al.*, 2012, Williams *et al.*, 2012), particularly the Southwest (Breshears *et al.*, 2005, Williams *et al.*, 2012). More broadly, warmer and drier conditions led to increases in both tree mortality rates (McDowell *et al.*, 2015, Smith *et al.*, 2015, van Mantgem *et al.*, 2009) and annual area

burned during recent decades in this region (Abatzoglou & Williams, 2016, Westerling *et al.*, 2006). Trees killed by drought and disturbance will gradually decompose and emit CO₂ back into the atmosphere over decades to centuries (Harmon *et al.*, 2011), which could amplify regional warming (Anderson-Teixeira *et al.*, 2012).

There are growing concerns that continued climatic change could further exacerbate drought-stress on forests in this region over the coming century (Allen *et al.*, 2015, Anderegg *et al.*, 2015a, McDowell *et al.*, 2015). Climate projections indicate that regional temperatures could rise another 3.8-5.5°C by the end of the century and that much of the region, particularly the areas that are characteristically dry like the Southwest, could become increasingly arid and prone to drought under a high GHG emission scenario (RCP 8.5; Cook *et al.*, 2015, Kunkel *et al.*, 2013, Walsh *et al.*, 2014). Tree-ring based reconstructions indicate that very persistent, severe, and extensive droughts ('mega-droughts') occurred over the past 1200 years in this region, particularly during an abnormally warm period from around AD 900 to 1300 (Cook *et al.*, 2004, Woodhouse *et al.*, 2010). Continued regional warming over the coming century could produce droughts that are much more severe and persistent than the documented historical mega-droughts (Cook *et al.*, 2015, Schwalm *et al.*, 2012, Williams *et al.*, 2012). The rapid velocity and trajectory of projected climate change could accelerate tree mortality and forest die-back in parts of the region, with implications for forest ecosystem services including carbon sequestration (Adams *et al.*, 2009, Jiang *et al.*, 2013, McDowell *et al.*, 2015).

It is crucial to better understand forest response to water availability and disturbance in the western US given the importance of forest ecosystem services (Williams, 2006), the potential forest-climate feedbacks (Anderson-Teixeira *et al.*, 2012), and the trajectory of ongoing climatic change (Cook *et al.*, 2015). The US Forest Service (USFS) recently highlighted that forest biomass, productivity, and disturbance by fires and insects are all sensitive to climate and thus should be monitored as indicators of national climatic change (Heath *et al.*, 2015). This dissertation presents three studies that investigated how forest carbon cycling was affected by water availability and disturbance in the western US (Berner & Law, 2015, Berner *et al.*, 2017, Berner *et al.*, in revision). These studies employed techniques from ecology, dendrochronology, climatology, and remote sensing to better understand forest dynamics across a range of spatial, temporal, and biological scales.

The first study (Chapter 2) investigated how forest carbon cycling and conifer morphological traits responded to variation in water availability among mature stands in the eastern Cascade Mountains, Oregon (Berner & Law, 2015). The Cascade Mountains exhibit

one of the steepest hydrologic gradients in North America, making this area an excellent natural laboratory for studying ecosystem response and plant adaptation to water availability. We established 12 field sites along this hydrologic gradient that included forests dominated by grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), and western juniper (*Juniperus occidentalis*). We then used a combination of stand survey, tree ring, and morphological measurements together with gridded climate data to test the following three hypotheses:

- I. Long-term average water availability constrains tree leaf area, productivity, and aboveground biomass at low- to mid-elevations in the eastern Cascade Mountains.
- II. Interannual fluctuations in water availability exert a stronger influence on tree growth in dry, low-elevation forests than in wet, mid-elevation forests.
- III. Trees respond to increased long-term water availability (i.e., reduced hydraulic stress) by increasing investment of resources to competition for light.

The second study (Chapter 3) explored how forest carbon cycling responded to spatial variation in water availability across the western US (Berner *et al.*, 2017). We hypothesized that long-term water availability constrains tree productivity, biomass, and carbon residence time in live biomass across mature forests in the western US. We tested these hypotheses first across Washington, Oregon, and California (WAORCA) using forest inventory measurements from nearly 2,000 field sites in mature stands (> 100 years old). We then tested these hypotheses across 18 Mha of mature forest in the western US using satellite remote sensing data sets that included three national biomass maps and net primary productivity derived using the Moderate Resolution Imaging Spectroradiometer (MODIS).

The final study (Chapter 4) assessed the magnitude and regional variation in tree mortality from fires, bark beetles, and timber harvest in the western US. The primary research question: “What was the magnitude and relative contribution of mean annual tree mortality from fires, bark beetles, and timber harvest from 2003-2012 both regionally and among the 11 western states?”. Specifically, we quantified tree mortality as the amount of carbon stored in aboveground woody biomass killed by disturbance. We developed spatially explicit estimates of annual tree mortality from fires and bark beetles for the region using remote sensing information on tree biomass, as well as the extent and severity of fire and beetle activity. We then estimated mean annual tree mortality from timber harvest for each state based on US Forest Service (USFS) national forest resource reports and ancillary information. We quantified uncertainty in tree mortality estimates using a Monte Carlo approach to that accounted for temporal variability and parameter error.

Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon

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CHAPTER 2. WATER LIMITATIONS ON FOREST CARBON CYCLING AND CONIFER TRAITS ALONG A STEEP CLIMATIC GRADIENT IN THE CASCADE MOUNTAINS, OREGON

Abstract

Severe droughts occurred in the western United States during recent decades and continued human greenhouse gas emissions are expected to exacerbate warming and drying in this region. We investigated the role of water availability in shaping forest carbon cycling and morphological traits in the eastern Cascade Mountains, Oregon, focusing on the transition from low-elevation, dry western juniper (*Juniperus occidentalis*) woodlands to higher-elevation, wetter ponderosa pine (*Pinus ponderosa*) and grand fir (*Abies grandis*) forests. We examined 12 sites in mature forests that spanned a 130 cm yr⁻¹ gradient in mean water year climate moisture index ($CMI_{\overline{wy}}$), computed annually (1964 to 2013) as monthly precipitation minus reference evapotranspiration and summed October to September. Maximum leaf area, annual aboveground productivity, and aboveground live tree biomass increased with $CMI_{\overline{wy}}$ ($r^2=0.67-0.88$, $P<0.05$), approximately 50-, 30-, and 10-fold along this drier to wetter gradient. Interannual fluctuations in CMI affected the annual radial growth of 91% of juniper, 51% of pine, and 12% of fir individuals from 1964 to 2013. The magnitude of the site-average growth-CMI correlations decreased with increased $CMI_{\overline{wy}}$ ($r^2=0.53$, $P<0.05$). All three species, particularly fir, experienced pronounced declines in radial growth from c. 1985 to 1994, coinciding with a period of sustained below-average $CMI_{\overline{wy}}$ and extensive insect outbreak. Traits of stress-tolerant juniper included short stature, high wood density for cavitation resistance, and high investment in water transport relative to leaf area. Species occupying wetter areas invested more resources in height growth in response to competition for light relative to investment in hydraulic architecture. Consequently, maximum tree height, leaf area:sapwood area ratio, and stem wood density were all correlated with $CMI_{\overline{wy}}$. The tight coupling of forest carbon cycling and species traits with water availability suggests that warmer and drier conditions projected for the 21st century could have significant biogeochemical, ecological, and social consequences in the Pacific Northwest.

Introduction

Droughts in the western United States (US) had severe impacts on human and natural systems during the past century (Allen *et al.*, 2010, Schwalm *et al.*, 2012, Williams *et al.*, 2012, Woodhouse & Overpeck, 1998) and sustained climatic warming due to human greenhouse gas emissions will likely exacerbate drought impacts over the coming century (Collins *et al.*, 2013, Dai, 2013, Williams *et al.*, 2012). Mean annual air temperatures in the western US increased 0.8-1.1°C from 1895 to 2011 (Kunkel *et al.*, 2013, Mote *et al.*, 2014) and could rise an additional 5.4°C by the end of the 21st century (Walsh *et al.*, 2014). Rising temperatures resulted in substantial reductions (up to 80%) in spring snowpack across most mountain ranges in the region since observations became widespread in the 1950s (Mote *et al.*, 2014, Mote *et al.*, 2005) and during April 2015 snowpack was less than 25% of the 30-yr average across the Cascade and Sierra Mountain Ranges (USDA Natural Resources Conservation Service, 2015).

Tree-ring based reconstructions indicate that very persistent, severe, and extensive droughts ('mega-droughts') occurred over the past 1200 years in the western US, especially during an abnormally warm period from around AD 900 to 1300 (Cook *et al.*, 2004, Woodhouse *et al.*, 2010), and suggest an increase in the area annually affected by drought over the 20th century (Cook *et al.* 2004). The most severe drought over the past 800 years occurred in 2000-2004 (Schwalm *et al.*, 2012) and continued regional warming over the 21st century is expected to produce droughts that are much more severe and persistent than the documented historical mega-droughts (Collins *et al.*, 2013, Dai, 2013, Schwalm *et al.*, 2012, Williams *et al.*, 2012), with widespread ecological and socioeconomic consequences (Diffenbaugh & Field, 2013, Jiang *et al.*, 2013, Mote *et al.*, 2014).

Water availability varies widely across the western US and shapes the distribution and composition of forests, as well as forest carbon cycling. Mean annual precipitation (1971-2000) ranged from <10 cm yr⁻¹ in parts of the Southwest to >500 cm yr⁻¹ in parts of the Pacific Northwest, with spatial patterns largely governed by proximity to the ocean and the distribution of mountain ranges (Daly *et al.*, 2008). Strong spatial gradients in water availability across this region play an important role in shaping the distribution of tree species and plant communities (Franklin & Dyrness, 1988, Mathys *et al.*, 2014). For instance, drought-tolerant western juniper (*Juniperus occidentalis*) form open woodlands in the dry foothills of the eastern Cascade Mountains, Oregon, while increased rainfall at higher elevations leads to a sequence of forest zones dominated by species with progressively lower

drought tolerance, such as ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis* Dougl.) and western hemlock (*Tsuga heterophylla*; Franklin & Dyrness 1988), and progressively higher leaf area, productivity and biomass (Gholz, 1982, Grier & Running, 1977). Warming-induced drought-stress contributed to increased tree mortality rates (Allen, 2009, Peng *et al.*, 2011, van Mantgem *et al.*, 2009) and wildfire activity (Dennison *et al.*, 2014, Westerling *et al.*, 2006) in parts of western North America over the 20th century and the rapid velocity of climate change projected for the 21st century (Loarie *et al.*, 2009) is expected to drive pronounced, though relatively uncertain changes in forest distribution (Coops & Waring, 2011, Jiang *et al.*, 2013, Rehfeldt *et al.*, 2006) and biogeochemical cycling (Hudiburg *et al.*, 2011, Jiang *et al.*, 2013, Kang *et al.*, 2014), with impacts dependent in part on species' morphological and physiological adaptations to drought stress (Law, 2014, McDowell & Allen, 2015).

Plants have evolved numerous adaptations to prevent hydraulic dysfunction, but adaptations that allow plants to withstand very arid conditions often reduce their ability to compete in wetter, more productive environments. Water is used for myriad physiological processes (e.g., photosynthesis, heat dissipation, osmotic regulation; Kozlowski *et al.*, 1991) and ascends from the soil into vascular plant canopies through xylem conduits, driven by tension imparted on the water column from molecules being evaporated from leaf substomatal chambers (Sperry, 2011, Tyree, 1997). Plants have adaptations to maintain xylem water potentials (Ψ) within physiologically operable ranges so as to prevent runaway cavitation of the water column and subsequent hydraulic and photosynthetic impairment (Pockman *et al.*, 1995, Sperry & Tyree, 1988) caused by low soil Ψ and high atmospheric vapor pressure deficit (VPD; Whitehead *et al.*, 1984). The xylem Ψ required for substantial hydraulic impairment [e.g. 50% loss of hydraulic conductance (P50)] varies both within (Domec *et al.*, 2009) and among species (Anderegg, 2015, Choat *et al.*, 2012, Willson *et al.*, 2008), depending in part on the mechanical strength of the xylem conduits, which tends to increase with wood density (Chave *et al.*, 2009, Hacke *et al.*, 2001, Jacobsen *et al.*, 2007). When conditions are dry, some plants reduce stomatal conductance to help maintain xylem Ψ within an operable range, yet this simultaneously reduces carbon assimilation and can lead to carbon starvation and mortality if sustained (McDowell, 2011). Plants can also manage xylem Ψ by shedding leaves or, more gradually, by increasing investment in sapwood (Maherali & DeLucia, 2001, Mencuccini & Grace, 1995), either of which lowers the leaf:sapwood area ratio (LA:SA). Holding other factors constant, taller trees experience lower (i.e. more negative) xylem Ψ at the top of the canopy due to increased gravitational pull and cumulative

path-length resistance (Koch *et al.*, 2004, Whitehead *et al.*, 1984), which is potentially a key factor limiting maximum tree height in a given environment (Koch *et al.*, 2004, Ryan & Yoder, 1997) and can predispose taller trees to drought-induced mortality (McDowell & Allen, 2015). Adaptations that enable plants to endure harsh abiotic stress (e.g. drought) often come at a competitive cost in more productive environments due to lower rates of resource acquisition and processing (Grime, 1974, Grime, 2001, Reich, 2014).

Given the potential socioeconomic and ecologic impacts it is imperative that we better understand how forest ecosystems in the western US respond to spatial and temporal variations in water availability. Our objective in this study was to investigate how forest carbon cycling and conifer morphological traits responded to variation in water availability across a network of field sites in the eastern Cascade Mountains, Oregon, which included forests dominated by western juniper, ponderosa pine, and grand fir. We used the average growing-year climate moisture index ($CMI_{\overline{wy}}$, 1964-2013) as an indicator of water availability (Berner *et al.*, 2013, Hogg & Hurdle, 1995), calculated as the difference between monthly precipitation (P) and reference evapotranspiration (ET_0) from October of year $t-1$ through September of year t . The Cascade Mountains exhibit one of the steepest $CMI_{\overline{wy}}$ gradients in North America (Fig. 2.1a), making it an excellent natural laboratory for studying plant adaptation and ecosystem response to water stress (e.g., Gholz, 1982, Law & Waring, 1994). We used a combination of stand survey, tree ring, and morphological measurements to test the following three hypotheses:

- I. Long-term water availability limits forest carbon cycling at low- to mid-elevations in the eastern Cascade Mountains. Building on prior analyses in the region (Gholz, 1982, Grier & Running, 1977, Law & Waring, 1994), we predicted that forest leaf area index (LAI), annual aboveground net primary productivity (ANPP), and aboveground live biomass (AGB) would increase with $CMI_{\overline{wy}}$.
- II. Interannual fluctuations in water availability exert a stronger influence on tree growth in dry, low-elevation forests than in wet, mid-elevation forests. We anticipated that the proportion of trees exhibiting a significant positive correlation between annual tree ring-width indices (RWI) and CMI over the past 50 years ($F_{RWI-CMI}$) would be highest among western juniper, followed by ponderosa pine and then grand fir. Furthermore, we predicted that the site-average strength of the RWI-CMI correlation ($\overline{r}_{RWI-CMI}$) across years would decrease with increasing $CMI_{\overline{wy}}$ across sites
- III. Trees respond to increased long-term water availability (i.e., reduced hydraulic stress) by increasing investment of resources to competition for light. We anticipated

that average stem wood density ($\overline{WD}$) would decrease with increased $CMI_{\overline{wy}}$, whereas maximum tree height (H_{max}) and LA:SA would increase with $CMI_{\overline{wy}}$.

Materials and methods

Study design

We employed a gradient analysis that included 12 sites evenly distributed among three forest types (western juniper, ponderosa pine, and grand fir) along the eastern slopes of the Cascade Mountains, Oregon, which ranged in elevation from 929 to 1560 m above sea level (Fig. 2.1a,b). Guided by maps of forest type (Kagan *et al.*, 2006), historical wildfires (Eidenshink *et al.*, 2007), and land ownership we selected sites in areas with mature (>80 years), publicly-owned forest that showed minimal evidence of recent natural (e.g. fire, insect) or human disturbance (e.g. thinning). Furthermore, sites were situated within 100 m of a road to facilitate access. We included the long-term AmeriFlux Metolius Mature Pine (US-Me2) eddy covariance flux tower (Law *et al.*, 2004) as one of our ponderosa pine sites. Additionally, we collected samples at three relatively young stands, one for each species, which included the Metolius Young Pine Burn flux tower site (US-Me6). These data are presented in Table A1, though were not included in our analysis given that the mean cambial age at breast height was 17 to 38 years, depending on site.

At each new site we established a randomly located 1-ha plot, as per the Global Terrestrial Observing System (GTOS) protocol (Law *et al.*, 2008), though used pre-existing plots at US-Me2 and US-Me6. The plot design, similar to that used by the USDA Forest Service Forest Inventory and Analysis program, included one central subplot and three subplots arranged in a circular pattern around the center and offset from the center by 35 m. Subplot radii were held consistent within a site, but varied among sites from 10-17 m for trees and from 5-17 m for saplings, depending on stem density. Stems with a diameter at breast height (DBH, 1.4 m) greater than 10 cm were considered trees, while those with DBH from 1-10 cm were considered saplings. We tagged every tree (n=730) and sapling (n=39) in the study with a unique identifier. Seedlings (DBH < 1 cm) were not sampled.

Field sampling

Field activities included stem survey measurements, collection of tree core and foliage samples, and optical measurements of leaf area, as per the GTOS protocol (Law *et al.*, 2008). We measured DBH and total height (H) of every tagged stem and then, within each subplot, randomly selected a subset of trees for intensive measurement. Tree H was measured using a laser range finder (Laser Technology Inc., Centennial, USA). We cored five trees of the dominant species per subplot (20 trees per plot) for growth measurements. Tree cores were extracted near breast height using a 5.15 mm increment borer and, if necessary, oriented perpendicular to the slope. We then randomly selected two or three of the five trees per subplot (10 trees total per plot) and collected an additional core from each tree for wood density and sapwood area measurements. For each of the 10 intensively measured trees we also excised mid-canopy, south-facing branches and collected foliage for measurements of leaf longevity (LL), specific leaf area (SLA), and foliar carbon (C) and nitrogen (N). For ponderosa pine and grand fir we estimated LL on the excised branches using the “counting cohorts” method (Pérez-Harguindeguy *et al.*, 2013). Since western juniper do not form distinct cohorts we calculated LL based on estimates of foliage biomass and annual leaf litter fall from a nearby site (Runyon *et al.*, 1994). Foliage was then stored following standard protocols prior to laboratory analysis (Pérez-Harguindeguy *et al.*, 2013). We collected additional tree cores and foliage samples when nondominant tree species were present in the subplots. The number of additional trees varied from one to six depending on the diversity and relative abundance of additional species. Lastly, we measured canopy gap fraction on each subplot using an optical LI-2200 Plant Canopy Analyzer for conifers (LI-COR, Lincoln, USA).

Sample processing

Tree radial growth, sapwood area, and stem wood density

We measured annual radial growth using 256 tree cores, focusing principally on the 50-year period from 1964 to 2013, and estimated tree age on cores that included the pith. The tree cores were processed using standard procedures (Pilcher, 1990). We measured annual ring-widths using a desktop scanner and WinDendro software (89% of cores) or a stereoscopic microscope, Velmex sliding stage, and MeasureJ2X software if the growth-rings were very

tight (11% of cores). We cross-dated the cores visually (Yamaguchi, 1991) and then statistically in R (R Core Team, 2015; version 3.2.0) using the Dendrochronology Program Library in R package (dplR; Bunn, 2010).

We estimated sapwood area and basic stem wood density initially using the same set of tree cores (n=144). Sapwood width was measured using calipers. Sapwood area at breast height was calculated for each sampled tree as the difference between stem basal area (excluding bark) and stem heartwood area, assuming a circular trunk. For each species DBH was a strong predictor of sapwood area ($r^2=0.85-0.93$, Table A2) and therefore we used these relationships to predict sapwood basal area for trees that were not sampled.

We estimated basic stem wood density following published guidelines (Williamson & Wiemann, 2010), which involved removing the bark, cutting each core into multiple segments and then measuring segment cross-sectional diameter and length using calipers. The core segments were oven-dried at 101-105°C for 72 hours and then immediately weighed. We calculated basic stem wood density (WD, g cm⁻³) for each core segment by dividing oven-dry mass (g) by the green volume (cm³). Since each segment represented a different portion of the total trunk cross-sectional area, we calculated an area-weighted mean WD across segments to account for potential variation in WD between the cambium and the pith (Muller-Landau, 2004). Williamson and Wiemann (2010) recommended estimating WD from tree cores only when the core includes the pith. Since 25% of our tree cores (n=43) did not include the pith, we tested, for each species, whether WD estimates differed significantly depending on whether the tree had been or had not been pithed. For fir and pine, the WD estimates did not differ significantly (t-tests, $P>0.05$) between samples with or without the pith; however, for juniper, the WD estimates were significantly lower for samples that did not include the pith ($P<0.05$). We therefore chose to exclude samples from 14 juniper trees that did not include the pith, yet retained all samples from fir and pine irrespective of whether the sample included the pith. In total, we analyzed samples from 120 trees.

Specific leaf area and foliar chemistry

We measured SLA [one-half of total leaf (i.e., hemisurface area) area per gram of carbon] and leaf chemistry (C and N) using samples collected from 186 trees in the middle of the growing season. Mid-growing season leaf characteristics tend to be representative of species-average conditions (e.g., Nippert & Marshall, 2003). We carefully trimmed the needles from each sample (usually about 0.5 g dry weight), measured the cumulative projected surface area

using a LI-3100C Area Meter (LI-COR, Lincoln, USA), dried each sample at 70°C for at least 72 hours, and then immediately weighed each sample (Pérez-Harguindeguy *et al.*, 2013). Samples were then finely ground and sent to Central Analytical Laboratory at Oregon State University for analysis of C and N content using a Leco CNS-2000 Macro Analyzer. We calculated SLA (cm² leaf g⁻¹ C) as

$$SLA = \frac{A \times \beta}{M \times C} \quad (1)$$

where A was the projected surface area (cm²); β was a species-specific conversion coefficient drawn from the literature that related A to one-half of total surface area (Table 2.1); M was oven-dry mass (g); and C was the species-average carbon content of leaf dry matter (%).

Forest leaf area, biomass, and productivity

Forest leaf area

We estimated LAI (one half of surface area of needles (m²) per square meter of ground) at 35-45 random points on each subplot based on optical measurements. We used the FV2200 software (LI-COR, Lincoln, USA) to calculate effective leaf area (L_e) from field measurements of canopy gap fraction, which implemented a foliage scattering and transmittance correction that permits measurements to be made during periods of direct sunlight (Kobayashi *et al.*, 2013). The LAI measurements were subsequently corrected for foliage (γ) and canopy clumping (Ω), as well as for light interception by branches and stems (Chen, 1996, Law *et al.*, 2008). We computed LAI as

$$LAI = L_e \left(\frac{\gamma}{\Omega} \right) - W \quad (2)$$

where species-specific γ were derived from the literature (Frazer *et al.*, 2000, Law *et al.*, 2001b) and Ω was derived directly from the LI-2200. We calculated wood area index (W) from stand basal area (BA , m² ha⁻¹) as

$$W = 2.061 \times (1 - e^{(-0.006 \times BA)}) \quad (3)$$

based on the strong relationship ($r^2=0.90$) observed between W and BA across 96 sites in Oregon (Law, unpublished data). For mixed species subplots we calculated a biomass-weighted mean γ .

Forest biomass

We estimated forest AGB (kg C m^{-2}) for each subplot as the total mass of bole, branch, bark, and leaf carbon of all trees and saplings, divided by the areal extent of each plot. Tree component biomass was computed using species-specific allometric equations based on tree DBH and H, while sapling biomass was calculated from height alone (Gholz *et al.*, 1979, Means *et al.*, 1994, Wenzel, 1977). Bole volume estimates were converted to dry matter using species-average WD measurements from our study sites. Bole, branch, and bark dry matter were assumed to be 51% carbon (Law *et al.* 2001). Leaf mass was computed by dividing LAI by ecosystem-averaged SLA, with ecosystem-average SLA calculated based on the relative biomass of each species present.

Forest productivity

We estimated forest ANPP ($\text{kg C m}^{-2} \text{ yr}^{-1}$) biometrically for each site by calculating the change in forest AGB (excluding leaf mass) between 2005 and 2014, divided by the number of intervening years, plus annual leaf turnover (e.g., Hudiburg *et al.*, 2009, Van Tuyl *et al.*, 2005). This necessitated hindcasting DBH and H for each tree using radial growth measurements and allometric models to predict H from DBH. We did not collect cores from every tree and therefore we divided the trees at each site into three equal-sized, species-specific groups based on DBH. We then took the available ring-width measurements within each size class and calculated the average diameter increment over the preceding 10 years, which was then subtracted from the DBH_{2014} of each tree in the size class to yield an estimate of DBH_{2005} . For each species we developed a nonlinear Weibull-type model (Yang *et al.*, 1978) to predict H from DBH ($r^2 = 0.66\text{--}0.87$, $\text{RMSE} = 1.55\text{--}3.21 \text{ m}$, Table A3). We estimated H_{2005} from DBH_{2005} for each tree and subsequently calculated forest AGB in 2005 (excluding leaf mass) for each subplot. Forest ANPP was then estimated for each subplot by differencing woody AGB from 2014 from that of 2005, divided by the 10 intervening years, plus annual leaf turnover computed by dividing leaf mass in 2014 by ecosystem-average leaf longevity measured at our sites.

Climate data and derivation of climate moisture index

We derived monthly estimates of CMI (Hogg, 1997) for each site as the difference between P and ET_0 using gridded climate data from 1964 to 2013. The climate data were produced by the Parameter-elevation Relationships on Independent Slopes Model (PRISM; <http://www.prism.oregonstate.edu/>; Daly *et al.*, 2008) based on climate station observations and spatial modeling at 4 km resolution. We calculated monthly ET_0 (mm month⁻¹) using a version of the Hargreaves equation (Hargreaves & Samani, 1985) modified by Droogers and Allen (2002):

$$ET_0 = 0.0013 \times 0.408R(T_{avg} + 17.0)(T_{rng} - 0.0123P)^{0.76} \quad (4)$$

which is based average daily extraterrestrial radiation (R ; MJ m⁻² d⁻¹), average daily temperature (T_{avg} , °C), daily temperature range (T_{rng} , °C), and precipitation (PPT , mm month⁻¹). Estimates of R were derived based on equations provided by Allen *et al.* (1998). Modeled monthly ET_0 and P agreed relatively well with meteorological measurements at the US-Me2 flux tower site from 2002 to 2012 ($r^2=0.57-0.64$, $P<0.01$) and at the US-Me6 flux tower from 2010 to 2013 ($r^2=0.58-0.65$, $P<0.01$). For each site we then summarized climate conditions over the water year (wy, October in year $t-1$ through September of year t), which involved calculating average T_{avg} , as well as cumulative P , ET_0 , and CMI (e.g. denoted CMI_{wy}). Lastly, we averaged growing-year climate conditions from 1964 to 2013 to produce 50-year climatologies for each variable (e.g. $CMI_{\overline{wy}}$).

Analyses

Constraints of long-term water availability on forest carbon cycling

For each site we computed the average and standard error (SE) of LAI, ANPP, and AGB among subplots and then examined the relationship between each of the variables and $CMI_{\overline{wy}}$ across sites. Scatterplots revealed nonlinear relationships between each variable and $CMI_{\overline{wy}}$, which could be described using power functions ($Y = aX^b$). Power function models were fit using the nonlinear least squares (*nls*) function in R (version 3.2.0) and model residuals were visually examined. For each model we calculated the root mean squared error (RMSE) and the coefficient of determination (r^2), which was computed based on the proportion of the total sum of squares explained by the model. We also examined the relationships among forest LAI, ANPP, and AGB using least squares linear regression.

Influence of interannual fluctuations in water availability on tree radial growth

We derived standardized tree ring-width indices (RWI) for each mature tree using functions in dlpR (Bunn, 2010) and then quantified the association between each RWI series and monthly CMI aggregated over the preceding 1 to 36 months. For each tree at least 70 years old ($n=216$) we subset measurements from 1964 to 2013, detrended the series using a flexible spline and then standardized the series by dividing the ring-width in year t by the value predicted for year t by the fitted function (Fritts, 2001). Splines were fit with the *detrend* function in dplR using a 30-year window and frequency response of 0.5. Next, we removed lag-1 autocorrelation (i.e. pre-whitened) from each RWI series by taking the residuals of an ordinary least squares regression that related the RWI from each year against that of the prior year. We then computed Pearson's correlations between each RWI series and monthly pre-whitened and linearly detrended CMI aggregated from 1 to 36 months. This approach resulted in 432 correlations per tree (12 months x 36 lags). For each tree we calculated the overall strength of the RWI-CMI correlation as the average of the 95% quantile of all computed correlations. We then summarized these responses by both species and site. For each of the three species we calculated the percent of trees that exhibited a significant ($P<0.05$) positive RWI-CMI correlation at each month x lag combination. Next, we computed an ecosystem-average RWI-CMI correlation ($\bar{r}_{RWI-CMI}$) for each site, based on the relative biomass of each species, and then examined how $\bar{r}_{RWI-CMI}$ changed with $CMI_{\overline{wy}}$. We also tested whether the percent of trees at each site that exhibited a significant RWI-CMI correlation ($F_{RWI-CMI}$) differed among the three forest types using a nonparametric Kruskal-Wallis rank sum test (Kruskal & Wallis, 1952), which assess the null hypothesis that all samples come from the same distribution. Lastly, we examined the relationship between RWI and other climate variables, including T_{avg} , T_{min} , T_{max} , VPD, number of freeze days, the standardized precipitation-evaporation index (SPEI; Vicente-Serrano *et al.*, 2010) and the climatic water deficit (i.e., monthly ET in excess of P), yet focused on CMI because trees were generally most sensitive to this climate variable. For completeness, we provide summaries of these additional growth-climate relationships in Figure A1 and Table A4.

Constraints of long-term water availability on tree morphological traits

To explore long-term hydraulic constraints on forest morphology we compared LA:SA (m^2 leaf cm^{-2} sapwood), $H_{\max}$ (m), and $\overline{\text{WD}}$ (g cm^{-3}) to $\text{CMI}_{\overline{\text{wy}}}$. For each subplot we calculated LA:SA as the ratio between LAI and sapwood basal area, $H_{\max}$ as the height of the tallest tree, and $\overline{\text{WD}}$ as the biomass-weighted average WD of each species present. We then computed the average and SE of each characteristic for each plot. Next, we modeled each trait as a function of $\text{CMI}_{\overline{\text{wy}}}$ using either linear or nonlinear regression.

Results

Climate conditions

Summary statistics in this section are for 1964 to 2013 and represent cross-site averages (± 1 SD) within each of the three forest types (site-level summaries are given in Table A4). Average $T_{\overline{\text{wy}}}$ decreased from 8.32 ± 0.80 °C at the juniper sites to 6.26 ± 0.72 °C at the fir sites, while $\text{CMI}_{\overline{\text{wy}}}$ increased from -125 ± 12 cm yr^{-1} to -28 ± 25 cm yr^{-1} (Table 2.2). Across forest types July was the climatically driest month, while December, conversely, was the climatically wettest month. At juniper sites, CMI tended to be negative (i.e. ET_0 exceeded P) for nine consecutive months each year (February-October), whereas CMI was generally negative at pine and fir sites for eight (March-October) and seven (April-October) consecutive months, respectively.

Large interannual fluctuation in CMI_{wy} occurred between 1964 and 2013 (Fig. 2.2a,b,c). For instance, 1982 and 1997 were abnormally wet, whereas 1977 and 1994 were abnormally dry. At the juniper sites, CMI_{wy} during these wet years was around 300-400 mm greater than during the dry years. At the fir sites the difference in CMI_{wy} between these abnormally wet and dry years was more pronounced, exceeding 1000 mm. Other notable dry years included 1973, 1992, 2001 and 2003. Conditions were consistently drier than normal from 1985 to 1994, with $\text{CMI}_{\text{wy}} < \text{CMI}_{\overline{\text{wy}}}$ for eight or nine years, depending on forest type (Fig. A2).

Constraints of long-term water availability on forest carbon cycling

The 12 sites spanned a gradient in $\text{CMI}_{\overline{\text{wy}}}$ from $-124 \pm 12 \text{ cm yr}^{-1}$ to $5 \pm 29 \text{ cm yr}^{-1}$ and across this gradient forest LAI, ANPP, and AGB increased significantly ($P < 0.05$) and nonlinearly with $\text{CMI}_{\overline{\text{wy}}}$, which explained 67-88% of the variability in these stand characteristics (Fig. 2.3, Table 2.3, A1, A4). After accounting for wood interception and clumping, LAI ranged from 0.09 ± 0.03 to 6.15 ± 1.12 across sites, with average ($\pm 1 \text{ SD}$) LAI in each forest type increasing progressively from the open-canopy juniper sites (0.26 ± 0.13) to the pine (1.92 ± 0.51) and then closed-canopy fir sites (4.54 ± 1.49 , Fig. 2.3a, Table 2.4). Annual productivity along this gradient increased from 11 ± 2 to $311 \pm 60 \text{ g C m}^{-2} \text{ yr}^{-1}$ and averaged 17 ± 4 , 185 ± 62 , and $238 \pm 54 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the juniper, pine and fir sites, respectively (Fig. 2.3b). Aboveground biomass also tended to be quite low at the juniper sites ($2.6 \pm 0.4 \text{ kg C m}^{-2}$), yet reached higher levels at sites dominated by pine ($10.6 \pm 4.1 \text{ kg C m}^{-2}$) and fir ($14.4 \pm 5.9 \text{ kg C m}^{-2}$). Across sites there was a significant ($P < 0.01$) positive linear relationship between LAI and ANPP ($r^2 = 0.75$). Furthermore, AGB was positively associated with both LAI ($r^2 = 0.57$) and ANPP ($r^2 = 0.68$, Table 2.3).

Influence of interannual fluctuations in water availability on tree radial growth

Annual radial growth varied considerable from 1964 to 2013 (Fig. 2.2d,e,f) and tracked CMI more closely at the chronically dry juniper sites than at the wetter pine and fir sites (Figs. 2.4, 5). Growth reductions in response to single-year drought events (e.g. 1977, 1994, and 2001) were evident at the juniper sites, whereas reductions were more modest at the pine and fir sites (Fig. 2.2d,e,f). For instance, the 1977 drought led to a 73% reduction in average radial growth among juniper in comparison to growth during 1976 ($0.66 \pm 0.05 \text{ mm}$ vs. $0.18 \pm 0.03 \text{ mm}$). In contrast, this drought drove a 35% reduction in average growth among pine ($1.74 \pm 0.14 \text{ mm}$ vs. $1.08 \pm 0.10 \text{ mm}$) and a 7% reduction among fir ($1.87 \pm 0.14 \text{ mm}$ vs. $1.74 \pm 0.14 \text{ mm}$).

The vast majority of juniper ($91 \pm 3\%$) exhibited a significant positive RWI-CMI correlation ($\bar{r}_{\text{RWI-CMI}} = 0.52 \pm 0.02$) and responded most strongly to CMI over the 6 to 12 months leading up to late spring and summer (Fig. 2.4a, Table A5). Around $51 \pm 6\%$ of pine ($\bar{r}_{\text{RWI-CMI}} = 0.27 \pm 0.02$) and $12 \pm 4\%$ of fir ($\bar{r}_{\text{RWI-CMI}} = 0.11 \pm 0.02$) also exhibited a significant positive correlation with CMI, yet the influence of CMI seasonality and timescale were less distinct than for juniper (Fig. 2.4b,c). The proportion of trees exhibiting a significant RWI-

CMI association differed significantly among the three forest types (Kruskal-Wallis, $X^2=8.77$, $P=0.01$) and among sites there was a significant negative relationship between $\bar{r}_{\text{RWI-CMI}}$ and $\text{CMI}_{\overline{y}}$ ($r^2=0.53$, $P<0.05$), with $\bar{r}_{\text{RWI-CMI}}$ decreasing from 0.57 ± 0.14 to -0.02 ± 0.07 as conditions became wetter (Fig. 2.5). There was a very strong linear relationship between $\bar{r}_{\text{RWI-CMI}}$ and $F_{\text{RWI-CMI}}$ across sites ($r^2=0.92$, $P<0.001$). Significant proportions of western juniper and, to a lesser extent, ponderosa pine also showed negative correlations between growth and VPD, T_{max} , climatic water deficit, as well as positive correlations with SPEI, while grand fir were largely unresponsive to any of the climate variables that we examined (Fig. A1, Table A5).

Each species showed relatively high growth around 1980 to 1984, followed by a general decline from c. 1985 to 1994 (Fig. 2.2 right panel) that corresponded with a period of relatively *sustained*, below-average CMI_{wy} (Fig. 2.2 left panel) and, as discussed below, a widespread western spruce budworm (*Choristoneura freeman*) outbreak. The growth decline was particularly severe among fir; average radial growth in 1993 (0.55 ± 0.04 mm) and 1994 (1.00 ± 0.09 mm) was 73% and 52% lower, respectively, than in 1985 (2.07 ± 0.14 mm). In contrast, pine growth was 38% lower (1.23 ± 0.09 mm vs. 1.83 ± 0.12 mm) and juniper growth 42% lower (0.38 ± 0.03 mm vs. 0.66 ± 0.03 mm) in 1994 than in 1985. Since disturbances can obscure RWI-climate relationship, we reevaluated the correlations using measurements from 1994 to 2013 and found that the correlations changed little in comparison to those computed from 1964 to 2013 (Table A5).

Constraints of long-term water availability on tree morphological traits

Notable changes in morphological traits were evident along the water availability gradient (Fig. 2.6a,b,c, Tables 2.3, 2.4, A1). In general, ecosystem-average stem wood density, $\overline{\text{WD}}$, decreased with increased $\text{CMI}_{\overline{y}}$ ($r^2=0.36$, Fig. 2.6a). Correspondingly, species-average stem WD of juniper (0.47 ± 0.02 g cm⁻³) was 4% higher than that of pine (0.45 ± 0.02 g cm⁻³) and 18% higher than that of fir (0.40 ± 0.03 g cm⁻³). Maximum tree height increased nonlinearly by 220% with $\text{CMI}_{\overline{y}}$ ($r^2=0.69$), from average H_{max} of 10.54 ± 0.53 m at the juniper sites to 33.54 ± 5.56 m at the fir-dominated sites (Fig. 2.6b). Many of the tallest trees at the fir-dominated sites were actually old pine, the tallest of which reached 41.2 m. Forest LA:SA also increased with $\text{CMI}_{\overline{y}}$ ($r^2=0.76$, Fig. 2.6c), ranging from 0.02 ± 0.01 to 0.19 ± 0.02 m² cm⁻². Average LA:SA was quite low at the juniper sites (0.04 ± 0.02 m² cm⁻²), and 75% to 300%

higher at the pine ($0.07 \pm 0.02 \text{ m}^2 \text{ cm}^{-2}$) and fir sites ($0.16 \pm 0.02 \text{ m}^2 \text{ cm}^{-2}$), respectively. Lastly, there were significant relationships among $H_{\max}$, $\overline{WD}$, and LA:SA across sites ($r^2=0.35-0.55$, $P<0.05$, Table 2.3).

Discussion and conclusions

Constraints of long-term water availability on forest carbon cycling

Consistent with predictions from our first hypothesis, forest ecosystem LAI, ANPP, and AGB increased with $CMI_{\overline{wy}}$, yet residual variance in the regression models implies that the characteristics were influenced by additional bioclimatic or disturbance-related factors. Our results, along with those of several prior field studies (Gholz, 1982, Grier & Running, 1977), indicate that water availability is the dominant constraint on forest leaf area of mature stands in the eastern Cascades. The constraint of water availability on forest leaf area in this environment is driven by the need to maximize carbon assimilation while simultaneously minimizing water loss. Net carbon uptake by trees (i.e., photosynthesis - respiration) occurs within the limits of the hydraulic system (Ruehr *et al.*, 2014), minimizing the risk of embolism when evaporative demand exceeds supply (Meinzer *et al.*, 2010). While $CMI_{\overline{gy}}$ explained 68% of the observed variance in LAI, differences among sites in soil nitrogen, stand age, and disturbance history (e.g., windthrow, insect outbreaks) might account for some of the residual variance (Gholz, 1982, Law *et al.*, 2003). For instance, we observed low-level leaf herbivory at several of the grand fir sites, possibly due to western spruce budworm, which has affected large areas of forest in this region over the past three decades (Meigs *et al.*, 2015b, Willamette National Forest, 1995). Defoliation could have temporarily reduced leaf area without killing the trees, drawing down stored carbohydrates during refoliation. Additionally, there is uncertainty in both destructive and nondestructive estimates of forest leaf area (Law *et al.*, 2001b, Runyon *et al.*, 1994) that could have further obscured the relationship with long-term climate. For example, summer maximum LAI at the Metolius Mature Pine flux site averaged about 2.5 over the past eight years, starting around 2.1 in 1997 (Law *et al.*, 2001b), and our estimate for 2014 was about 2.0. The substantial increase in forest leaf area from the dry western juniper woodlands to the more mesic grand fir forests highlights the importance of long-term water availability in controlling light-harvesting potential and subsequent carbon accumulation.

Forest productivity is highly dependent on leaf area (Gholz, 1982, Waring, 1983, Waring *et al.*, 2014) and therefore the observed increase in forest ANPP with CMI_{wy} can be largely explained by the concomitant increase in leaf area. Forest leaf area and CMI_{gy} respectively explained 75% and 88% of the variation in ANPP across sites. Forest leaf area largely determines the interception of photosynthetically active radiation (IPAR; Runyon *et al.*, 1994), while subsequent utilization of IPAR for photosynthesis depends on physiological constraints imposed by environmental conditions (Landsberg & Waring, 1997, Runyon *et al.*, 1994, Tezara *et al.*, 1999). For instance, Runyon *et al.* (1994) found at seven sites in Oregon that annual IPAR increased linearly with LAI ($r^2=0.95$), while subsequent ANPP depended on utilized IPAR ($r^2=0.99$), which was calculated by reducing IPAR based on constraints imposed due to low soil moisture, high VPD, and the duration of subfreezing temperatures. Differences in biotic and abiotic constraints among our sites could explain some of the remaining variance in the ANPP- CMI_{wy} relationship (e.g. summer VPD, extent of freezing days each year, soil fertility and ratio of above- to belowground C allocation; Schwarz *et al.*, 2004).

Our estimates of ANPP for ponderosa pine over the past 10 years ($125\text{--}262\text{ g C m}^{-2}\text{ yr}^{-1}$) were within the range reported by Law *et al.* (2003) for six mature to old stands ($103\text{--}473\text{ g C m}^{-2}\text{ yr}^{-1}$) in the region and agreed to within 14% at the Mature Pine flux tower site (210 ± 23 vs. $242\pm 57\text{ g C m}^{-2}\text{ yr}^{-1}$). Productivity at our four ponderosa pine sites was about 20–60% higher than at sites examined by Gholz (1982; $\approx 110\text{ g C m}^{-2}\text{ yr}^{-1}$) and Runyon *et al.* (1994; $\approx 95\text{ g C m}^{-2}\text{ yr}^{-1}$), whereas ANPP at our western juniper sites ($11\text{--}21\text{ g C m}^{-2}\text{ yr}^{-1}$) was considerably lower than at sites examined by either Gholz (1982; $\approx 60\text{ g C m}^{-2}\text{ yr}^{-1}$) or Runyon *et al.* (1994; $\approx 80\text{ g C m}^{-2}\text{ yr}^{-1}$). Spatial differences in soil water holding capacity in the rocky volcanic soils (Peterman *et al.*, 2013) could account for some of the discrepancy in productivity, as could differences in stand density or age. Western juniper at our sites were generally quite old and had accumulated considerably higher overall AGB ($2\text{--}3\text{ kg C m}^{-2}$ vs. $\approx 0.5\text{ kg C m}^{-2}$). Overall, forest ANPP increased with long-term average water availability, largely owing to the increased leaf area, but potentially also due to reductions in abiotic constraints on carbon assimilation.

Forest AGB reflects the long-term integration of ANPP minus carbon loss (e.g. litterfall, herbivory, tree mortality) and therefore higher biomass observed at wetter sites was likely driven by higher rates of ANPP sustained over centennial timescales. Forest AGB increased with CMI_{wy} ($r^2=0.67$) and achieved a carbon density, when averaged across the grand fir sites, that was 6% greater than the average AGB estimated for temperate forests

worldwide ($\approx 13.5 \text{ kg C m}^{-2}$; Houghton et al. 2009). We found that $CMI_{\overline{gy}}$ explained less of the variance in forest AGB than ANPP ($r^2=0.88$), potentially as a result of differences among sites in tree mortality rates. For instance, there was little sign of recent tree mortality at the western juniper or ponderosa pine sites, yet there were several large, freshly wind-thrown trees at two of the grand fir sites (GF-1 and GF-4) that could somewhat account for lower AGB at these sites ($8.8\text{-}10.4 \text{ kg C m}^{-2}$) compared with the other two grand fir sites ($16.9\text{-}21.6 \text{ kg C m}^{-2}$). Additionally, differences among sites in growth impairment and mortality from periodic, historic outbreaks of spruce budworm and mountain pine beetle (*Dendroctonus ponderosae*; Meigs et al. 2015) could account for some of the unexplained variance in the AGB- $CMI_{\overline{wy}}$ regression model. Our findings, and those of prior field (Franklin & Dyrness, 1988, Gholz, 1982, Grier & Running, 1977) and modeling (Kang et al., 2014, Runyon et al., 1994) analyses, demonstrate that steep gradients in water availability are a key factor shaping forest distribution and carbon cycling in the Pacific Northwest, with regional forests further molded by disturbances such as timber harvest, wildfire, and insect outbreaks (Law et al., 2004, Law & Waring, 2015, Meigs et al., 2015b).

Influence of interannual fluctuations in water availability on tree radial growth

We found evidence to support the hypothesis that interannual fluctuation in water availability exerted less influence over tree growth as conditions became wetter; however, we unexpectedly observed a pronounced growth decline across species from c. 1985 to 1994 that was particularly severe among grand fir and potentially associated with relatively sustained, dry conditions over that decade. We observed that as $CMI_{\overline{wy}}$ increased there was a decline in the proportion of trees at each site that showed a significant correlation between radial growth and CMI, as well as a decline in the magnitude of that correlation. This suggests that, on an annual basis, water tends to limit the growth of western juniper to a greater extent than that of either ponderosa pine or grand fir, a finding consistent with results from a modeling study that showed that drought imposed greater physiological reductions on the utilization of annual IPAR by western juniper than by ponderosa pine or other conifers at higher elevations in the eastern Cascade Mountains (Runyon et al., 1994). Western juniper trees occupy sites with chronically low rainfall, high summer VPD and ET, and often thin, rocky soils, leading to generally low soil moisture that is highly dependent on annual recharge. Thus, annual photosynthesis and subsequent stem wood production of western juniper track the annual

water balance to a greater extent than ponderosa pine or grand fir, which occupy sites with not only higher rainfall, but reduced summer VPD and ET. Furthermore, soils in the ponderosa pine and grand fir zones tend to be deeper and have greater water storage capacity than in the western juniper zone (Kern, 1995). Soil depth averaged about 0.5 m at a nearby juniper site (Anthoni *et al.*, 1999) and about 2 m at the Metolius Mature Pine site (Law, unpublished data). Our analysis focused on changes in tree growth-climate relations over tens of kilometers, yet evidence from tree-ring and remote sensing analyses at regional (Huang *et al.*, 2015, Littell *et al.*, 2008, Wilmsking & Juday, 2005), hemispheric (Vicente-Serrano *et al.*, 2014) and global scales (Vicente-Serrano *et al.*, 2013) suggest that as landscapes become wetter, annual tree growth generally becomes increasingly decoupled from interannual fluctuations in water availability, yet trees in characteristically wet landscapes can still be vulnerable to drought-induced mortality (Allen *et al.*, 2010).

What factor, or complex of factors, were responsible for the notable cross-species decline in tree radial growth from c. 1985 to 1994, and why was the decline most severe in grand fir? Ponderosa pine at low and high elevations in southern Oregon also experienced reduced growth during these years (Knutson & Pyke, 2008). This 10-year period was characterized by nine years in which CMI_{wy} was at or below the 50-year average and punctuated by very dry conditions in 1994, the second most severe single-year drought over the record examined. This period corresponded with the most extensive mountain pine beetle and western spruce budworm outbreaks to have occurred in the eastern Cascades since 1970 (Meigs *et al.*, 2015b). The inspection of aerial survey data collected annually since the 1940s by federal and state agencies (available online: <http://www.fs.usda.gov/detail/r6/forest-grasslandhealth/>) revealed that from 1985 to 1994 our grand fir sites showed signs of western spruce budworm defoliation for between two to eight years, depending on the site. Western spruce budworm defoliation was also detected at three of our four ponderosa pine sites in 1986. Our woodland western juniper sites were not surveyed. We speculate that a multi-year drawdown of soil moisture due to insufficient recharge could have triggered the growth declines; which, in the case of grand fir and, to a lesser extent, ponderosa pine, were further exacerbated by insect attack. We suspect that grand fir growth is buffered against single-year meteorological droughts by ample soil water storage and recharge during wet years, but is potentially vulnerable to soil water draw down due to sustained, multi-year periods of below average recharge. Soil moisture buffering might explain the lack of significant RWI-CMI correlations among grand fir. Although beyond the scope of this study, additional lines of evidence to support or refute this hypothesis could be drawn from tree-ring isotopes, remote-

sensing observations, and detailed hydraulic and ecological modeling. This presents an intriguing possibility that although annual growth tends to become decoupled from interannual fluctuations in water as conditions become wetter, forests occupying generally wet zones could experience greater impact from infrequent, multi-year periods of below-normal soil water recharge due to increased biotic pressure (e.g. insects) and morphological investment in competition for light over water.

Dendroecological analyses often involve sampling trees at multiple sites and then producing a mean ring-width chronology, at the site or regional level, that is used to reconstruct paleoclimatic conditions (e.g., Fritts, 2001) or assess spatial variability in historic forest growth (Berner *et al.*, 2011, Bunn *et al.*, 2013); however, growth and climate sensitivity of neighboring trees can vary widely (Berner *et al.*, 2013, Bunn *et al.*, 2005, Lloyd *et al.*, 2010) and additional ecological information can be gained by examining growth-climate relations on an individualistic basis (Carrer, 2011). Our study demonstrates that not all trees within a site responded uniformly to drought, particularly at the ponderosa pine and grand fir sites. We did not explore the underlying mechanisms responsible for differences in drought response among individual trees within a site; however, factors such as age, genotype, competition, and microclimate could have contributed to these differences (Bunn *et al.*, 2011, Bunn *et al.*, 2005, Hultine *et al.*, 2013, Loranty *et al.*, 2010) and warrant further investigation. The substantial intra- and interspecific variation in drought sensitivity that we observed highlights the need for fine spatial and taxonomical resolution when modeling potential climate change impacts on mixed-species forests in mountainous terrain.

Constraints of long-term water availability on tree morphological traits

As conditions became wetter, forest $\overline{WD}$ declined, while $H_{\max}$ and LA:SA increased, suggesting that trees responded to reduced hydraulic stress by increasing investment in competition for light to the extent that xylem tensions were maintained within an operable range. These morphological changes, together with the observed differences in forest productivity and growth-climate relations across our network of sites, highlight trade-offs associated with investment in stress tolerance versus competitive ability (Grime, 2001, Reich, 2014). Since cavitation resistance (e.g. P50) tends to increase with WD (Chave *et al.*, 2009, Hacke *et al.*, 2001, Jacobsen *et al.*, 2007), the decline in stem $\overline{WD}$ that we observed between the juniper and fir communities is generally congruent with prior research showing that small

western juniper branches are more resistant to drought-induced cavitation ($P_{50} = -9.0$ MPa; Willson *et al.*, 2008) than those of ponderosa pine ($P_{50} = -4.5$ to -4.8 ; Domec *et al.*, 2009) or grand fir ($P_{50} = -3.6$ to -6.1 MPa; Cochard, 2006, McCulloh *et al.*, 2011) and, furthermore, that ponderosa pine stems are more cavitation-resistant ($P_{50} = -2.5$ to -4.1 ; Domec *et al.*, 2009) than those of grand fir ($P_{50} = -1.1$ to -1.0 ; McCulloh *et al.*, 2011). Several previous syntheses similarly found general declines in WD (Swenson & Enquist, 2007, Wiemann & Williamson, 2002) and increases in P_{50} (Choat *et al.*, 2012, Maherali *et al.*, 2004) as conditions become wetter, yet these relationships tend to be quite weak since trees have evolved a variety of strategies to maintain hydraulic integrity, which depends on a suite of traits integrated at the organism level (e.g. stomatal regulation, xylem capacitance, embolism repair, LA:SA plasticity; Meinzer *et al.*, 2010, Whitehead *et al.*, 1984). High WD helps enable trees to endure hydraulic and mechanical stress, yet could come at a competitive cost in productive environments since dense wood is carbon-intensive to construct (Chave *et al.*, 2009), generally has low hydraulic conductivity (Hacke *et al.*, 2009, Reich, 2014), and limits the maximum height that a tree can obtain before buckling under its own weight (Swenson & Enquist, 2007).

Canopy height plays an important role in competition for light among plants (Hartmann, 2011, King, 1990) and, in trees, might ultimately be constrained by low leaf water potential inhibiting cell expansion and growth (Koch *et al.*, 2004, Sala & Hoch, 2009) and/or photosynthesis (Koch *et al.*, 2004, Ryan & Yoder, 1997) at the top of the canopy. In the juniper woodlands, low stem density (99-157 trees ha^{-1}) and high water stress would place little premium on height growth, whereas ponderosa pine (127-334 trees ha^{-1}) and grand fir (205-645 trees ha^{-1}) formed progressively denser stands where greater canopy height would be more competitively beneficial and hydraulically feasible, which potentially explains the nearly three-fold increase in $H_{\max}$ that occurred among these forest communities. While taller trees can compete more effectively for light, the additional height causes them to experience lower xylem Ψ (Whitehead *et al.*, 1984) and could render these trees more vulnerable to drought impacts if conditions become increasingly arid (Hartmann, 2011, McDowell & Allen, 2015).

As with $H_{\max}$, forest LA:SA increased nearly three-fold between the western juniper and grand fir stands, demonstrating that trees responded to increased water availability by increasing investment in light absorption relative to water transport. In a review of conifer LA:SA, Waring *et al.* (1982) reported that LA:SA varied from 0.14 to 0.75 $\text{m}^2 \text{cm}^{-2}$ across 14 conifer species and noted qualitatively that taxa with low LA:SA occurred in desiccating

environments (e.g. *J. occidentalis*), whereas taxa with high LA:SA occupied mild climates (e.g. *Abies lasiocarpa*). Our results provide quantitative support for this earlier observation. Several studies have additionally shown that pine inhabiting sites with contrasting climatic conditions can adjust LA:SA to maintain xylem Ψ within a narrow range that prevents cavitation (Maherali & DeLucia, 2001, Mencuccini & Grace, 1995). Low LA:SA enables trees to maintain higher leaf-specific hydraulic conductance, which helps regulate leaf Ψ (Maherali & DeLucia, 2001, Mencuccini & Grace, 1995), and is likely an important adaptation allowing western juniper to inhabit such arid sites. While low LA:SA helps ease leaf Ψ , this must be balanced against the increase in stem respiration resulting from greater investment in sapwood, given that stem respiration increases with both sapwood volume and temperature (Ryan *et al.*, 1995). Relative to western juniper, the high LA:SA observed at the grand fir stands likely enables greater light absorption and photosynthate production, yet reduced water transport capabilities that could render these trees more susceptible to significant changes in water availability. Our findings demonstrate several adaptive responses to shifts in water availability, highlighting trade-offs between hydraulic stress tolerance and competition for light and suggesting potential changes in forest community morphological characteristics that could result from future changes in water availability due to sustained regional warming. Investigating the extent and causes of variation in traits across species and regions is a critical step towards understanding and modeling ecosystem properties and their responses to environmental change (Anderegg, 2015, Law, 2014, Westoby & Wright, 2006).

Limitations

We note several limitations associated with using an observational study to elicit the response of plant form and function to variation in climate, as well as with using CMI as an indicator of water availability. The observational approach makes it very challenging to separate the effect of a single environmental factor on plant form or function given that it is not possible to control the suite of environmental factors that can influence plant processes. For instance, although we focused on CMI as a dominant driver of carbon cycling and trait characteristics, there were additional differences among sites in climate (e.g. VPD, frost frequency, snow pack), soil, and disturbance history that independently, or interactively, could affect the processes of interest. Observational studies can elucidate existing spatial and temporal variation in plant response to climate or other controlling factors and are strengthened when

coupled with experimental and modeling studies focused on the underlying mechanisms of response.

We used the CMI as an indicator of plant water availability and acknowledge that while useful, it is a rather simple index with several shortcomings. The index is easy to calculate from gridded climate data and serves as the water balance calculation underpinning the SPEI (Vicente-Serrano *et al.*, 2010); together, they have been used to examine hydroclimatic controls over forest distribution (Hogg, 1997), productivity (Berner *et al.*, 2013, Vicente-Serrano *et al.*, 2014, Vicente-Serrano *et al.*, 2013), and wildfire (Williams *et al.*, 2014). The CMI is sensitive to changes in temperature and integrates both atmospheric inputs and withdrawals; however, it does not account for spatial variation in soil depth, soil water holding capacity, or snowpack that, along with rooting depth and architecture, further determine plant water availability. Additionally, we estimated CMI at each site using gridded PRISM climate data and an empirical equation for calculating ET_0 from T, PPT, and R. Different climate data sets, or means of estimating ET_0 , could affect the statistical relationships that we observed, yet it is the overall tendencies, rather than the absolute statistical parameters, that we are most interested in capturing.

Implications and future efforts

Forests ecosystems in the Pacific Northwest are a critical element of the regional economy, culture, biodiversity and biophysics, yet future changes in water availability due to sustained regional warming could have significant adverse impacts on these unique and valuable ecosystems. Uncertainty in forest physiologic, demographic and disturbance-related responses to changing environmental settings hinder projections of future forest conditions (Fisher *et al.*, 2010, Hudiburg *et al.*, 2013a, Law, 2014, van der Molen *et al.*, 2011) and thus our adaptation and mitigation capabilities. For instance, CO₂ fertilization might ameliorate some impacts of reduced water availability by increasing plant water-use efficiency (WUE), yet the potential magnitude of this response is unclear. Ecological simulations suggest that warming and increased WUE could lead to a ~20% increase in plant net primary productivity by 2100 (Hudiburg *et al.*, 2013b, Kang *et al.*, 2014), or, conversely, that conifer forest NPP, carbon storage, and extent could decline substantially over this period due to reduced water availability and increased heat stress, despite increased WUE (Jiang *et al.*, 2013). These divergent projections underscore the need to further reduce uncertainty in ecological models, which will necessitate investment in high-performance computing, experiments to elucidate

physiologic mechanisms driving intra- and interspecific differences in drought and heat sensitivity, regional field studies (such as ours) to provide physiological measurements for model parameterization, and a combination of remote-sensing and eddy covariance flux tower measurements to hone and validate model predictions. By understanding current climatic controls over forest ecosystem function and refining prognostic models of ecosystem processes, we can better anticipate the potential impacts of climate change and thus improve our mitigation and adaptation capabilities.

Tables

Table 2.1. Species conversion coefficients (β) relating leaf projected surface area to one half of total surface area. These coefficients were drawn from published sources.

Species	β	Source	Notes
Western juniper	1.57	Hicks and Dugas (1998)	
Lodgepole pine	1.28	Barclay (1998)	
Ponderosa pine	1.20	Cregg (1994)	average of values in table 4
Incense cedar	1.14	Barclay and Goodman (2000)	coefficient for western red cedar
Grand fir	1.09	Barclay and Goodman (2000)	also used for noble fir

Table 2.2. Average (± 1 SD) growing-year climate conditions from 1964 to 2013 for sites dominated by western juniper, ponderosa pine, and grand fir in the eastern Cascade Mountains, Oregon. The growing-year extended from October of year t-1 through September of year t. Climate variables include average daily temperature (T_{wy}), precipitation (P_{wy}), reference evapotranspiration (ET_{0wy}) and climate moisture index ($CMI_{wy} = P_{wy} - ET_{0wy}$) calculated from monthly PRISM climate data (Daly et al. 2008). We averaged the climate time series for each of the four sites in a given forest type prior to calculating summary statistics.

Forest type	T_{wy} (° C)	P_{wy} (cm yr ⁻¹)	ET_{0wy} (cm yr ⁻¹)	CMI_{wy} (cm yr ⁻¹)
Western juniper	8.32 ± 0.80	29 ± 7	154 ± 70	-125 ± 12
Ponderosa pine	6.90 ± 0.72	61 ± 15	137 ± 70	-75 ± 19
Grand fir	6.26 ± 0.72	95 ± 21	123 ± 70	-28 ± 25

Table 2.3. Regression equations relating forest community carbon cycling, morphological characteristics, and long-term (1964-2013) mean growing-year climate moisture index ($\text{CMI}_{\overline{\text{wy}}}$, cm yr^{-1}) across 12 sites in the eastern Cascade Mountains, Oregon. Forest characteristics include leaf area index (LAI, half of total surface area; $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$), annual aboveground net primary productivity (ANPP, $\text{g C m}^{-2} \text{ yr}^{-1}$), aboveground live biomass (AGB, kg C m^{-2}), leaf:sapwood area ratio (LA:SA, $\text{m}^2 \text{ leaf cm}^{-2} \text{ sapwood}$), maximum tree height (H_{max} , m), and average stem wood density ($\overline{\text{WD}}$, g cm^{-3}). Also included are the community-average correlation between tree ring-width indices (RWI) and CMI from 1964 to 2013 ($\overline{r}_{\text{RWI-CMI}}$, unitless) and the fraction of individual trees in the community that exhibited a significant ($P < 0.05$) positive RWI-CMI correlation ($F_{\text{RWI-CMI}}$, %). Equations are either power form ($Y = aX^b$) or linear ($Y = a + bX$), where a and b are fitted coefficients, with X and Y in units provided above. All relationships were significant at $\alpha < 0.05$.

Explanatory	Response	Form	a	a (SE)	b	b (SE)	r^2
$\text{CMI}_{\overline{\text{wy}}}$	LAI	power	0.02	0.03	0.79	0.30	0.68
	ANPP	power	2.47	2.23	0.66	0.13	0.88
	AGB	power	0.24	0.33	0.59	0.20	0.67
	$\overline{r}_{\text{RWI-CMI}}$	linear	0.02	0.07	-0.00037	0.00008	0.65
	$F_{\text{RWI-CMI}}$	linear	4.90	13.10	-0.07	0.02	0.63
	LA:SA	power	0.008	0.008	0.456	0.159	0.65
	H_{max}	power	4.25	2.25	0.30	0.08	0.69
	$\overline{\text{WD}}$	linear	0.41	0.01	-0.00005	0.00002	0.36
LAI	ANPP	linear	42.05	23.97	46.82	8.11	0.75
	AGB	linear	3.66	1.85	2.48	0.63	0.57
ANPP	AGB	linear	1.84	1.81	0.05	0.01	0.68
$\overline{r}_{\text{RWI-CMI}}$	$F_{\text{RWI-CMI}}$	linear	2.08	5.53	174.97	15.29	0.92
$\overline{\text{WD}}$	LA:SA	linear	0.98	0.18	-1.96	0.40	0.71
	H_{max}	linear	118.14	36.20	-214.39	82.23	0.35
	H_{max}	linear	0.009	0.042	0.0047	0.0016	0.46

Table 2.4. Summary of carbon cycling, growth-climate, morphological, and chemical characteristics for western juniper, ponderosa pine, and grand fir in the eastern Cascade Mountains, Oregon. Both stand- and tree-level characteristics are included. The stand-level characteristics provided for grand fir actually represent an average mixture of two thirds grand fir and one third ponderosa pine. The mean, standard deviation, and sample size are provided for each characteristic.

Characteristic	Level	Units	Species		
			Juniper	Pine	Fir
LAI	Stand	$\text{m}^2 \text{m}^{-2}$	0.26 ± 0.13 (4)	1.92 ± 0.51 (4)	4.54 ± 1.49 (4)
ANPP	Stand	$\text{g C m}^{-2} \text{yr}^{-1}$	17 ± 4 (4)	185 ± 62 (4)	238 ± 54 (4)
AGB	Stand	kg C m^{-2}	2.6 ± 0.4 (4)	10.6 ± 4.1 (4)	14.4 ± 5.9 (4)
$\bar{r}_{\text{RWI-CMI}}$	Stand	unitless	0.52 ± 0.18 (72)	0.27 ± 0.21 (82)	0.11 ± 0.13 (62)
$F_{\text{RWI-CMI}}$	Stand	%	91 ± 3 (72)	51 ± 6 (82)	12 ± 4 (62)
LA:SA	Stand	$\text{cm}^2 \text{m}^{-2}$	0.05 ± 0.02 (4)	0.10 ± 0.03 (4)	0.21 ± 0.04 (4)
H_{max}	Stand	m	10.5 ± 0.5 (4)	27.9 ± 5.3 (4)	33.5 ± 5.6 (4)
WD	Tree	g cm^{-3}	0.47 ± 0.02 (32)	0.45 ± 0.02 (52)	0.40 ± 0.03 (36)
SLA	Tree	$\text{cm}^2 \text{HSA g}^{-1} \text{C}$	63 ± 6 (40)	91 ± 11 (47)	100 ± 16 (42)
Leaf longevity	Tree	years	5.6^b	4.3 ± 1.0 (59)	9.2 ± 2.1 (50)
Leaf C	Tree	%	48.2 ± 0.8 (40)	48.3 ± 0.5 (47)	47.8 ± 0.5 (42)
Leaf N	Tree	%	0.89 ± 0.13 (40)	1.14 ± 0.12 (47)	0.83 ± 0.13 (42)
Leaf C:N	Tree	unitless	55 ± 9 (40)	43 ± 4 (47)	59 ± 10 (42)

^b Western juniper leaf longevity was calculated as the ratio of foliage biomass to annual leaf fall using measurements from Runyon et al. (1994).

Figures

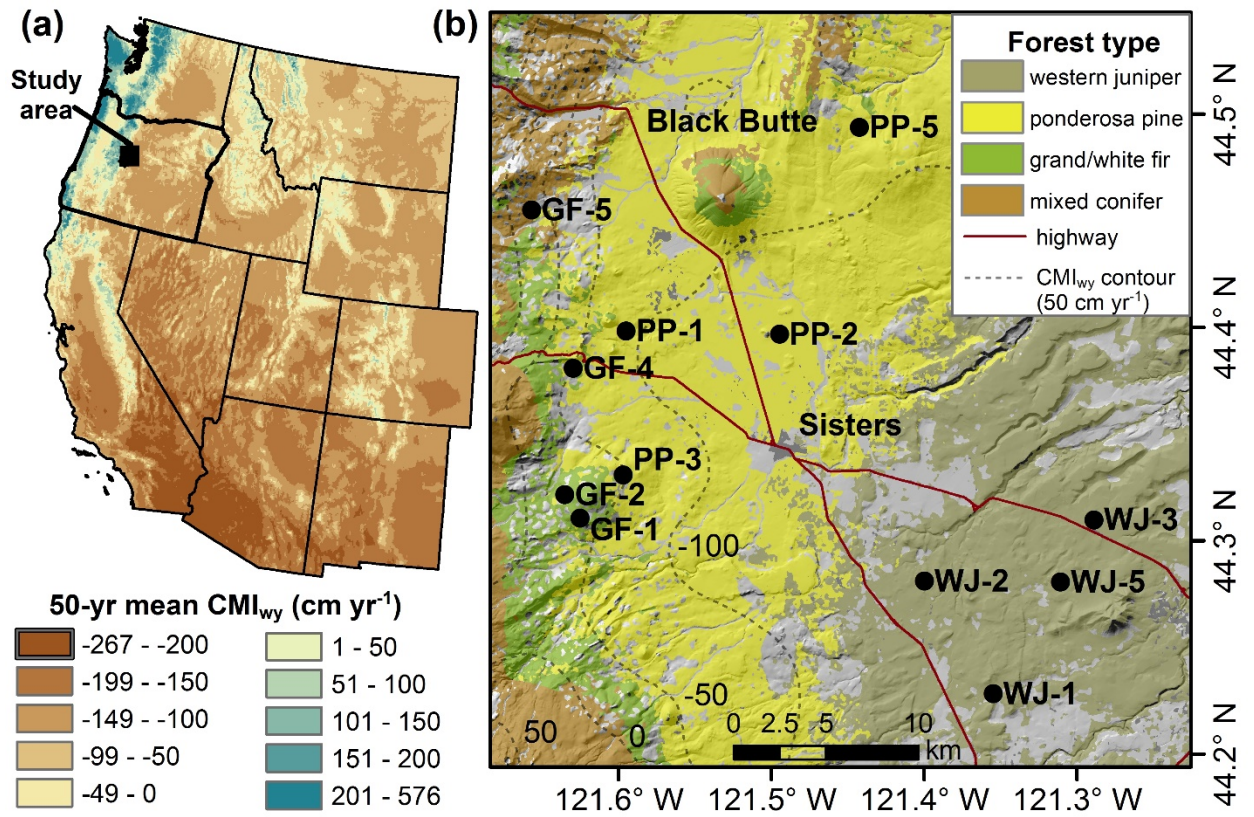


Figure 2.1. (a) Locator map depicting study area location and mean growing-year climate moisture index from 1964 to 2013 (CMI_{wy} , $cm\ yr^{-1}$) across the western United States. (b) Field sites (points) were located in the eastern Cascade Mountains (Oregon) and spanned three forest types that occur along a steep gradient in CMI_{wy} . Contours (dotted lines) depict CMI_{wy} in 50 $cm\ yr^{-1}$ increments. We derived CMI_{wy} from PRISM climate data (Daly *et al.*, 2008), while data on forest type were from Kagan *et al.* (2006).

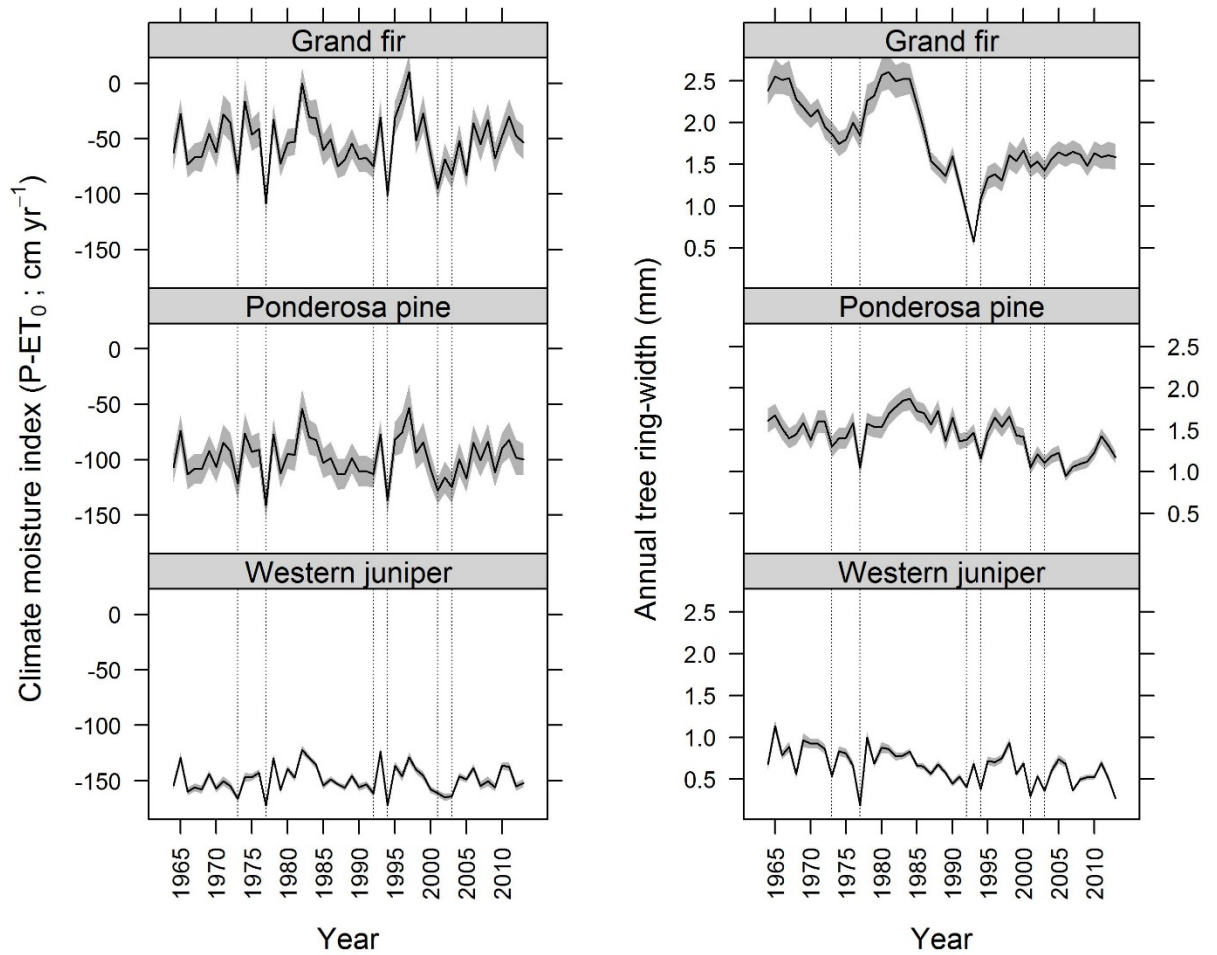


Figure 2.2. Growing-year climate moisture index (CMI_{wy}) from 1964 to 2013 averaged (± 1 SE) across sites ($n=4$) in three forest types (left panel). Average (± 1 SE) annual radial growth at breast height for grand fir ($n = 62$), ponderosa pine ($n = 82$), and western juniper ($n = 72$) from 1964 to 2013, with trees pooled irrespective of site (right panel). In both panels the dotted vertical lines depicted six notably dry years (1973, 1977, 1992, 1994, 2001 and 2003) over the 50-year record.

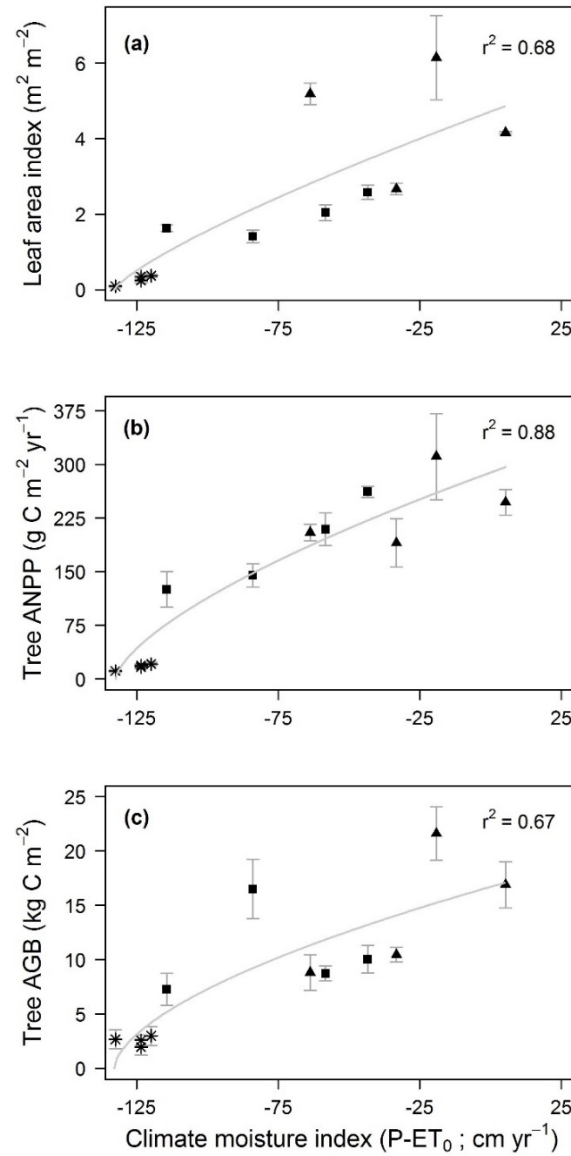


Figure 2.3. Forest community (a) leaf area index, (b) 10-year average annual aboveground net primary production and (c) aboveground live biomass plotted against the average growing-year climate moisture index from 1964 to 2013 (CMI_{wy}) for 12 mature conifer sites in the eastern Cascade Mountains, Oregon. We calculated CMI_{wy} by summing monthly precipitation (P) minus reference evapotranspiration (ET_0) from October to through September and then averaged the growing-year values from 1964 to 2013. Each point represents the mean (± 1 SE) of four subplots. Regression coefficients are given in Table 2.3.

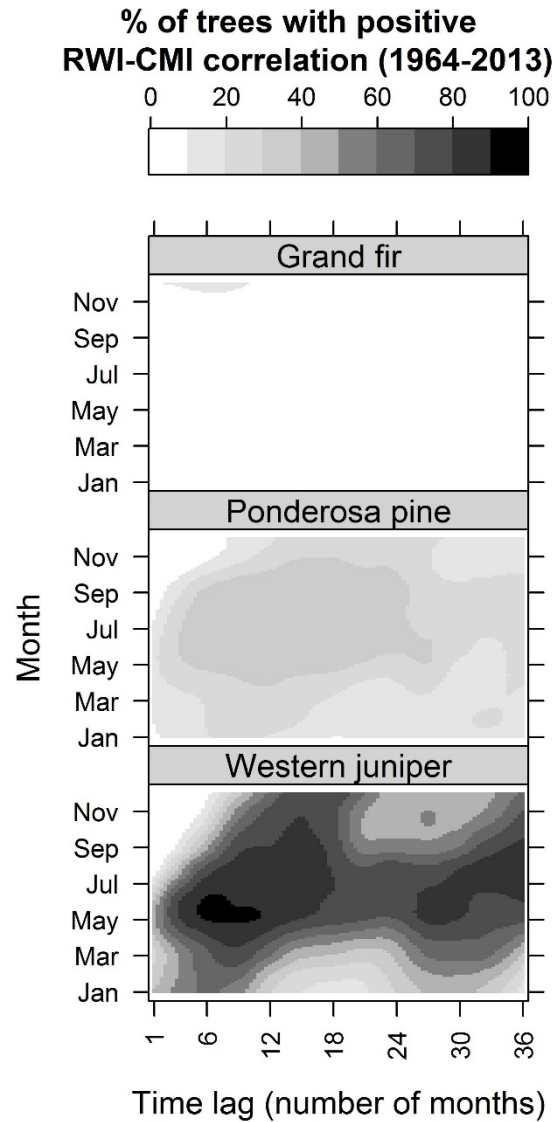


Figure 2.4. Correlations between annual tree radial growth and the climate moisture index ($\text{CMI} = P - \text{ET}_0$) from 1964 to 2013 for three tree species in the eastern Cascades, Oregon. Depicted is the proportion of trees with a significant positive correlation between annual ring-width indices (RWI) and CMI calculated for each month at time lags extending from 1 to 36 months. See Fig. A1 and Table A4 for correlations between RWI and additional climate variables.

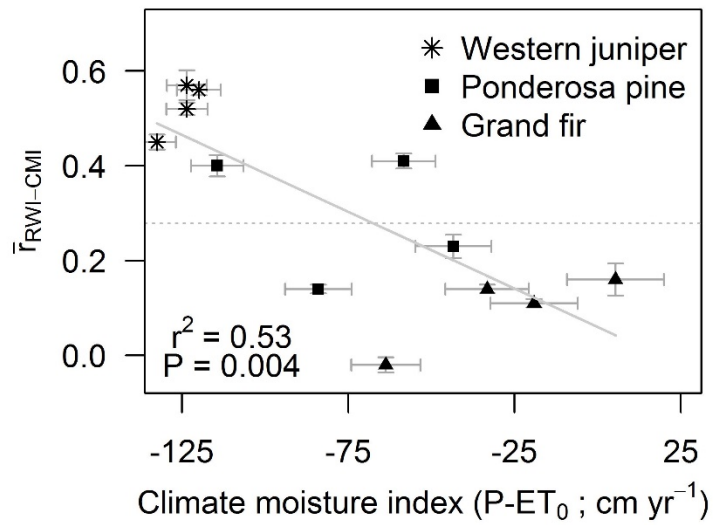


Figure 2.5. Mean ecosystem-weighted correlation ($\bar{r}_{\text{RWI-CMI}}$) between annual tree ring-width indices (RWI) and the climate moisture index (CMI = $P - ET_0$) plotted against the 50-year mean (± 1 SE) water year CMI. The dashed horizontal line denotes statistical significance at $\alpha=0.05$. The 12 sites were located in the eastern Cascade Mountains and represented forest types dominated by western juniper, ponderosa pine and grand fir. Regression coefficients are given in Table 2.3.

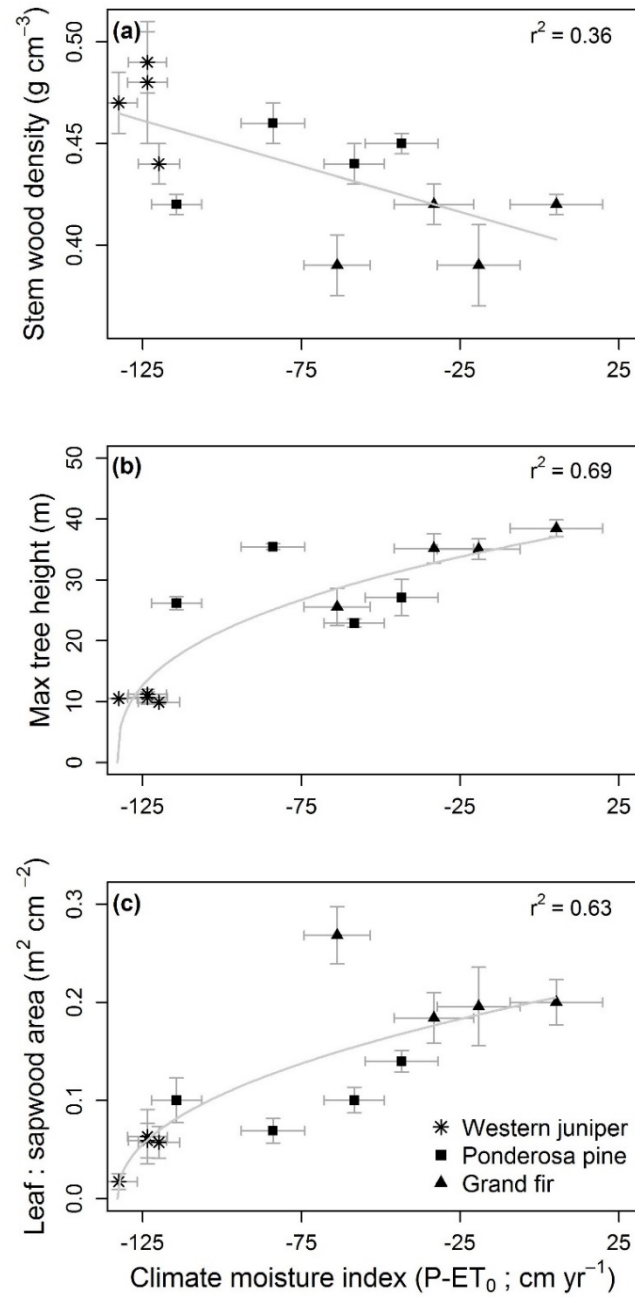


Figure 2.6. Forest ecosystem (a) average stem wood density, (b) maximum tree height, and (c) leaf:sapwood area ratio plotted against the average growing-year climate moisture index from 1964 to 2013 (CMI_{wy}). Each point represents the mean (± 1 SE) of four subplots sampled at each site. Regression coefficients are given in Table 2.3.

**Water availability limits tree productivity, carbon stocks, and carbon residence time in
mature forests across the western United States**

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CHAPTER 3. WATER AVAILABILITY LIMITS TREE PRODUCTIVITY, CARBON STOCKS, AND CARBON RESIDENCE TIME IN MATURE FORESTS ACROSS THE WESTERN UNITED STATES

Abstract

Water availability constrains the structure and function of terrestrial ecosystems and is projected to change in many parts of the world over the coming century. We quantified the response of tree net primary productivity (NPP), live biomass (BIO), and mean carbon residence time ($CRT = BIO/NPP$) to spatial variation in water availability in the western US. We used forest inventory measurements from 1,953 mature stands (>100 years) in Washington, Oregon, and California (WAORCA) along with satellite and climate data sets covering the western US. We summarized forest structure and function in both domains along a 400 cm yr^{-1} hydrologic gradient, quantified with a climate moisture index (CMI) based on the difference between precipitation and reference evapotranspiration summed over the water year (October-September) and then averaged annually from 1985-2014 ($CMI_{\overline{wy}}$). Median NPP, BIO, and CRT computed at 10 cm yr^{-1} intervals along the $CMI_{\overline{wy}}$ gradient increased monotonically with increasing $CMI_{\overline{wy}}$ across both WAORCA ($r_s = 0.93-0.96$, $p < 0.001$) and the western US ($r_s = 0.93-0.99$, $p < 0.001$). Field measurements from WAORCA showed that median NPP increased from 2.2 to $5.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ between the driest and wettest 5% of sites, while BIO increased from 26 to 281 Mg C ha^{-1} and CRT increased from 11 to 49 years. The satellite data sets revealed similar changes over the western US, though these data sets tended to plateau in the wettest areas, suggesting that additional efforts are needed to better quantify NPP and BIO from satellites in high-productivity, high-biomass forests. Our results illustrate that long-term average water availability is a key environmental constraint on tree productivity, carbon storage, and carbon residence time in mature forests across the western US, underscoring the need to assess potential ecosystem response to projected warming and drying over the coming century.

Introduction

Water availability strongly constrains the distribution of plants on Earth's land surface (Holdridge, 1947, Major, 1963) and the resulting structure and function of terrestrial ecosystems (Churkina & Running, 1998, Law *et al.*, 2002, Schuur, 2003). For instance, desert (Whittaker & Niering, 1975), grassland (Yang *et al.*, 2008) and forest productivity (Berner & Law, 2015, Law *et al.*, 2002, Schuur, 2003) differ widely among sites with contrasting water availability. Water availability is shaped by regional climate (e.g., precipitation, atmospheric evaporative demand), as well as by local topography and soils (Webb *et al.*, 1983). Water availability is projected to change in many parts of the world over the coming century in response to continued atmospheric warming from sustained anthropogenic greenhouse gas emissions (Collins *et al.*, 2013, Dai, 2013, Walsh *et al.*, 2014). Societies depend on the goods and services provided by terrestrial ecosystems (e.g., forests; Williams, 2006) and thus it is imperative to elucidate climatic controls over ecosystem structure and function to help anticipate and mitigate potential impacts of ongoing climatic change.

The western United States (US) is a region where pronounced spatial variation in water availability exerts a strong influence over forest structure and function. For instance, average annual precipitation varies over 500 cm yr⁻¹ across this region, with particularly steep hydrologic gradients in the Pacific Northwest (Daly *et al.*, 2008). Differences in water availability gives rise to forest communities that range from dry, low-productivity woodlands to high-productivity coastal temperate rainforests where live tree biomass (BIO) attains levels thought to be exceeded only by primary *Eucalyptus regnans* forests in southern Australia (Keith *et al.*, 2009, Waring & Franklin, 1979).

Prior studies drew on small networks of field sites ($n < 20$) to investigate how tree net primary productivity (NPP) and BIO varied among mature stands spread along hydrologic gradients in parts of this region (Berner & Law, 2015, Gholz, 1982, Webb *et al.*, 1983, Whittaker & Niering, 1975). Tree BIO and NPP can vary widely with stand age (Hudiburg *et al.*, 2009) and thus these studies focused on mature stands (stand age generally > 100 years) where BIO and NPP had somewhat stabilized after reaching their "climatic potential." These studies showed that BIO and NPP tended to increase linearly or curvilinearly across sites as average water availability increased (Berner & Law, 2015, Gholz, 1982, Webb *et al.*, 1983, Whittaker & Niering, 1975). These spatial relationships are thought to reflect long-term climatic constraints on ecosystem structure (e.g., BIO) and function (e.g., NPP) that are

shaped by gradual shifts in community composition and population size (Jin & Goulden, 2014). The field studies mentioned above make a compelling case that water availability is an important determinant of BIO and NPP in mature stands, yet these studies were based on a small number of field sites selected using a set of criteria (e.g., mature stands near a road) rather than on a large sample of mature stands in the region.

Several of these earlier field studies also indicated that plant communities accumulated more BIO per unit of NPP in progressively wetter areas, suggesting slower turnover of plant BIO as climate became wetter (Webb *et al.*, 1983, Whittaker & Niering, 1975). Mean carbon residence time (CRT) describes the average duration that a carbon molecule will remain in a specific pool (Waring & Running, 2007) and for CRT in live biomass it can be computed as BIO/NPP, assuming that BIO remains constant over time (Friend *et al.*, 2014, Whittaker, 1961). CRT in live biomass is also known as the *biomass accumulation ratio* (Whittaker, 1961) and ranged, for instance, from ~2 years in a hot desert shrubland to ~75 years in a wet, old-growth Douglas-fir forest (Webb *et al.*, 1983). Differences in CRT among plant communities with contrasting climate are potentially associated with shifts in carbon allocation (e.g. short-lived fine roots and foliage vs. long-lived stem wood) and disturbance regimes (Girardin *et al.*, 2010). Together, these field studies illustrate that forest structure and function are constrained by water availability in parts of the western US; however, additional efforts are needed to assess these relationships on larger scales across the region, particularly given that climate models project a pronounced shift towards hotter, drier conditions over much of the region during the coming century (Collins *et al.*, 2013, Cook *et al.*, 2015, Walsh *et al.*, 2014).

Our objective in this study was to explore how forest structure and function change along spatial gradients in water availability across the western US. We used the average water year climate moisture index ($\text{CMI}_{\overline{\text{wy}}}$; 1985-2014) as an indicator of long-term water availability (Hogg & Hurdle, 1995, Webb *et al.*, 1983), which we computed as the cumulative difference between precipitation (P) and reference evapotranspiration (ET_0) over the approximate seasonal cycle of soil water recharge and draw-down (October-September). Furthermore, we focused on forest stands that were at least 100 years old because field surveys from the region indicated that BIO and NPP reached much of their climatic potential after a century. However, we acknowledge that BIO tends to gradually increase and NPP remains stable or gradually declines during subsequent centuries (Hudiburg *et al.*, 2009). Building on prior field studies (e.g., Berner & Law, 2015, Gholz, 1982, Webb *et al.*, 1983), we hypothesized that long-term water availability limits tree NPP, BIO, and CRT in mature

forest stands across the region. We thus predicted that tree NPP, BIO, and CRT in mature forests would increase with increasing CMI_{wy} . Tree NPP, BIO, and CRT were based on above and belowground components. We tested these hypotheses first across Washington, Oregon, and California (WAORCA) using forest inventory measurements from 1,953 sites and then across 18 Mha of mature forest in the western US using satellite remote sensing data sets. These data sets included three national biomass maps, along with NPP derived from the Moderate Resolution Imaging Spectroradiometer (MODIS). Forest inventories provide rigorous, though spatially limited field measurements of forest structure and function, while satellite remote sensing provides spatially continuous, albeit modeled estimates of forest structure and function across large domains.

Materials and methods

Data sets and preprocessing

Field estimates of tree biomass, productivity, and carbon residence time

We used field measurements to estimate BIO ($\text{BIO}_{\text{field}}$, Mg C ha^{-1}), NPP ($\text{NPP}_{\text{field}}$, $\text{Mg C ha}^{-1} \text{ yr}^{-1}$), and CRT ($\text{CRT}_{\text{field}}$, year) at 1,953 forest inventory sites located in mature stands spread across WAORCA. These 1-ha sites were surveyed by the US Forest Service Forest Inventory and Analysis (FIA) program between 2001 and 2006 and comprise a representative sample of forest lands (tree cover > 10%) in the region (Bechtold & Patterson, 2005). The inventory sites occurred at elevations ranging from 5 m to 3,504 m, with an average ($\pm 1\text{SD}$) elevation of 1429 ± 677 m. We included sites in our analysis when stand age was at least 100 years. Stand age was defined as the average age of the oldest 10% of trees, where individual tree age was determined at survey plots using increment cores (Van Tuyl *et al.*, 2005). $\text{BIO}_{\text{field}}$ and $\text{NPP}_{\text{field}}$ were computed for each site as part of a prior study (Hudiburg *et al.*, 2011). $\text{BIO}_{\text{field}}$ was estimated using regional allometric equations for tree components (e.g., stem, branch, bark, foliage, and coarse roots) based on tree diameter and/or height (Law *et al.*, 2001a, Means *et al.*, 1994), along with estimates of fine-root mass derived from a relationship with leaf area index (LAI, $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$; Van Tuyl *et al.* 2005). $\text{NPP}_{\text{field}}$ was estimated based on changes in above and belowground woody biomass over a 10-year interval plus annual foliage and fine-root turnover. See Hudiburg *et al.* (2011) for additional details. We then computed $\text{CRT}_{\text{field}}$ in live-tree biomass as the ratio of $\text{BIO}_{\text{field}}$ to $\text{NPP}_{\text{field}}$.

Remote sensing estimates of tree biomass, productivity, and carbon residence time

We used satellite remote sensing and ancillary data sets to estimate BIO (BIO_{sat}), NPP (NPP_{sat}), and CRT (CRT_{sat}) across mature forests in the western US. Tree BIO_{sat} included the same component carbon pools as BIO_{field} (i.e. stem, branch, bark, foliage, coarse-roots and fine-roots). We quantified the amount of carbon in stems, branches, and bark using an ensemble of three satellite-derived data sets that depicted live-tree aboveground biomass (AGB, excluded foliage) circa 2000 to 2008 (Blackard *et al.*, 2008, Kelldorfer *et al.*, 2012, Wilson *et al.*, 2013). Each map was generated using satellite and geophysical (e.g., climate, topography) data sets to spatially extrapolate forest inventory measurements over the conterminous US. We acquired these maps at 250-m spatial resolution and then converted two of the maps (Blackard *et al.*, 2008, Kelldorfer *et al.*, 2012) from dry biomass to carbon assuming a 50% conversion factor (Smith *et al.*, 2006). We then reprojected these maps onto a uniform grid in an equal area projection, masked them to the common forest extent, and then averaged the AGB for each pixel across the three biomass maps. We used the biomass map ensemble average in the subsequent analysis, recognizing that pixel-wise estimates of AGB can vary notably among individual maps (Neeti & Kennedy, 2016).

After deriving spatial estimates of carbon storage in AGB, we then estimated carbon storage in coarse-roots, fine-roots, and foliage for each 250-m forested pixel. As with AGB, we assumed that roots and foliage were 50% carbon (Berner & Law, 2016, Smith *et al.*, 2006). We computed coarse root biomass based on an empirical relationship with AGB (Cairns *et al.*, 1997) and fine root biomass based on an empirical relationship with peak summer LAI (Van Tuyl *et al.*, 2005). Spatial estimates of LAI were available globally at 1-km resolution from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) as part of the MOD15A2 (Collection 5) data set (Myneni *et al.*, 2002). We obtained these LAI estimates at 8-day intervals during July and August (late summer) from 2000 to 2014 for the western US. We then (1) excluded poor-quality pixels using the quality control flags, (2) computed average late-summer LAI over the 15-year period, and (3) reprojected and resampled the data set to the common 250-m resolution equal area grid. We used average late-summer MODIS LAI to compute both fine-root biomass (as described above) and foliage biomass. Foliage biomass was estimated for each pixel by dividing LAI by the average specific leaf area (SLA, $g\ C\ m^{-2}\ leaf$) of the forest type found in that pixel. We aggregated an existing map of forest type (Ruefenacht *et al.*, 2008) into nine classes (e.g.,

Pinus ponderosa, true fir) and then varied SLA among classes using species-, genus-, or division-specific estimates of average SLA from a recent leaf trait synthesis (Berner & Law, 2016). We then estimated BIO_{sat} for each 250-m resolution pixel by summing the above and belowground carbon pools.

We quantified regional NPP using the satellite-derived MODIS primary productivity data set (NPP_{sat} , MOD17A3 v. 55). The MODIS light-use efficiency model predicts annual NPP at 1 km resolution across global terrestrial ecosystems by incorporating estimates of absorbed photosynthetically active radiation (APAR), LAI, and land cover derived from MODIS together with plant physiological characteristics and climate data (Running *et al.*, 2004, Zhao *et al.*, 2010). The model first predicts daily gross primary productivity (GPP) based APAR and the efficiency with which APAR is converted to biomass (ϵ), which is affected by low temperatures (frost) and high vapor pressure deficit (VPD) inducing stomatal closure. The model then estimates plant respiration (R) at daily-to-annual increments and subsequently computes annual NPP as the cumulative difference between GPP and R. These estimates thus reflect NPP allocated both above and belowground. We acknowledge a degree of circularity in relating NPP_{sat} to CMI given that both computations incorporate temperature data, specifically, temperature effects on VPD. We obtained annual NPP estimates from 2000 to 2014 for the western US, reprojected the data onto an equal area grid, and then averaged the data over years.

Several additional preprocessing steps were required after deriving forest BIO_{sat} and NPP_{sat} . These included masking both BIO_{sat} and NPP_{sat} to areas mapped as forest by the MODIS land cover map (Friedl *et al.*, 2010) and then further masking these data sets to include only areas where stand age was at least 100 years. The map of stand age reflected conditions around 2006 and was produced by Pan *et al.* (2011b) by combining forest inventory measurements, information on historical fires, and optical satellite imagery. We applied these 1 km resolution masks to the 250 m resolution BIO_{sat} assuming homogenous land cover and stand age within each 1 km pixel. We then aggregated BIO_{sat} from 250 m to 1 km resolution and computed CRT_{sat} as the ratio of BIO_{sat} to NPP_{sat} .

Climate data sets and derivation of the climate moisture index

We quantified water availability using a climate moisture index (CMI) that was computed at monthly time steps as precipitation minus ET_0 (Hogg, 1994, Webb *et al.*, 1983). We summed monthly CMI over each water year (October in year $t-1$ to September in year t) from 1985 to

2014 and then averaged over years to produce a 30-year climatology ($\text{CMI}_{\overline{\text{wy}}}$, cm yr^{-1}). The water year represents the approximate annual cycle of soil water recharge and withdrawal (Thomas *et al.*, 2009). We obtained estimates of monthly precipitation from the Parameter-elevation Relationships on Independent Slopes Model (PRISM; Daly *et al.*, 2008), which interpolated weather station measurements onto a 4-km resolution grid. We then estimated monthly ET_0 using the Food and Agricultural Organizations (FAO) Penman-Monteith equation (FAO-56; Allen *et al.*, 1998), where

$$\text{ET}_0 = \frac{0.408\Delta (R_n - G) + \gamma \left(\frac{900}{T + 273} \right) U(e_s - e_a)}{\Delta + \gamma (1 + 0.34 U)}$$

Variables included net incoming radiation (R_n), soil heat flux (G), mean daily temperature (T), wind speed (U), and both saturation (e_s) and actual vapor pressure (e_a), as well as the psychrometric constant (γ) and the slope of the vapor pressure curve (Δ). We quantified R_n and U using monthly climatologies from the North American Land Data Assimilation System-2 (NALDAS-2, ~12-km resolution) that were based on measurements from 1980-2009 (Mitchell *et al.*, 2004). We derived G , T , e_s , and e_a from PRISM temperature data following Zotarelli *et al.* (2010). We also computed $\text{CMI}_{\overline{\text{wy}}}$ based on ET_0 derived using the modified-Hargreaves approach (Droogers & Allen, 2002, Hargreaves & Samani, 1985) and found that our analysis was robust to differences in methods used to compute ET_0 (results not shown). After computing $\text{CMI}_{\overline{\text{wy}}}$, we then resampled these data using the nearest neighbor approach to match the footprints of both the 1-km NPP and 250-m BIO remote sensing data sets.

Analysis

We quantified the response of forest NPP, BIO, and CRT to changes in $\text{CMI}_{\overline{\text{wy}}}$ across both WAORCA and the broader western US. We specifically focused on areas where $\text{CMI}_{\overline{\text{wy}}}$ was between -200 and 200 cm yr^{-1} , conditions which occurred both in WAORCA and in the broader region. This range encompassed 98% of forest area in the western US; the paucity of data in the remaining 2% of forest area that was either drier or wetter precluded rigorous analysis. We divided the landscape along this gradient into 10 cm yr^{-1} nonoverlapping bins and then summarized forest characteristics in each bin by computing the median, along with the 10th, 25th, 75th and 90th percentiles. Forest characteristics were summarized separately for the field and remote sensing data sets. There were a minimum of 10 and a maximum of 114

field sites in each bin. We then assessed the association between the median forest characteristic (i.e., NPP, BIO, and CRT) in each bin and $\text{CMI}_{\overline{\text{wy}}}$ across the bioclimatic gradient using nonparametric Spearman's rank correlation. This test yields a coefficient (r_s) between -1 and +1, where a value of +1 indicates a perfect monotonically increasing relationship, a value of zero indicates no covariation between the two variables, and a value of -1 indicates a perfect monotonically decreasing relationship. The test is analogous to Pearson's correlation where the data were first ranked. We assessed the association between forest characteristics and $\text{CMI}_{\overline{\text{wy}}}$ using Spearman's correlation rather than nonlinear regression because our intent was to describe the general relationship rather than develop a predictive model. We performed data preprocessing, analysis, and visualization using ArcGIS 10 (ESRI, Redlands, CA) and *R* statistical software (R Core Team, 2015), relying extensively on the *R* packages *raster* (Hijmans & van Etten, 2013) and *dplyr* (Wickham & Francois, 2015).

Results

Average annual water availability varied widely across both WAORCA and the broader western US from 1985-2014 (Fig. 3.1a, b). The $\text{CMI}_{\overline{\text{wy}}}$ ranged from a minimum of -330 cm yr^{-1} in southern California and Arizona to a maximum of 490 cm yr^{-1} in the Olympic Mountains in northwestern Washington. Forests mapped by MODIS occurred in areas where $\text{CMI}_{\overline{\text{wy}}}$ was between -340 and 490 cm yr^{-1} , though 98% of forest area occurred between -200 and 200 cm yr^{-1} , and 72% occurred between -100 and 100 cm yr^{-1} . Average ($\pm 1 \text{ SD}$) $\text{CMI}_{\overline{\text{wy}}}$ in forested areas was $-40 \pm 80 \text{ cm yr}^{-1}$. The Coast Range and Cascade Mountains in Washington and Oregon were the wettest areas, with $\text{CMI}_{\overline{\text{wy}}}$ generally $> 100 \text{ cm yr}^{-1}$. Water availability decreased rapidly in the rain shadows east of the Cascades and Sierra Nevada, giving rise to very steep $\text{CMI}_{\overline{\text{wy}}}$ gradients. For instance, annual $\text{CMI}_{\overline{\text{wy}}}$ in northern Oregon decreased nearly 350 cm over $\sim 30 \text{ km}$ between high-elevation forests in the Cascades and low-elevation woodlands in the eastern foothills of the Cascades. The range in $\text{CMI}_{\overline{\text{wy}}}$ encountered along this gradient in the Cascades almost spanned the full range in $\text{CMI}_{\overline{\text{wy}}}$ that supported 98% of forest area in the western US. Dry forests occurred along the low-elevation margins of mountain ranges throughout continental areas, though the largest tract of dry forest was found in Arizona and New Mexico.

Forest NPP, BIO, and BIO residence time varied substantially across both WAORCA and the broader western US in response to variation in CMI_{wy} (Fig. 3.1, 2, Table 3.2). We focused on forests in areas where CMI_{wy} was between -200 and 200 cm yr^{-1} given the paucity of land and measurements in the 2% of forest area that was either drier or wetter. Median $\text{NPP}_{\text{field}}$, $\text{BIO}_{\text{field}}$, and $\text{CRT}_{\text{field}}$ all exhibited a strong, positive association with CMI_{wy} ($r_s=0.93-0.96$, $p<0.001$). Median $\text{NPP}_{\text{field}}$ increased 155% between the driest and wettest 5% of sites in WAORCA (Fig. 3.2a), while median $\text{BIO}_{\text{field}}$ and $\text{CRT}_{\text{field}}$ increased 997% and 358%, respectively, between these sites (Fig. 3.2b, c, Table 3.2). The relationship in each case was slightly curvilinear. There were also strong, positive relationships among median $\text{NPP}_{\text{field}}$, $\text{BIO}_{\text{field}}$, and $\text{CRT}_{\text{field}}$ along the WAORCA bioclimatic gradient ($r_s=0.90-0.96$, $p<0.001$).

Broadly similar patterns were evident when forest NPP_{sat} , BIO_{sat} , and CRT_{sat} were examined across the western US using remote sensing data sets (Fig. 3.1b, c, d, 2c, d, Table 3.2). Median NPP_{sat} , BIO_{sat} , and CRT_{sat} all showed a strong, positive relationship with CMI_{wy} ($r_s=0.93-0.99$, $p<0.001$). Median NPP_{sat} increased 97% between the driest and wettest 5% of forested areas along the regional CMI_{wy} gradient (Fig. 3.2d, Table 3.2). Similarly, median BIO_{sat} and CRT_{sat} increased 410% and 160%, respectively, between the driest and wettest areas (Fig. 3.2e, f, Table 3.2). The response of median NPP_{sat} , BIO_{sat} , and CRT_{sat} to increased CMI_{wy} was more curvilinear than the field measurements and plateaued in areas where CMI_{wy} exceeded $\sim 100 \text{ cm yr}^{-1}$. Furthermore, while magnitude of NPP_{sat} and $\text{NPP}_{\text{field}}$ response to CMI_{wy} were similar, the magnitude of BIO_{sat} and CRT_{sat} responses to increased CMI_{wy} were much more muted than the magnitude of response in $\text{BIO}_{\text{field}}$ and $\text{CRT}_{\text{field}}$. Nevertheless, field- and satellite-derived estimates of median NPP, BIO, and CRT were strongly correlated ($r_s=0.90-0.95$, $p<0.001$). Furthermore, there were again strong relationships among median NPP_{sat} , BIO_{sat} , and CRT_{sat} along the western US bioclimatic gradient ($r_s=0.93-0.97$, $p<0.001$).

Discussion and conclusions

Climate moisture index

Water availability exerted a strong influence on NPP, BIO, and CRT among mature forests in the western US. We chose to quantify water availability using an index that accounted for both precipitation and energy-mediated ET_0 , recognizing that both of these factors contribute to the relative water stress experienced by plants within an ecosystem (Webb *et al.*, 1983).

We acknowledge that this index has several shortcomings. For instance, the index does not account for spatial variation in soil water storage capacity, which can be crucial for determining plant performance during drought (Peterman *et al.*, 2013). This might explain some of the variation in NPP and BIO among areas with similar CMI_{wy} ; however, quantifying soil water storage capacity even at individual sites is challenging given uncertainty in soil structure and plant rooting capacity (Running, 1994). The index also does not account for water added via fog drip, which has been shown to supply 13-45% of the water transpired by redwood forests (*S. sempervirens*) (Dawson, 1998) and sustain other forest ecosystems along the California coast (Fischer *et al.*, 2016, Johnstone & Dawson, 2010). This potentially explains why there were areas with low CMI_{wy} along the central and northern coast of California that supported forests with higher NPP and BIO than other forests with similar CMI_{wy} . Furthermore, the index does not account for spatial variation in runoff and thus likely overestimates water availability in the wettest areas since the fraction of water lost as runoff increases with precipitation (Sanford & Selnick, 2013). Despite its relative simplicity, prior studies showed that CMI was a useful index for explaining interannual variability in fire activity in the southwestern US (Williams *et al.*, 2014), as well as forest productivity in northern Siberia (Berner *et al.*, 2013), southern Canada (Hogg *et al.*, 2002), and central Oregon (Berner & Law, 2015). Several studies also found that the index, or its inverse (i.e. $ET_0 - P$), explained substantial spatial variability in mature forest gross photosynthesis (Law *et al.*, 2002), productivity and biomass across a range of ecosystems (Berner & Law, 2015, Hogg *et al.*, 2008, Webb *et al.*, 1983). Our current study further demonstrates that CMI is a useful empirical index for assessing climatic constraints on forest ecosystems on large spatial scales.

Tree net primary productivity

Median forest NPP in mature stands approximately doubled between the driest and wettest areas in both WAORCA and the western US, though in both cases the rate at which NPP increased with CMI_{wy} slowed in the wettest areas. Prior field studies conducted at a limited number of field sites in the western US over the past four decades have similarly documented increased forest NPP along spatial gradients of increasing water availability (Berner & Law, 2015, Gholz, 1982, Webb *et al.*, 1983, Whittaker & Niering, 1975). Building on these prior efforts, our current study demonstrates a robust relationship between mature forest NPP and

water availability using field measurements from nearly 2,000 inventory plots along with satellite remote sensing estimates of NPP covering ~18 Mha of forestland.

The NPP-CMI_{wy} relationship was similar when NPP was assessed using field measurements from across WAORCA or using MODIS covering the western US. MODIS did show NPP leveling off in the wettest parts of WAORCA (CMI_{wy} $\approx$ 100-200 cm yr⁻¹), whereas this was less evident in the field measurements. The inventory sites and MODIS forestland occurred at similar elevations along the CMI_{wy} gradient in WAORCA, suggesting that this discrepancy in NPP was not due to MODIS systematically including cold, high-elevation areas not sampled by the inventory sites. One possibility is that MODIS NPP did not increase in the wettest areas because MODIS becomes less sensitive to increases in the fraction of photosynthetically-active radiation (FPAR) absorbed by plant canopies in densely vegetated areas (Yan *et al.*, 2016). A recent MODIS analysis similarly found that the amount of photosynthetically-active radiation absorbed by plant canopies (APAR = FPAR x PAR) increased asymptotically with increasing mean annual precipitation across plant communities in California (Jin & Goulden, 2014). Forests had higher APAR than other plant communities and, furthermore, exhibited the smallest increase in APAR per unit increase in precipitation of any plant community, suggesting that forest productivity was less sensitive to changes in precipitation than productivity of other plant communities (Jin & Goulden, 2014). In contrast with the field measurements, the asymptotic response of MODIS NPP and APAR to increasing water availability in wet areas suggests that climate impact assessments based on MODIS could underestimate the sensitivity of plant productivity to changes in water availability in wet areas with high biomass.

Mechanistically, the strong NPP-CMI_{wy} association reflects the coupling between carbon and water cycling at leaf (Ball *et al.*, 1987)-to-ecosystem scales (Law *et al.*, 2002). Forest NPP depends on regionally specific relations with leaf area (Schroeder *et al.*, 1982, Waring, 1983), which largely determine the proportion of incoming solar radiation that is absorbed and thus potentially available to fuel photosynthesis (Runyon *et al.*, 1994). Leaf photosynthesis inevitably leads to transpiration water loss (Ball *et al.*, 1987), which must be balanced against water uptake from the soil so as to prevent the formation of excessive tension on the internal water column that could result in hydraulic failure (Ruehr *et al.*, 2014, Williams *et al.*, 1996). As soil water availability increases, trees are able to support greater leaf area while maintaining water column tensions within physiologically operable ranges, which consequently leads to more photosynthate available to fuel NPP unless trees are limited by other resources (e.g., nitrogen). The decreasing rate at which NPP increased with

CMI_{wy} in the wettest areas is likely due to low temperatures constraining productivity at high elevations (Nakawatase & Peterson, 2006, Runyon *et al.*, 1994) and heavy cloud cover limiting solar radiation and thus photosynthesis in coastal areas (Carroll *et al.*, 2014, Zhao *et al.*, 2010). Forest NPP is affected by many biotic (e.g., age) and abiotic factors (e.g., nutrients), yet water availability emerges as a key environmental constraint in the western US.

Tree carbon stocks

Mature forest BIO increased notably with increasing CMI_{wy} across both WAORCA and the broader western US, reflecting underlying shifts in NPP and, likely, BIO mortality rates due to natural disturbance. BIO is determined by the rates at which carbon is gained via NPP and lost due to tissue senescence and mortality integrated over annual to centennial timescales (Olson, 1963). Hence, the increase in NPP with increasing CMI_{wy} explains some of the concomitant increase in BIO. Our analysis did not investigate how tissue senescence or mortality varied along the regional bioclimatic gradient, though a recent study found that BIO mortality rates due to bark beetles and fires were very low in the wettest parts of the western US (e.g., Coast Range and Cascades), while considerably higher in most drier areas (Hicke *et al.*, 2013). Furthermore, the field and satellite data sets also incidentally revealed that there was an increase in the median age of stands over 100 years as conditions became wetter, with median stand age at ~140 years in the driest areas and 200-240 years in the wettest areas. The general increase in mature forest BIO with increasing water availability is thus likely due to higher rates of productivity and potentially lower BIO mortality rates from natural disturbance.

The observed increase in mature forest BIO with increasing water availability was generally consistent with prior field studies from this region, yet our study demonstrates this response over a much broader bioclimatic gradient. For instance, early work by Whittaker and Niering (1975) showed that mature forest BIO tended to increase with a moisture index inferred from community composition along an elevational gradient in Arizona's Santa Catalina Mountains. Subsequent studies focused on five long-term ecological research (LTER) sites spread across the conterminous US (Webb *et al.*, 1983) and at 8-12 sites in Oregon (Berner & Law, 2015, Gholz, 1982) similarly showed a general increase in tree biomass with increasing water availability. Our study included sites that ranged from dry

woodlands with little BIO to temperate rainforests with BIO exceeded in few other regions (e.g. max BIO $\approx 950 \text{ Mg C ha}^{-1}$). BIO in our study area has been reported to reach over 2,000 Mg C ha^{-1} in old-growth coastal redwood stands in northern California (Waring & Franklin, 1979), which is thought to be exceeded only by the $>3,000 \text{ Mg C ha}^{-1}$ attained by old-growth *Eucalyptus regnans* stands in southern Australia (Keith *et al.*, 2009). A global synthesis suggested that average AGB among high-biomass stands in wet temperate forests ($\sim 377 \text{ Mg C ha}^{-1}$) was over two times that of high-biomass stands in wet tropical forests ($\sim 179 \text{ Mg C ha}^{-1}$) and nearly six times that of high-biomass stands in wet boreal forests ($\sim 64 \text{ Mg C ha}^{-1}$) (Keith *et al.*, 2009). The range in mature forest BIO included in our analysis of WAORCA thus spanned much of the observed global range in BIO.

Both field and satellite measurements revealed that median BIO increased with CMI_{wy} , yet the satellite data set showed less of an increase than the field measurements. Median forest $\text{BIO}_{\text{field}}$ increased nearly 1,000% between the dry woodlands and coastal temperate rainforests in WAORCA, yet the increase in BIO_{sat} with increasing CMI_{wy} was less pronounced ($\sim 410\%$ increase) when assessed across the western US. Furthermore, median BIO_{sat} plateaued around 175 Mg C ha^{-1} in areas where CMI_{wy} was $\sim 100\text{-}200 \text{ cm yr}^{-1}$. The response of BIO to increasing CMI_{wy} was likely more muted when assessed using the satellite-derived maps than the field measurements for several reasons. The maps are largely derived from optical, multispectral satellite imagery that is not very sensitive to variation in BIO in high-biomass forests. Additionally, areas with high BIO often occur as small patches set in a matrix of stands with lower BIO (Spies *et al.*, 1994) and thus the moderate-resolution satellite imagery used in developing these maps records the spectral signature of this larger area rather than just the patch with high BIO. In other words, the satellite imagery has a larger sampling footprint relative to that of a field plot, which thus averages BIO over a larger area, reducing peak values. Advances in satellite remote sensing, such as NASA's new Global Ecosystem Dynamics Investigation Lidar (GEDI) instrument, are anticipated to help overcome some of these challenges (Goetz & Dubayah, 2011). Nevertheless, current BIO maps (e.g., Kellndorfer *et al.*, 2012, Wilson *et al.*, 2013) proved to be a valuable tool for ecologic and natural resource assessments (Berner *et al.*, 2012, Goetz *et al.*, 2014, Krankina *et al.*, 2014).

Carbon residence time in tree biomass

We computed CRT as BIO/NPP and found that median CRT_{field} increased persistently with CMI_{wy} from ~11 years in the driest forests to over 49 years in the wettest forests, highlighting a fundamental change in ecosystem function along this broad bioclimatic gradient. One limitation of our study is that computing CRT in this manner assumes that BIO is constant over time (Friend *et al.*, 2014). We focused on mature stands (>100 years) to minimize the change in BIO over time, though we acknowledge that BIO can gradually increase during subsequent centuries (Hudiburg *et al.*, 2009), which would have led us to underestimated CRT. Conversely, drought and insect-induced defoliation in the early 2000s could have suppressed NPP (Berner & Law, 2015, Schwalm *et al.*, 2012) without a proportional reduction in BIO, which could have inflated our estimates of CRT in some areas.

Nevertheless, our results agree well with a prior study focused on 11 LTERs spread across the conterminous US that found that CRT increased from ~2 years in a desert shrubland to ~73 years in a 450-year-old Douglas-fir stand at the Andrews LTER in the Cascade Mountains in Oregon (Webb *et al.*, 1983). For comparison, we looked at five old-growth Douglas-fir stands (336-555 years old) near the Andrews LTER and found that CRT_{field} averaged 79 ± 23 years ($\pm 1SD$) among these stands. An increase in the CRT of aboveground tissues was also observed among plant communities along an elevational moisture gradient in the Santa Catalina Mountains of Arizona (Whittaker & Niering, 1975) and across nine mature stands in a range of forest communities in Oregon (Gholz, 1982). Although this pattern has been previously documented on small scales, the underlying mechanisms remain unclear.

We speculate that the increase in CRT with increased water availability was associated with underlying changes in NPP allocation, BIO mortality rates, and stand age. Trees invest a larger proportion of NPP into aboveground tissue production as conditions become wetter and competition for light intensifies (Law *et al.*, 2003, Runyon *et al.*, 1994). Our field measurements revealed that the fraction of NPP allocated aboveground increased from ~0.45 in the driest areas to ~0.64 in the wettest areas and, furthermore, that CRT in aboveground tissues averaged twice as long as CRT in belowground tissues. Thus, a shift in NPP allocation toward longer-lived aboveground tissues likely contributed to longer CRT in wetter areas. Longer CRT in wetter areas could also be related to forests in these areas (e.g., Coast Range) experiencing lower BIO mortality rates from wildfire and bark beetles than forests in drier, continental areas (Hicke *et al.*, 2013). We also found that mature stands

tended to be older in wetter areas and that older stands tended to have longer CRT, likely as a result of these stands having higher BIO and similar NPP (Hudiburg *et al.*, 2009).

Consequently, the CRT-CMI_{wy} relationships that we observed incorporate an age-related effect; however, the effect was quite small relative to the climate-effect. This can be illustrated by comparing median CRT between mature (100-200 years) and old (>200 years) stands occupying very dry (CMI_{wy} < -100 cm yr⁻¹) and very wet (CMI_{wy} > 100 cm yr⁻¹) areas. Median CRT differed by 6% (16 vs. 17 years) between mature and old stands in very dry areas and by 10% (47 vs. 52 years) in very wet areas. Conversely, median CRT of mature stands differed 98% (16 vs. 47 years) between very dry and very wet areas, while the median CRT of old stands differed 101% (52 vs. 17 years) between very dry and very wet areas. In other words, the difference in CRT between stands in contrasting climates is much greater than difference in CRT between mature and old stands within the same climate zone. Our study demonstrates that CRT in live-tree biomass was strongly influenced by water availability; however, additional efforts are needed to determine the underlying mechanism by which changes in water availability affect CRT, particularly given that CRT is a primary source of uncertainty in global vegetation model projections of future terrestrial carbon cycling (Friend *et al.*, 2014).

Predicting ecosystem response to environmental change

Water availability is projected to decline in much of the western US over the coming century, in part due to higher temperatures increasing atmospheric evaporative demand (Cook *et al.*, 2015, Dai, 2013, Walsh *et al.*, 2014). Predicting the timing, magnitude and extent of ecological response to regional climate change remains a challenge. Our study showed that water availability is a key determinant of forest structure and function in the western US, broadly suggesting that chronic reductions in regional water availability could reduce the NPP, BIO, and CRT of mature stands. Nevertheless, it is problematic to predict the temporal response of extant forest communities to near-term climatic change based on bioclimatic relationships derived from spatial data. For instance, recent studies found that the slope of the NPP-precipitation relationship was much steeper when derived from spatial data than when derived from the temporal response of NPP to interannual variation in precipitation (Jin & Goulden, 2014, Wilcox *et al.*, 2016). Near-term effects of climate variability depend on the physiological characteristics of species in the extant plant community; however, bioclimatic

relationships derived from spatial data reflect gradual adjustment of community composition and population size to climate over long periods of time (Jin & Goulden, 2014, Wilcox *et al.*, 2016). Furthermore, bioclimatic models derived from spatial data cannot account for other ecophysiological impacts of environmental change, such as (1) enhanced plant water use efficiency from CO₂ fertilization (Soulé & Knapp, 2015), (2) increased likelihood of tree mortality due to hotter drought (Adams *et al.*, 2009), or (3) novel changes in disturbance regimes (Dale *et al.*, 2001, Hicke *et al.*, 2006). Consequently, predicting ecological response to environmental change over the coming century will require the use of mechanistic ecosystem models that account for physiologic, demographic, and disturbance processes at fine taxonomic and spatial scales (Hudiburg *et al.*, 2013a, Law, 2014). Although spatial models may not be suitable for near-term projection of ecosystem change, they do provide insight into long-term ecosystem adaptation to local climate and, furthermore, can be used to validate and refine mechanistic models if constructed from a representative sample of forestland.

Summary and conclusions

Water availability varies widely across the western US, giving rise to forests that range from dry, low-biomass woodlands to temperate rainforests that are among the highest biomass forests found anywhere in the world. In this study we quantified changes in tree productivity, live biomass, and carbon residence time along spatial gradients in water availability using field inventory measurements from WAORCA and satellite remote sensing data sets spanning the western US. Our multi-method, multi-scale analysis revealed that tree productivity, live biomass, and carbon residence time all increased notably with water availability, which we computed using an index that accounted for both precipitation and reference evapotranspiration. The observed increase in productivity was likely due to the close coupling between carbon and water cycling at leaf-to-ecosystem scales, while the observed increase in live biomass was associated with higher productivity and longer carbon residence. The increase in carbon residence time in wetter areas was linked with greater carbon allocation to long-lived aboveground tissues, older stand age, and, possibly, lower biomass mortality rates from natural disturbances (e.g., bark beetles, fires). Tree productivity and biomass derived from field and satellite measurements exhibited similar responses to increasing water availability, though the satellite data sets tended to plateau in the wettest areas, suggesting that additional efforts are needed to better quantify productivity and biomass from satellites in

high-productivity, high-biomass forests. The pronounced increase in tree productivity, biomass, and carbon residence time between the driest and wettest areas illustrates the gradual adjustment of ecosystem structure and function to long-term variation in water availability; however, the observed bioclimatic relationships are not suitable for near-term projections of future ecosystem response to regional drying. Predicting near-term ecosystem response to drying and other environmental change (e.g., increased CO₂) will require mechanistic ecosystem models, which can be evaluated against bioclimatic relationships developed using inventory sites from a representative sample of forestlands (e.g., Forest Service inventory sites). Overall, our results indicate that water availability is a key determinant of tree productivity, live biomass, and carbon residence time in mature stands ranging from dry woodlands to coastal temperate rainforests. Future efforts are needed to anticipate and mitigate the impacts of projected warming and drying on forest ecosystems in the western US and elsewhere around the world.

Tables

Table 3.1. Summary of tree net primary productivity (NPP, $\text{Mg C ha}^{-1} \text{ yr}^{-1}$), live biomass (BIO, Mg C ha^{-1}), and carbon residence time (CRT, year) for stands over 100 years old across both WAORCA and the broader western United States. Forest characteristics were quantified for WAORCA using field measurements from 1,953 sites and for the western United States using satellite-derived data sets covering 18 Mha of mature forest. Satellite data sets included MODIS NPP and an estimate of BIO derived by combining existing maps of aboveground biomass with additional estimates of carbon storage in coarse-root, fine-roots, and foliage. CRT describes the average duration, in years, that a molecule of carbon will remain in live tree biomass and was computed as $\text{CRT} = \text{BIO}/\text{NPP}$. These carbon stocks and fluxes combine above and belowground components.

Domain	Variable	Units	Time span	Mean (SD)	Range
WAORCA	$\text{NPP}_{\text{field}}$	$\text{Mg C ha}^{-1} \text{ yr}^{-1}$	2001-2006	4.3 (2.5)	0.6 – 20.9
	$\text{BIO}_{\text{field}}$	Mg C ha^{-1}	2001-2006	158 (135)	2 – 947
	$\text{CRT}_{\text{field}}$	year	2001-2006	33 (19)	2 – 137
Western US	NPP_{sat}	$\text{Mg C ha}^{-1} \text{ yr}^{-1}$	2000-2014	5.3 (2.0)	0.1 – 22.7
	BIO_{sat}	Mg C ha^{-1}	2000-2008	83 (54)	2 – 669
	CRT_{sat}	year	2000-2008	15 (9)	2 – 1390

Table 3.2. Changes in tree net primary productivity (NPP, Mg C ha⁻¹ yr⁻¹), live biomass (BIO, Mg C ha⁻¹), and carbon residence time (CRT, year) for stands over 100 years old along gradients in a climate moisture index (CMI_{wy}, cm yr⁻¹) in both WAORCA and the broader western US. Forest characteristics were quantified using field measurements in WAORCA and satellite remote sensing data sets covering the western US. The analysis incorporated forests in areas where CMI_{wy} was between -200 cm yr⁻¹ and 200 cm yr⁻¹. Summaries include (1) median forest characteristics in the driest 5% and wettest 95% of sites or pixels, (2) the corresponding change, and (3) Spearman's correlation (r_s) between CMI_{wy} and the median forest characteristics computed at 10 cm yr⁻¹ CMI_{wy} intervals. All correlations were statistically significant at $\alpha < 0.001$.

Domain	Variable	Units	Median of...		Change...		CMI _{wy} cor. r_s
			Driest 5%	Wettest 95%	Abs.	%	
WAORCA	NPP _{field}	Mg C ha ⁻¹ yr ⁻¹	2.2	5.6	3.4	155	0.93
	BIO _{field}	Mg C ha ⁻¹	26	281	255	997	0.96
	CRT _{field}	year	11	49	38	358	0.96
Western US	NPP _{sat}	Mg C ha ⁻¹ yr ⁻¹	3.4	6.7	3.3	97	0.93
	BIO _{sat}	Mg C ha ⁻¹	32	165	133	410	0.97
	CRT _{sat}	year	10	26	16	160	0.99

Figures

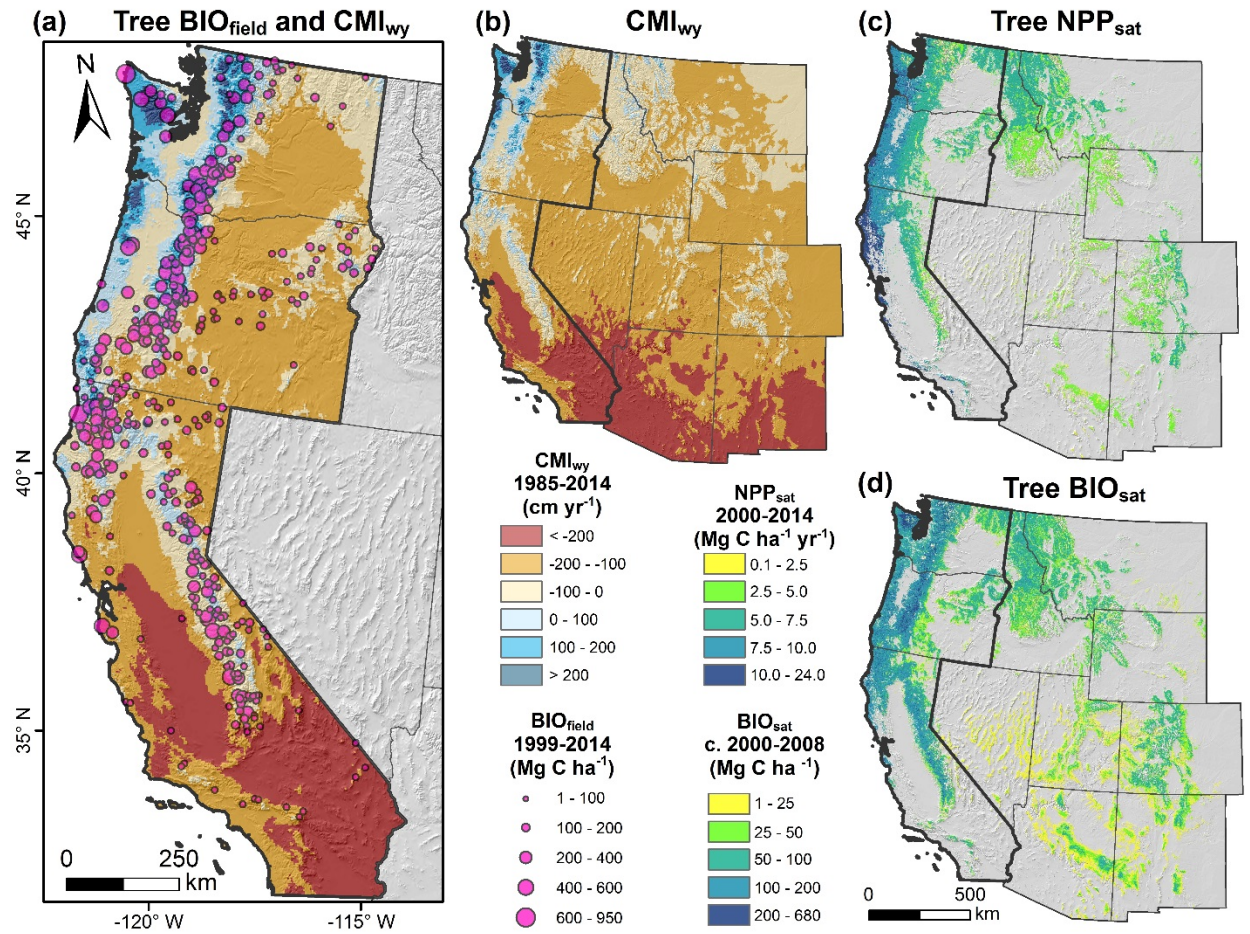


Figure 3.1. Mean climatic moisture index (CMI_{wy} , $cm\ yr^{-1}$), tree net primary productivity (NPP , $Mg\ C\ ha^{-1}\ yr^{-1}$), and live tree biomass (BIO , $Mg\ C\ ha^{-1}$) in the western United States. (a) BIO derived from field measurements (BIO_{field}) at mature sites (>100 years) in WAORCA. For visual clarity only 20% of the 1,953 sites are depicted. (b) CMI_{wy} was computed as monthly precipitation minus reference evapotranspiration summed over the annual water year (October-September) and then averaged from 1985-2014. (c) Mean annual NPP was quantified using MODIS satellite data from 2000-2014 (NPP_{sat}). (d) BIO was quantified using satellite-derived estimates of carbon stocks (BIO_{sat}).

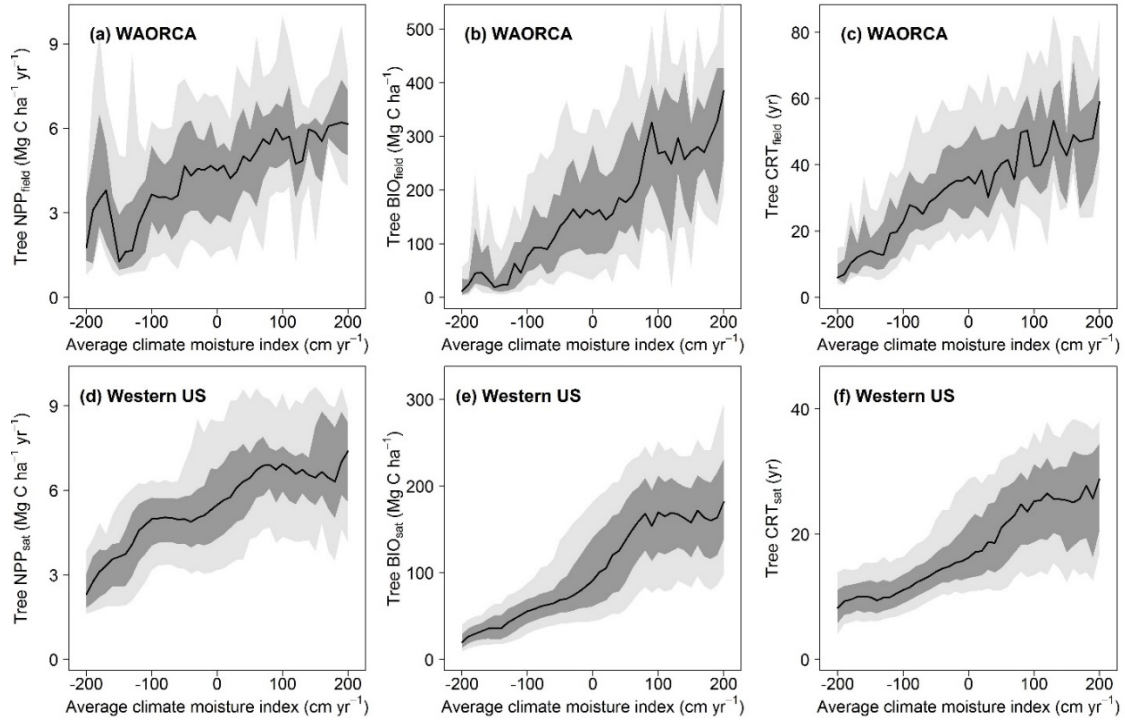


Figure 3.2. Tree net primary productivity (NPP, $\text{Mg C ha}^{-1} \text{ yr}^{-1}$), live biomass (BIO, Mg C ha^{-1}), and carbon residence time (CRT, years) increased with increasing water availability across both WAORCA (a-c) and the broader western United States (d-f). Forest characteristics were derived from field measurements on 1,953 inventory plots in WAORCA (a-c) and from satellite remote sensing data sets across 18 Mha of mature forest in the western United States (d-f). Tree NPP_{sat} was characterized using MODIS data averaged annually from 2000 to 2014. Tree BIO_{sat} was quantified based on an ensemble of aboveground biomass maps plus estimates of coarse-root, fine-root, and foliage biomass. Tree CRT was computed for each field plot and pixel as BIO / NPP . Water availability was quantified using a climate moisture index ($\text{CMI} = \text{P} - \text{ET}_0$) summed over the water year (October-September) and then averaged from 1985-2014 (CMI_{wy}). The region was partitioned into 10 cm yr^{-1} (nonoverlapping) CMI_{wy} bins, pixels/plots were allocated to bins, and then forest characteristics were summarized within each bin. In each panel, the bold line denotes the median, the dark gray band the 25-75th percentiles, and the light gray band the 10-90th percentiles. Note the different y-axis scales between (b) and (e), as well as (c) and (f).

CHAPTER 4. TREE MORTALITY FROM FIRES, BARK BEETLES, AND TIMBER HARVEST DURING A HOT, DRY DECADE IN THE WESTERN UNITED STATES (2003-2012)

Abstract

High temperatures and severe drought contributed to extensive tree mortality from fires and bark beetles during the 2000s in parts of the western United States. Several states in this region have greenhouse gas (GHG) emission targets and would benefit from information on the amount of carbon stored in tree biomass killed by disturbance. We quantified mean annual tree mortality from fires, bark beetles, and timber harvest from 2003-2012 for each state in this region. We estimated tree mortality from fires and beetles using tree aboveground carbon (AGC) stock and disturbance data sets derived largely from remote sensing. We quantified tree mortality from harvest using data from US Forest Service reports. In both cases we used Monte Carlo analyses to track uncertainty associated with parameter error and temporal variability. Regional tree mortality from harvest, beetles, and fires ($MORT_{H+B+F}$) together averaged 45.8 ± 16.0 Tg AGC yr^{-1} ($\pm 95\%$ confidence interval), indicating a mortality rate of $1.10 \pm 0.38\%$ yr^{-1} . Harvest accounted for the largest percentage of $MORT_{H+B+F}$ ($\sim 50\%$), followed by beetles ($\sim 32\%$), and fires ($\sim 18\%$). Tree mortality from harvest was concentrated in Washington and Oregon, where harvest accounted for $\sim 80\%$ of $MORT_{H+B+F}$ in each state. Tree mortality from beetles occurred widely at low levels across the region, though the most pronounced impacts occurred in Colorado and Montana, where beetles accounted for $\sim 80\%$ of $MORT_{H+B+F}$. Tree mortality from fires was highest in California, though fires accounted for the largest percentage of $MORT_{H+B+F}$ in Arizona and New Mexico ($\sim 50\%$). Our results highlight that opportunities and challenges to managing GHG emissions from forest ecosystems differ appreciably among states. Rising temperatures and greater risk of drought will likely increase tree mortality from fires and bark beetles during coming decades in parts of this region, thus sustained monitoring and mapping of tree mortality is necessary to inform forest and GHG management.

Introduction

Forests provide important natural resources and help regulate Earth's climate in part by storing carbon in woody biomass (Bonan, 2008, Pan *et al.*, 2011a); however, rising temperatures and hotter droughts are increasing tree mortality and driving forest dieback across the globe (Allen *et al.*, 2010, Kautz *et al.*, 2016, Peng *et al.*, 2011). Tree mortality increased during recent decades in the western United States (US; Hicke *et al.*, 2015, McDowell *et al.*, 2015, Smith *et al.*, 2015, van Mantgem *et al.*, 2009), likely associated with drought and recent warming (Kunkel *et al.*, 2013, Mote *et al.*, 2014). Rising temperatures contributed to increases in the extent, frequency, and severity of drought (Cook *et al.*, 2004, Diffenbaugh *et al.*, 2015, McCabe *et al.*, 2004) and from 2000-2004 the region experienced the most severe drought in the past 800 years (Schwalm *et al.*, 2012). Projections indicate that regional temperature could rise another ~3.8-5.5°C by the end of the 21st century and that much of the region, particularly the southwest, could become increasingly arid and prone to drought under a high greenhouse gas emission (GHG) scenario (RCP 8.5; Cook *et al.*, 2015, Kunkel *et al.*, 2013, Walsh *et al.*, 2014). These changes in regional climate could accelerate tree mortality, affecting resource availability and reducing forest carbon uptake and storage (Adams *et al.*, 2009, Berner *et al.*, 2017, Jiang *et al.*, 2013, McDowell *et al.*, 2015, Mote *et al.*, 2014).

Hot, dry conditions can directly kill trees (e.g., hydraulic failure, carbon starvation) as well as exacerbate tree mortality from fires and insects (Anderegg *et al.*, 2015b, Meddens *et al.*, 2015, Williams *et al.*, 2012). These conditions can increase fire occurrence (Littell *et al.*, 2016), the likelihood that a tree will die after a fire occurs (van Mantgem *et al.*, 2013), and make trees more vulnerable to attack by insects such as bark beetles (Creeden *et al.*, 2014, Raffa *et al.*, 2008). Consequently, high temperatures and severe drought contributed to extensive tree mortality from fires and bark beetles during the 2000s in parts of the western US (Creeden *et al.*, 2014, Williams *et al.*, 2012). The US Forest Service (USFS) recently recommended that metrics related to fire and insect effects be used to track national climate change impacts (Heath *et al.*, 2015), underscoring the importance of quantifying the magnitude and regional variation in tree mortality from these types of disturbance.

Tracking the amount of carbon stored in trees killed by disturbance is important in addition to the areal extent of tree mortality (Hicke *et al.*, 2013, Powell *et al.*, 2014, Williams *et al.*, 2016). Tree biomass is about 46-55% carbon (Berner & Law, 2016, Lamblom & Savidge, 2003) and biomass killed by disturbance decomposes over decades to centuries,

gradually transferring carbon back to the atmosphere (Harmon *et al.*, 2011). Mortality can be quantified over large areas in terms of carbon using remote sensing estimates of tree aboveground biomass (AGB) together with information on disturbance extent and severity (e.g., Baccini *et al.*, 2012, Hicke *et al.*, 2013, Powell *et al.*, 2014). Several states in the western US (e.g., Oregon, California) have established GHG reduction targets and thus benefit from information on the magnitude of carbon lost and primary causes of tree mortality.

In this study we quantified mean annual tree mortality from fires, bark beetles, and timber harvest from 2003-2012 among states in the western US using a combination of remote sensing data sets, harvest statistics, and other information. The main research question was: “What was the magnitude and relative contribution of mean annual tree mortality from fires, bark beetles, and timber harvest from 2003-2012 both regionally and among the 11 western states?” Specifically, we quantified tree mortality as the amount of carbon stored in tree AGB (i.e., AGC) killed by disturbance (e.g. Mg AGC ha⁻¹ or Tg AGC state⁻¹). We focused on this decade because forests in the region experienced extensive tree mortality from disturbance (e.g., Hicke *et al.*, 2015, Powell *et al.*, 2014) and also because of data availability and methodological constraints. We developed spatially explicit estimates of annual tree mortality from fires and bark beetles across regional forestland using remote sensing data sets. Our approach built from an earlier study (Hicke *et al.*, 2013) that used remote sensing to quantify tree biomass killed by disturbance based on the extent and severity of fire and beetle activity. Our current approach incorporated several new aspects that result in a more complete and robust analysis. Specifically, we included (1) three tree AGB data sets (Blackard *et al.*, 2008, Kelldorfer *et al.*, 2012, Wilson *et al.*, 2013); (2) variation in the carbon content of tree AGC (Lamloom & Savidge, 2003); (3) variation in the fraction of tree AGC killed by fires of varying severity and forest type derived from field observations (Ghimire *et al.*, 2012); (4) a routine that tracked prior tree mortality within a grid cell; and (5) an uncertainty analysis based on a Monte Carlo approach. In addition to the remote sensing analysis, we estimated mean annual tree mortality from timber harvest for each state using US Forest Service (USFS) reports (Oswalt *et al.*, 2014, Smith *et al.*, 2009), ancillary information, and a Monte Carlo analyses to propagate uncertainty.

Methods

Geospatial data sets and preprocessing

General information

We quantified tree mortality from fires ($MORT_{fire}$) and bark beetles ($MORT_{beetle}$) from 2003-2012 across 802,575 km² of forestland located in the western US (Fig. 4.1, 31.3°N-49.0°N, 102.0°W-124.5°W). Forestlands were included if consistently mapped as forest by three separate tree AGB data sets (described below). We conducted the analysis on a 1-km resolution grid in an Albers Equal Area projection, with the resolution chosen to match the bark beetle data set (Meddens *et al.*, 2012). We analyzed and visualized the data using ArcGIS 10 (ESRI, Redlands, CA) and *R* statistical software (version 3.2; R Core Team, 2015), along with the *R* packages *raster* (Hijmans & van Etten, 2013) and *dplyr* (Wickham & Francois, 2015). Our approach for estimating tree mortality due to fires and bark beetles using remote sensing is illustrated in Fig. 4.2.

Tree carbon stocks

We estimated tree AGC using three tree AGB geospatial data sets together with information on the fraction of dry biomass that is carbon (f_{carbon}). The tree AGB data sets were produced by spatially interpolating USFS inventory measurements (FIA) using satellite and geophysical data sets in conjunction with machine learning algorithms (Blackard *et al.*, 2008, Kellndorfer *et al.*, 2012, Wilson *et al.*, 2013). Wilson *et al.* (2013) provided estimates of tree AGC assuming that f_{carbon} was 50%; we converted these estimates back to tree AGB by multiplying by 2. We acquired each data set at 250-m spatial resolution, reprojected it to an Albers Equal Area projection, and then applied a common mask that identified pixels consistently classified as forest among all data sets. Next, we aggregated from 250-m to 1-km resolution by computing total tree AGB in each 1-km pixel (i.e., Mg AGB pixel⁻¹).

We quantify tree mortality from 2003-2012 and required estimates of tree AGB prior to disturbance. Two of these data sets represented tree AGB circa 2000 (Blackard *et al.*, 2008, Kellndorfer *et al.*, 2012), whereas the third depicted tree AGB circa 2000-2008 (Wilson *et al.*, 2013). The data set from Wilson *et al.* (2013) depicted tree AGB following disturbances that occurred from 2003-2008 and thus we needed to estimate pre-disturbance tree AGB in pixels

that were disturbed during these six years. We did this following an existing approach (Hicke *et al.*, 2013) that involved comparing tree AGB in fire and beetles disturbed pixels against the average tree AGB of undisturbed pixels from the same forest type (Ruefenacht *et al.*, 2008) and ecoregion (Omernik, 1987). If tree AGB in the disturbed pixel was less than the average tree AGB of undisturbed pixels, then we set tree AGB in the disturbed pixel to this average, but otherwise left the disturbed pixel unaltered. After implementing this correction, we then computed the average and standard error (SE) of tree AGB for each pixel over the three data sets ($\overline{AGB}$, SE_{AGB}). Lastly, we estimated the average and SE of f_{carbon} ($\overline{f_{carbon}}$, SE_{carbon}) for angiosperm ($48.49 \pm 0.42\%$ C) and gymnosperm ($50.87 \pm 0.63\%$ C) forest types using measurements from tree species (n=8 and 11, respectively) found in this region (Lamloom & Savidge, 2003).

Forest fires

We used annual maps of fire severity from 2003-2012 produced by the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink *et al.*, 2007). These maps were derived from 30-m resolution Landsat images acquired before and after fires larger than ~405 ha in the western US. Fire severity was mapped using the differenced Normalized Burn Ratio (dNBR) and then each pixel was classified as one of five thematic severity classes. We focused on pixels that burned at low-, moderate-, or high-severity and excluded those that were unburned or showed post-fire greening. We identified fire in forests by generating a 30-m resolution forest mask based on non-agricultural forestland in either of two national land cover maps (Homer *et al.*, 2007, Rollins, 2009). We then computed the annual fraction of forest area in each 1-km pixel that burned at each severity (A_s). Lastly, we estimated the average (and SE) fraction of tree biomass killed at each severity (f_{fire}) for angiosperm and gymnosperm forest types ($\overline{f_{fire}}$, SE_{fire}) using 116 estimates of f_{fire} synthesized from 29 field studies conducted in the western US (Table C1; Ghimire *et al.*, 2012).

Bark beetles

We used annual maps depicting the areal extent of tree canopy mortality due to 12 bark beetle species that were produced from aerial surveys, forest inventory measurements, and high-resolution satellite imagery (Meddens *et al.*, 2012). The USFS National Forest Health

Monitoring program conducts aerial detection surveys (ADS) that provide a coarse snapshot of insect and other forest disturbance at a landscape scale (Johnson & Wittwer, 2008). Trained observers conduct surveys from fixed-wing aircraft that involve sketch-mapping the extent of areas affected by insect outbreaks and then visually estimating the number of dead trees within affected areas. Meddens *et al.* (2012) used the ADS observations to estimate annual canopy mortality area due to bark beetles across the western US from 1997-2010, with estimates then extended through 2012 (Hicke *et al.*, 2015).

Canopy mortality area was estimated at 1-km resolution based on the number of recently killed trees and the average canopy area of each tree species. The ADS observations underestimated the number of trees killed by bark beetles in comparison with field observations and QuickBird (2.4-m resolution) satellite imagery from Colorado, Idaho, and New Mexico. This led to the development of adjustment factors for several forest types based on the ratio of dead trees mapped from satellite to ADS tree kill counts. These adjustment factors were then used to modify ADS tree kill counts, resulting in high and middle (most realistic) estimates as well as low estimates based on unaltered ADS numbers (more details in: Hicke *et al.*, 2015, Meddens *et al.*, 2012). The data set includes bark beetle species that cumulatively killed at least 100,000 trees across the domain from 1997-2010. Specifically, it includes (from greatest to least mortality area) mountain pine beetle (*Dendroctonus ponderosae* Hopkins), piñon ips (*Ips confusus* (LeConte)), Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), western balsam bark beetle (*Dryocoetes confuses* (Swaine)), and fir engraver (*Scolytus ventralis* LeConte), as well as seven additional beetle species that killed fewer trees. We masked these data to our domain and then summed canopy mortality area across bark beetle species for each 1-km pixel in a given year (i.e., a voxel) from 2003-2012. We then calculated annual tree canopy mortality fraction (f_{beetle}) for each voxel by dividing canopy mortality area by forest cover fraction. We incorporated the lower, middle, and upper estimates of f_{beetle} into our analysis.

Tree mortality from bark beetles and fires

We developed spatially explicit estimates of annual $MORT_{beetle}$ and $MORT_{fire}$ from 2003-2012 and also quantified uncertainty in these estimates using a Monte Carlo approach (e.g., Gonzalez *et al.*, 2015, Harmon *et al.*, 2007). The Monte Carlo involved generating 100 realizations of annual tree mortality in each voxel, where each realization iteratively varied tree $\overline{AGC}$, $\bar{f}_{carbon}$, f_{beetle} , and $\bar{f}_{fire}$ based on uncertainty in each term. We assumed that tree

AGC within a pixel only changed due to disturbance (i.e., no tree growth); consequently, cumulative tree mortality within a pixel could not exceed the initial tree AGC. For each realization r we first computed tree AGC for pixel p of year $t = 2003$ as

$$\overline{AGC}_{r,p,t} = (\overline{AGB}_{p,t} + a_{AGB,r} \times SE_{AGB,p}) \times (\bar{f}_{carbon} + a_{carbon,r} \times SE_{carbon}) \quad (\text{Eqn. 1})$$

where $\bar{f}_{carbon}$ and SE_{carbon} varied by forest type and a_x was a random number from a normal distribution (mean=0, SD=1) that differed for each variable with each realization. The other variables are defined above. We then calculated $MORT_{beetle}$ as

$$MORT_{beetle,r,p,t} = \overline{AGC}_{r,p,t} \times \hat{f}_{beetle,p,t} \quad (\text{Eqn. 2})$$

where $\hat{f}_{beetle,p,t}$ was an estimate of f_{beetle} drawn randomly from a triangular distribution defined uniquely for each voxel using the low, middle, and high estimates of f_{beetle} . Each distribution was fit using the *triangle* package in R (Carnell, 2016). Next, we computed $MORT_{fire}$ as

$$MORT_{fire,r,p,t} = (\overline{AGC}_{r,p,t} - MORT_{beetle,r,p,t}) \times \sum_s^{severity} [A_{p,t,s} \times (\bar{f}_{fire,s} + a_{fire,s,r} \times SE_{fire,s})] \quad (\text{Eqn. 3})$$

We then reduced tree AGC stocks at the start of year $t+1$ to account for mortality in year t , such that

$$\overline{AGC}_{r,p,t+1} = \overline{AGC}_{r,p,t} - (MORT_{beetle,r,p,t} + MORT_{fire,r,p,t}) \quad (\text{Eqn. 4})$$

We repeated Eqns. 2-4 annually through 2012 and then repeated the entire process 100 times. We then computed the mean and standard deviation (SD) of these multiple estimates of tree mortality for each voxel, where the SD represented uncertainty due to parameter error (e.g., SE_{AGB} , SE_{fire}). Altogether, this process yielded spatially explicit estimates of annual tree mortality (and uncertainty) caused by fires and bark beetles from 2003-2012 across forestland in the western US.

Following the geospatial analysis, we estimated mean annual tree mortality from fires ($\overline{MORT}_{fire}$) and bark beetles ($\overline{MORT}_{beetle}$) for each state from 2003-2012 and used a Monte Carlo analysis to propagate uncertainty in these estimates associated with parameter error and temporal variability. As illustrated for fires (identical for beetles), we first derived 1,000 realizations r of annual tree mortality in each state from $t = 2003$ to 2012, as per

$$MORT_{fire,r,state,t} = \sum_{p=1}^{N_{pixels}} (MORT_{fire,p,t} + a_r \times SD_{MORT_{fire,p,t}}) \quad (\text{Eqn. 5})$$

and then summarized (mean and SD) each set of realizations. We used these annual statewide summaries to then repeatedly ($N_r=1,000$) estimate both the mean and SE of annual mortality from 2003-2012 for each state, where each realization randomly varied annual statewide

mortality by its parameter error (i.e., SD computed above). We again summarized (mean and SD) each set of realizations for both statistics. This yielded an estimate of $\overline{\text{MORT}}_{\text{fire}}$ for each state and also produced estimates of uncertainty in $\overline{\text{MORT}}_{\text{fire}}$ due to parameter error (i.e., SD of estimates of $\overline{\text{MORT}}_{\text{fire}}$) and temporal variability (i.e., mean of estimates of SE of annual mortality).

In the final step, we derived a 95% confidence interval (CI) around each estimate of $\overline{\text{MORT}}_{\text{fire}}$ that accounted for both parameter error and temporal variability. This involved repeatedly estimating $\overline{\text{MORT}}_{\text{fire}}$ for each state, where each realization randomly varied $\overline{\text{MORT}}_{\text{fire}}$ by uncertainty associated with both parameter error and temporal variability. We then computed the 95% CI (Gonzalez *et al.*, 2015) for each state, as per

$$95\% \text{ CI} = \frac{\overline{\text{MORT}}_{\text{fire}}^{97.5} - \overline{\text{MORT}}_{\text{fire}}^{2.5}}{2} \quad (\text{Eqn. 6})$$

where $\overline{\text{MORT}}_{\text{fire}}^{97.5}$ and $\overline{\text{MORT}}_{\text{fire}}^{2.5}$ were the 97.5th and 2.5th percentiles of 1,000 realizations of $\overline{\text{MORT}}_{\text{fire}}$. Overall, this approach yielded estimates of mean annual tree mortality ($\pm 95\%$ CI) due to fires and bark beetles from 2003-2012 for each state in the western US. We present these estimates both in terms of absolute tree mortality (Tg AGC yr⁻¹) and mortality rate (i.e., % of statewide $\overline{\text{AGC}}$ in tree biomass killed each year).

Tree mortality from timber harvest

We estimated mean annual tree mortality from timber harvest from 2003-2012 for each state ($\overline{\text{MORT}}_{\text{harvest}}$) using timber product output from several USFS reports along with ancillary information. We again used a Monte Carlo analysis to propagate uncertainty in $\overline{\text{MORT}}_{\text{harvest}}$ that was associated with parameter error and temporal variability. The USFS provided harvest estimates for each state in terms of mean annual growing stock volume (GSV) removed by forest type (angiosperm or gymnosperm) from c. 2003 to 2007 (Smith *et al.*, 2009) and c. 2008 to 2012 (Oswalt *et al.*, 2014). We computed the average GSV removed across these two time periods for both forest types in each state ($\overline{\text{GSV}}$). We then repeatedly ($N_r=1,000$) estimated $\overline{\text{MORT}}_{\text{harvest}}$ for each state, where each realization randomly permuted each variable based on its uncertainty, such that

$$\overline{MORT}_{harvest,r,state} = \sum_{forest}^{both} \left(\begin{array}{l} (\overline{GSV}_{state,forest} + a_{GSV,r} \times SE_{GSV}) \times \\ (\bar{R}_{forest} + a_{R,r} \times SE_{R,forest}) \times \\ (\overline{WD}_{state,forest} + a_{WD,r} \times SE_{WD,state,forest}) \times \\ (\bar{f}_{carbon,forest} + a_{carbon,r} \times SE_{carbon,forest}) \end{array} \right) \quad (\text{Eqn. 7})$$

where R was the ratio of total aboveground tree volume to GSV and WD was wood density, with other variables defined above. It was not possible to compute the SE of GSV removed for each state because annual harvest data were not available. We therefore assumed that the SE was 4.6% of $\overline{GSV}$ based annual harvest data from Oregon, which accounted for 35% regional harvest (Oregon Department of Forestry, 2017). We used estimates of average R ($\bar{R}$) that varied by forest type and among states in different USFS regions (Birdsey, 1992), assuming in each case that the SE was 2% of $\bar{R}$ (Levy *et al.*, 2004). We computed average WD ($\overline{WD}$) and its uncertainty (SE_{WD}) for both forest types in each state by first identifying the four tree species that accounted for the largest proportions of total tree AGB on USFS inventory plots surveyed 2003-2012 (Smith, 2002) and then summarizing WD measurements among these species (Miles & Smith, 2009). After repeatedly estimating $\overline{MORT}_{harvest}$, we then derived the average and associated 95% CI from each set of 1,000 realizations (e.g., Eqn. 6). We report $\overline{MORT}_{harvest}$ ($\pm 95\%$ CI) for each state both in terms of absolute mortality (Tg AGC yr⁻¹) and mortality rate (% yr⁻¹).

Results

Regional tree mortality from disturbance

Taken together, mean annual tree mortality from timber harvest, bark beetles, and fires ($\overline{MORT}_{H+B+F}$) was 45.8 ± 16.0 Tg AGC yr⁻¹ from 2003-2012 across the western US. Regional tree $\overline{AGC}$ stocks totaled 4.16 ± 0.12 Pg, suggesting that the tree mortality rate was $1.10 \pm 0.38\%$ yr⁻¹. Timber harvest accounted for the largest percentage of $\overline{MORT}_{H+B+F}$ (50%), followed by bark beetles (32%) and then fires (18%, Fig. 4.3, Table C2).

Tree mortality from fire

Mean annual tree mortality from fires ($\overline{\text{MORT}}_{\text{fire}}$) was 8.2 ± 6.2 Tg AGC yr^{-1} and the mortality rate was $0.20 \pm 0.15\%$ yr^{-1} from 2003-2012 in the western US (Fig 4.3, 4a, 5, Table B2).

Absolute $\overline{\text{MORT}}_{\text{fire}}$ was highest in northern California, central Idaho, and western Montana, with these states accounting for 64% of regional $\overline{\text{MORT}}_{\text{fire}}$. Forests in Arizona and New Mexico experienced the highest annual rates of $\overline{\text{MORT}}_{\text{fire}}$ (0.36 - 0.57% yr^{-1}), as well as the highest percentage of $\overline{\text{MORT}}_{\text{H+B+F}}$ caused by fire (51-55%). Conversely, forests in Colorado, Oregon, and Washington had the lowest rates of $\overline{\text{MORT}}_{\text{fire}}$ (0.03 - 0.08% yr^{-1}) and also the lowest percentage of $\overline{\text{MORT}}_{\text{H+B+F}}$ caused by fire (2-8%). Fires that occurred in Oregon and Washington were largely concentrated along the eastern slopes of the Cascade Range.

Tree mortality from bark beetles

Mean annual tree mortality from bark beetles ($\overline{\text{MORT}}_{\text{beetle}}$) was 14.6 ± 7.0 Tg AGC yr^{-1} and the mortality rate was $0.35 \pm 0.17\%$ yr^{-1} from 2003-2012 in the western US (Fig. 4.3, 4b, 5, Table B2). Absolute $\overline{\text{MORT}}_{\text{beetle}}$ was highest in northern Colorado, western Montana, and central Idaho, with these states accounting for 52% of regional $\overline{\text{MORT}}_{\text{beetle}}$ (Table B2).

Forests in Colorado and Wyoming had the highest annual rates of $\overline{\text{MORT}}_{\text{beetle}}$ (1.12 - 1.22% yr^{-1}) and the highest percentage of $\overline{\text{MORT}}_{\text{H+B+F}}$ caused by bark beetles (80-93%).

Conversely, Oregon and Washington had not only two of the lowest rates of $\overline{\text{MORT}}_{\text{fire}}$, but also two of the lowest rates of $\overline{\text{MORT}}_{\text{beetle}}$ (0.10 - 0.20% yr^{-1}).

Tree mortality from timber harvest

Mean annual tree mortality from timber harvest ($\overline{\text{MORT}}_{\text{harvest}}$) was 23.0 ± 2.8 Tg AGC yr^{-1} and the mortality rate was $0.55 \pm 0.07\%$ yr^{-1} from 2003-2012 in the western US (Fig. 4.3, 5, Table B2). Timber harvest in Oregon and Washington accounted for 67% of regional $\overline{\text{MORT}}_{\text{harvest}}$. These two states had the highest rates of $\overline{\text{MORT}}_{\text{harvest}}$ (0.85 - 0.86% yr^{-1}) and the highest percentage of $\overline{\text{MORT}}_{\text{H+B+F}}$ caused by harvest (76-83%). Conversely, forest in Colorado, Utah, and New Mexico had the lowest rates of $\overline{\text{MORT}}_{\text{harvest}}$ (0.04 - 0.06% yr^{-1}) and among the lowest percentage of $\overline{\text{MORT}}_{\text{H+B+F}}$ caused by harvest (3-10%).

Discussion

Uncertainty and improvements in estimating tree mortality

We advanced a remote sensing approach for estimating tree mortality and its uncertainty across the western US, though acknowledge remaining uncertainty and limitations. Our current estimates of cumulative (2003-2012) regional tree mortality from fires and bark beetles were both ~40% lower than earlier best estimates (Hicke *et al.*, 2013). Our current study improved representation of pre-disturbance tree AGB by using three AGB data sets (Blackard *et al.*, 2008, Kelldorfer *et al.*, 2012, Wilson *et al.*, 2013) rather than a single (older) data set (Blackard *et al.*, 2008); a change that accounted for ~10% of the decrease in each case. We potentially underestimated tree mortality in areas with sparse tree cover (e.g., southern California) due to focusing on forestland common to all three AGB data sets; however, incorporating multiple data sets with Monte Carlo analyses allowed us to better account for uncertainty in AGB when estimating tree mortality. Our current analysis also included more nuanced characterization of fire impacts, specifically varying tree mortality fraction by forest type and fire severity based on field observations (Ghimire *et al.*, 2012) rather than assuming complete tree mortality in areas that burned at moderate or high severity (Hicke *et al.*, 2013). Inconsistencies in regional MTBS burn severity mapping do introduce uncertainty in this approach (Kolden *et al.*, 2015). The extent and severity of bark beetle outbreaks remains an important source of uncertainty that would benefit from future research (Gartner *et al.*, 2015, Meddens *et al.*, 2012). Overall, this remote sensing approach allowed us to estimate tree mortality from two important types of disturbance across a large, ecologically diverse region during a decade with unusually hot, dry climate conditions.

Regional tree mortality

Our estimates of regional tree mortality from disturbance were comparable with several prior studies and illustrated the extent of tree mortality caused by timber harvest, bark beetles, and fires during the early 21st century in the western US. For instance, we estimated that the tree mortality rate from fires and bark beetles was ~0.56% yr⁻¹, while regional forest inventories indicated that tree mortality rates from “natural causes” were ~0.72-0.92% yr⁻¹ during the 2000s (Oswalt *et al.*, 2014). This suggests that fires and bark beetles might have accounted for ~60-80% of regional tree mortality from “natural causes,” with additional mortality

caused by different insect groups (e.g., defoliators), pathogens, wind, and other factors (Meigs *et al.*, 2015b, Reilly & Spies, 2016).

Our estimates of regional $MORT_{H+B+F}$ were quite similar to results from a prior remote sensing analysis that estimated tree mortality from all forms (undifferentiated) of disturbance from 1986-2004 using a stratified sample of Landsat scenes from the region (Powell *et al.*, 2014). In fact, our estimates differed by $\pm 5\%$ during 2003 and 2004 (the overlap between studies). This suggests that timber harvest, bark beetles, and fires were primary causes of tree mortality during the 2000s in this region. It also suggests that the Landsat analysis might have underestimated tree mortality associated with disturbances that occurred widely at low levels (e.g., pathogens; Reilly & Spies, 2016) and had a more subtle impacts on canopy spectral reflectance than harvest or fire (Cohen *et al.*, 2016). Regional timber harvest declined about 40% since the 1980s (Oswalt *et al.*, 2014) yet still caused significantly more tree mortality than bark beetles or fires during the 2000s, which was a period with extensive beetle and fire activity relative to the last several decades (Cohen *et al.*, 2016, Hicke *et al.*, 2015).

The carbon in trees killed by disturbance will be emitted to the atmosphere as dead trees decompose in the forest and as harvested trees are processed into wood products with varying efficiency and longevity (e.g., paper, lumber). Ignoring pyrogenic emissions, mean annual tree mortality from fire and beetles could together lead to emission of around 0.8 Tg C yr^{-1} during the following decade assuming exponential decay and an intermediate rate constant ($k = 0.04$; Harmon *et al.*, 1986). Actual decomposition rates will depend on snag fall rate, microclimate, biochemistry, tree anatomy, and other factors (Harmon *et al.*, 2011, Weedon *et al.*, 2009). Similarly, mean annual tree mortality from harvest could lead to emission of around 1.3 Tg C yr^{-1} during the following decade assuming that (1) 58% of harvested material went to fuels, paper, and residues that lasted < 5 years and that (2) the remaining 42% of material went to longer term storage that remained unchanged (Harmon *et al.*, 1990). In other words, tree mortality from harvest, bark beetles, and fires averaged 45.8 ± 16.0 Tg AGC yr^{-1} , yet annual emissions are likely closer to 2.1 Tg C yr^{-1} during the first decade following disturbance and will persist for decades to centuries. By comparison, total fossil fuel emissions from these states averaged ~ 260 Tg C yr^{-1} during this period, though varied widely among states (U.S. Energy Information Administration, 2015). More accurate assesment of emission rates will require using robust ecosystem models and life cycle assessments (Ghimire *et al.*, 2015, Hudiburg *et al.*, 2011).

Regional variation in tree mortality from disturbance

Tree mortality due to timber harvest, bark beetles and fire varied notably across the western US during the 2000s, reflecting both human and environmental factors. Tree mortality from timber harvest was highest in Oregon and Washington and accounted for ~80% of $\overline{\text{MORT}}_{\text{H+B+F}}$ in these states. Much of the timber harvest in these states occurs in highly productive forests of the Coast Range, where rates of timber extraction per unit of forest area are the highest in the country (Law & Waring, 2015). These coastal forests were a net source of carbon to the atmosphere during the 1980s due to high rates of timber harvest, though declines in harvest following implementation of the Northwest Forest Plan in 1994 led forests on public lands to become a net carbon sink during the 2000s (Turner *et al.*, 2011). Forest carbon storage could be nearly doubled in Oregon and northern California in absence of timber harvest and other disturbances (Hudiburg *et al.*, 2009). We show that recent tree mortality from timber harvest far exceeded tree mortality caused by both bark beetles and fires in the Pacific Northwest, highlighting that reductions in timber harvest could help these states meet GHG emission reduction targets.

Bark beetles were the dominant cause of disturbance-induced tree mortality in the Rocky Mountains, where a combination of stand structure, rising temperatures, and severe drought increased forest susceptibility to bark beetle outbreaks. We estimated that bark beetles were responsible for ~80% of $\overline{\text{MORT}}_{\text{H+B+F}}$ in Colorado and Wyoming, with prior research showing that much of the tree mortality occurred among lodgepole pine (*Pinus contorta*) due to attack by mountain pine beetle (Hicke *et al.*, 2015, Meddens *et al.*, 2012). Lodgepole pine stands in these areas were generally of an age (80-120 years) and stem density (>500 stems ha^{-1}) that rendered them highly susceptible to bark beetle attack (Hicke & Jenkins, 2008). Long-term increases in temperature have also increased beetle pressure by reducing beetle mortality during winter and accelerating beetle development (Creeden *et al.*, 2014, Logan & Powell, 2001). Furthermore, severe drought during this period weakened tree defense against beetle attack (Creeden *et al.*, 2014, Hart *et al.*, 2014). Together, these factors created a set of conditions that were conducive to extensive tree mortality from bark beetles.

Fires caused the most tree mortality among forests in the Southwest, where conditions were hot and dry during the 2000s. We found that absolute tree mortality from fire peaked in California (~ 2.6 Tg AGC yr^{-1}), while tree mortality rates were highest among forests in Arizona and New Mexico. Our results are broadly consistent with a recent study

focused on all Californian ecosystems, which estimated that plant mortality from fire averaged $\sim 4.3 \text{ Tg AGC yr}^{-1}$ from 2001-2010 (Gonzalez *et al.*, 2015). Extensive fire activity in the Southwest during the 2000s was related to a combination of high temperatures and low moisture, which dried fuels and made forests more prone to fire (Dennison *et al.*, 2014, Williams *et al.*, 2012, Williams *et al.*, 2014). Consequently, the federal government spent $\sim \$800$ million per year on fire suppression in the western US during this period, with $\sim \$400$ million per year spent in California (Kenward & Raja, 2013). Nevertheless, plant mortality from fire and other disturbances led to an estimated 8% net reduction in plant AGC in California from 2001-2010, complicating efforts to reduce statewide GHG emissions (Gonzalez *et al.*, 2015). Projected shifts towards a hotter, drier climate could potentially increase fire activity in the Southwest and other dry parts of the region over the coming century (Spracklen *et al.*, 2009, Williams *et al.*, 2014), contributing to increases in tree mortality, cost of wildfire management, and GHG emissions.

Conclusions

Timber harvest, bark beetles, and fires were important causes of tree mortality from 2003-2012 across forests in the western US. Regional tree mortality from these disturbances together averaged $45.8 \pm 16.0 \text{ Tg AGC yr}^{-1}$, with harvest accounting a significantly largest percentage (50%) than bark beetles (32%) or fires (18%). The amount of carbon in tree aboveground biomass killed each year by these disturbances was equivalent to 18% of regional carbon emissions from fossil fuel consumption during this period. Unlike fossil fuel emissions, this carbon will be emitted to the atmosphere over the coming years to centuries. Tree mortality from timber harvest was concentrated in the high-biomass forests of the Northwest, where it accounted for $\sim 80\%$ of the mortality caused by these three types of disturbance. Shifts in management priorities in the Northwest could reduce tree mortality and subsequent GHG emissions as a means of mitigating climate change. Bark beetles caused extensive tree mortality in the Rocky Mountains, likely due to high stand susceptibility, increased beetle pressure from rising air temperatures, and drought-induced reductions in tree defense against beetle attack. Tree mortality from fires was concentrated in the Southwest, where forests experienced extremely high air temperatures and severe drought. Tree mortality from bark beetles and fires will likely increase in parts of the regions over the coming decades as anthropogenic GHG emissions drive higher temperatures and increased risk of drought. Efforts to track climate change impacts, manage natural resources, and meet GHG

emission targets will all benefit from better understanding of the magnitude, location, and causes of tree mortality.

Figures

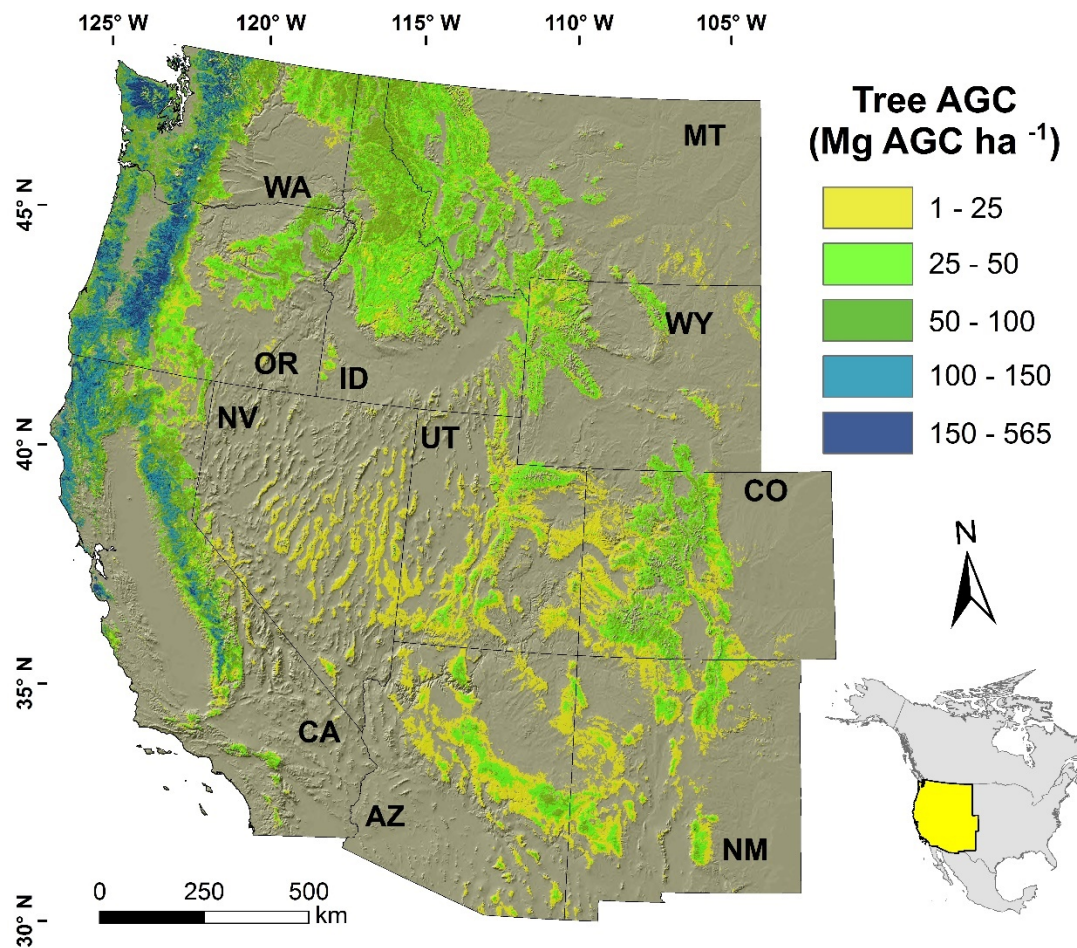
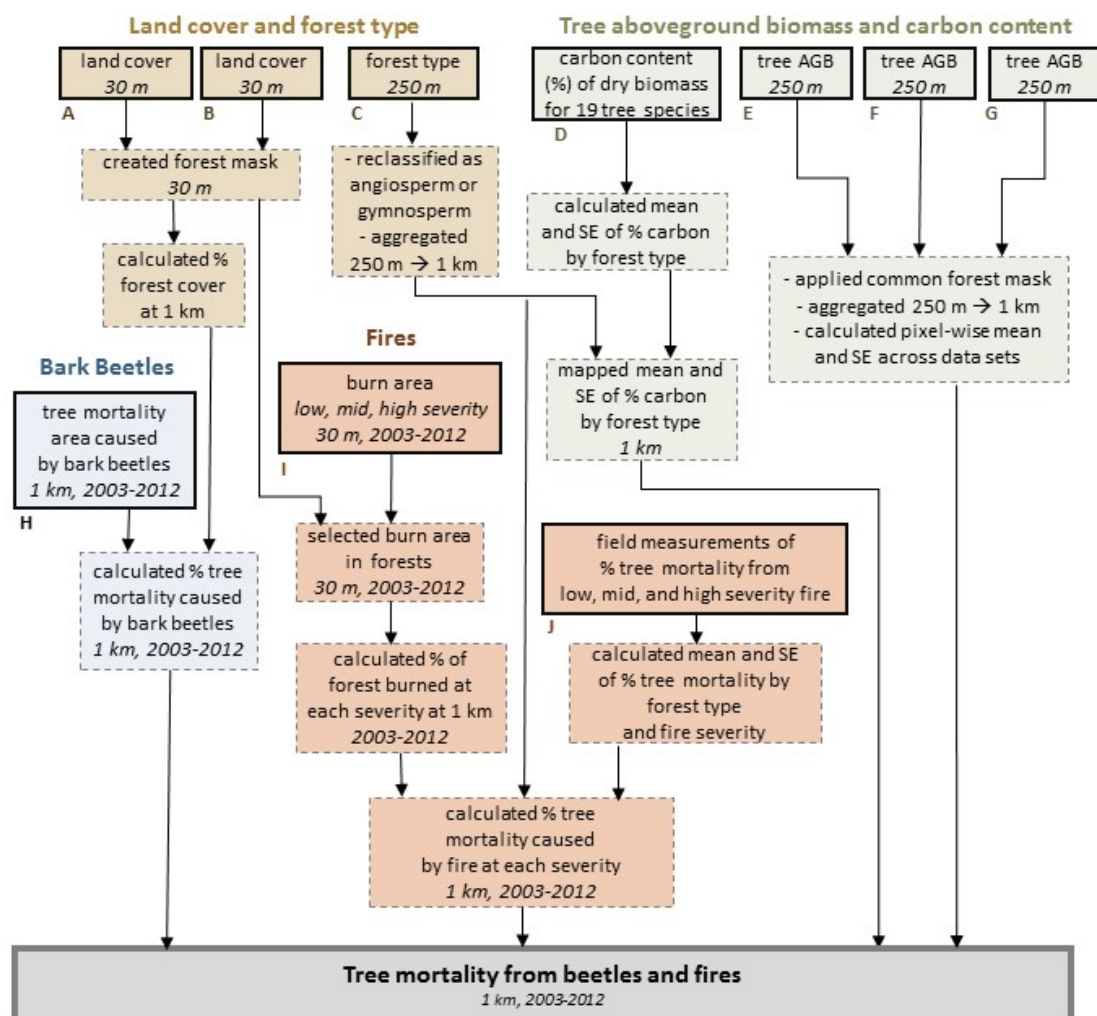


Figure 4.1. Study area extent, state boundaries, and live tree aboveground carbon (AGC; Mg AGC ha⁻¹) stocks on forestland in the western United States. Tree AGC stocks reflect conditions during the 2000s and are based on the ensemble-average of three recent data sets (Blackard *et al.*, 2008, Kelldorfer *et al.*, 2012, Wilson *et al.*, 2013).



Data set key

A Rollinset al.(2009) C Ruefenacht et al.(2008) E Kelldorfer et al.(2012) G Wilson et al.(2013) I Eidenshink et al.(2007)
 B Homer et al.(2007) D LamIom and Savidge (2003) F Blackard et al.(2012) H Meddens et al.(2012) J Ghimire et al.(2012)

Figure 4.2. Workflow illustrating data sets (solid boxes) and processing steps (dashed boxes) for estimating tree mortality due to bark beetles and fires from 2003-2012 across the western United States (thick solid box). Data citations, spatial resolutions, and temporal ranges are shown where applicable.

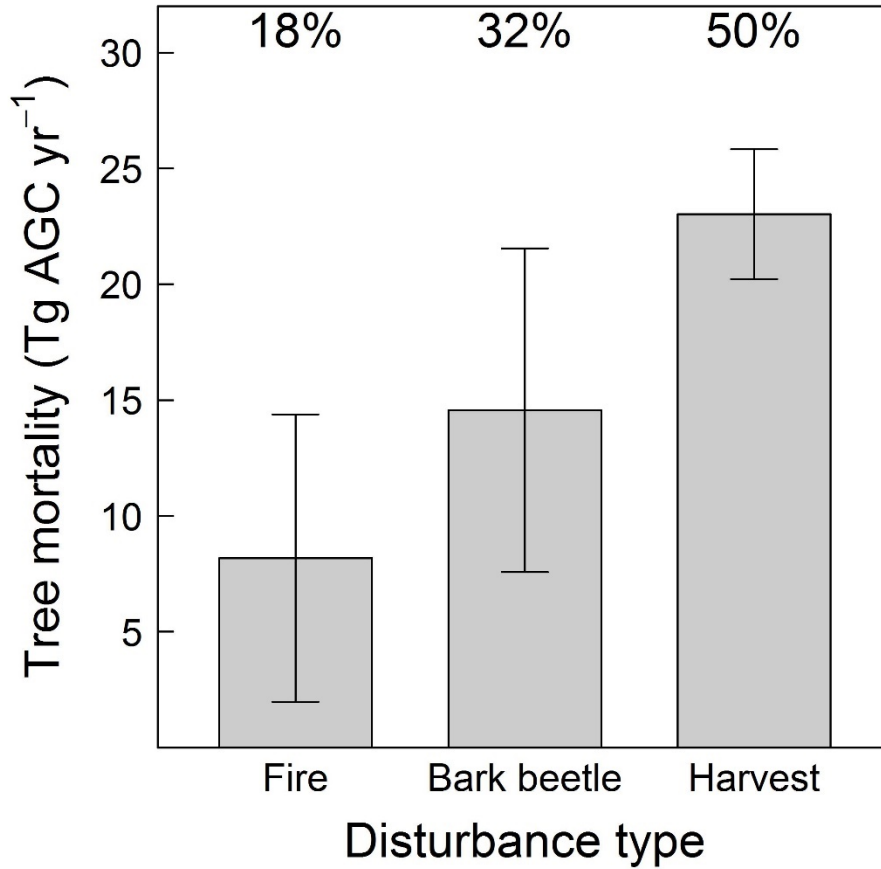


Figure 4.3. Regional mean annual tree mortality from fires, bark beetles, and timber harvest from 2003-2012 on forestland in the western United States. Tree mortality was quantified as the amount of aboveground carbon (AGC) stored in tree biomass killed by disturbance (Tg AGC yr⁻¹). Tree mortality from bark beetles and fires was derived using remote sensing, whereas harvest was derived from USFS forest resource assessments (Oswalt *et al.*, 2014, Smith *et al.*, 2009). Error bars depict 95% confidence intervals (CI) that account for temporal variability and parameter error computed using Monte Carlo analysis. We estimated that regional mean annual tree mortality from fires, beetles, and harvest was 45.8 ± 19.7 Tg AGC yr⁻¹ from 2003-2012, with fires, beetles, and harvest accounting for 18%, 32%, and 50% of annual mortality, respectively.

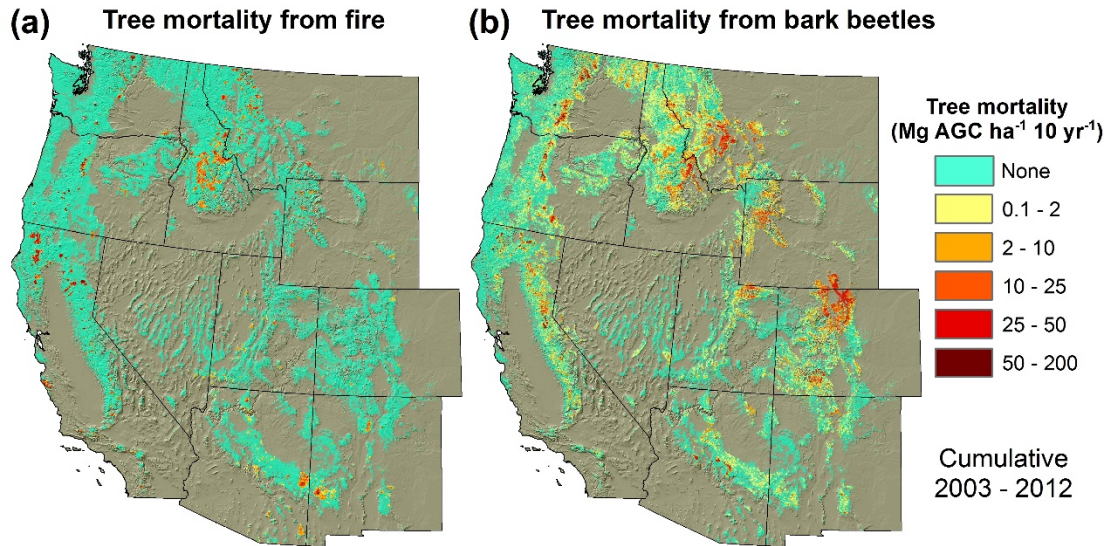


Figure 4.4. Cumulative tree mortality due to (a) fires and (b) bark beetles from 2003-2012 on forestland in the western United States. Tree mortality was quantified as the amount of aboveground carbon (AGC) stored in tree biomass killed by disturbance (e.g., Mg AGC ha⁻¹). Note that (a) tree mortality from fire was concentrated in northern California, central Idaho, and southern Arizona/New Mexico, whereas (b) tree mortality from bark beetles occurred widely, but was highest in northern Colorado and western Montana.

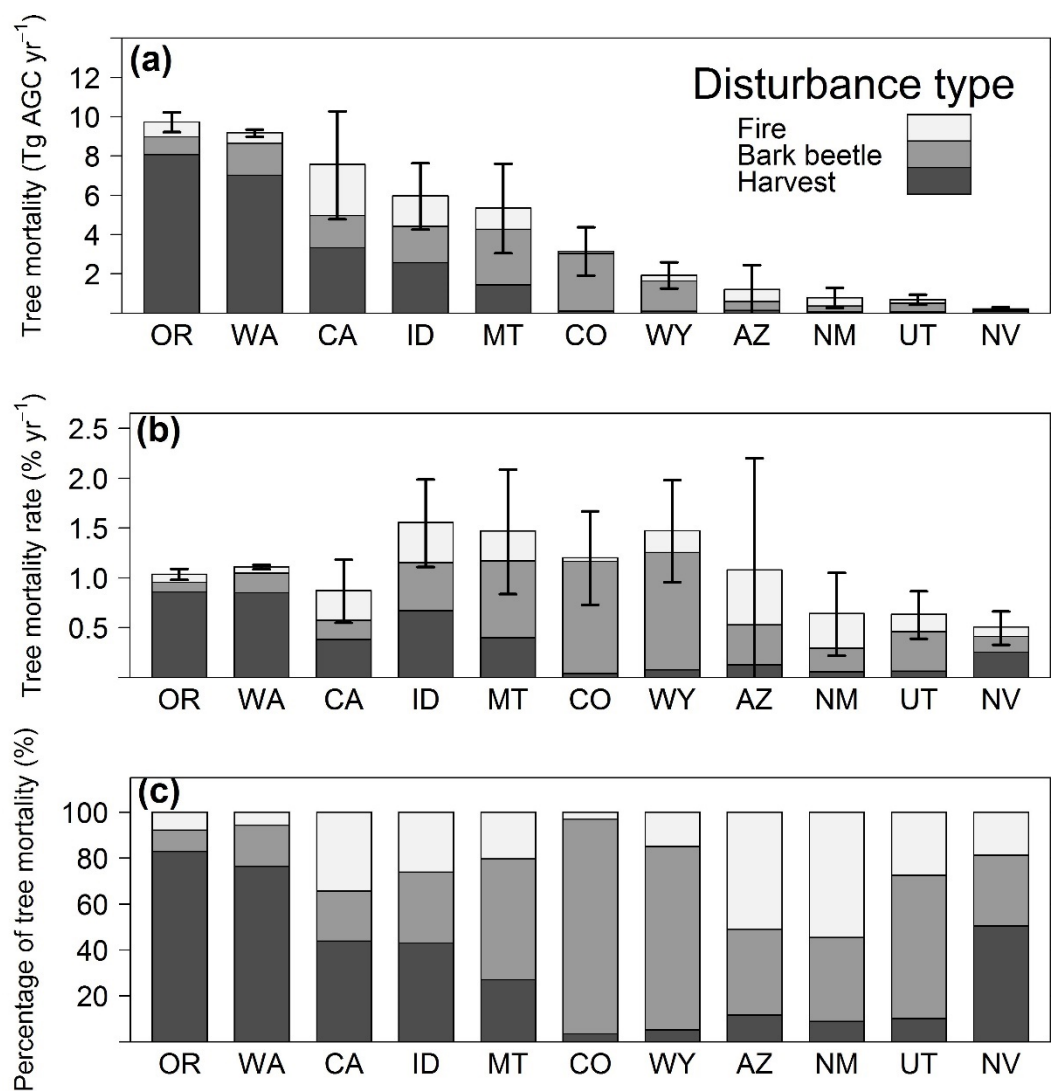


Figure 4.5. Mean annual tree mortality from fires, bark beetles, and timber harvest on forestland from 2003-2012 for each state in the western United States. Tree mortality is summarized in terms of (a) absolute mortality [Tg ACC yr⁻¹], (b) mortality rate [percentage of statewide AGC in tree biomass killed per year], and (c) proportion of mortality caused by each type of disturbance [%]. Tree mortality was quantified as the amount of aboveground carbon (AGC) stored in tree biomass killed by disturbance. Tree mortality from bark beetles and fires was derived using remote sensing, whereas harvest was derived from USFS forest resource assessments (Oswalt *et al.*, 2014, Smith *et al.*, 2009).

CHAPTER 5. SUMMARY AND CONCLUSIONS

Earth's atmosphere is warming due to carbon emissions from human fossil fuel consumption and land-use activities (IPCC, 2013, Melillo *et al.*, 2014). Forests store a similar amount of carbon as the atmosphere (Houghton, 2013), yet ongoing climatic change is affecting forest carbon uptake and storage (Allen *et al.*, 2015, Nemani *et al.*, 2003) in ways that could amplify or mitigate ongoing climatic change (Anderson-Teixeira *et al.*, 2012). It is therefore important better understand forest carbon cycling and its relation to climate. In this series of studies, we investigated forest response to recent variation in water availability and disturbance across the western United States (Berner & Law, 2015, Berner *et al.*, 2017, Berner *et al.*, in revision). These studies illustrate that forest carbon uptake and storage are widely sensitive to changes in water availability, suggesting that continued warming and drying could reduce forest carbon sequestration in some areas over the coming century. These studies also illustrate that human land use is a dominant cause of regional tree mortality, highlighting that human activities both directly and indirectly exert a strong influence on forests in the western US.

Summary of Chapter 2

In the first study (Chapter 2), we investigated how forest carbon cycling and tree morphology were affected by water availability in the eastern Cascade Mountains, Oregon (Berner & Law, 2015). The study focused on 12 sites located in three forest types (western juniper, ponderosa pine, and grand fir) spread along a steep hydraulic gradient and was based on analysis of climate, forest inventory, tree-ring, and tree morphology measurements. We used the average water-year climate moisture index ($CMI_{\overline{wy}}$; Oct.-Sept.; 1964-2013) as an indicator of long-term water availability that is represented by the net of precipitation and reference evapotranspiration (Hogg & Hurdle, 1995, Webb *et al.*, 1983). We found that $CMI_{\overline{wy}}$ varied $\sim 100 \text{ cm yr}^{-1}$ among the three forest types and that tree leaf area index (LAI), aboveground net primary productivity (ANPP), and aboveground biomass (AGB) increased markedly with $CMI_{\overline{wy}}$ between the driest and the wettest sites. Furthermore, we found strong relationships among tree LAI, ANPP, and AGB across sites. These findings suggest that average water availability constrains the amount of light-harvesting leaf area that a forest can

support, which subsequently constrains productivity and long-term accumulation of tree biomass. This analysis, together with prior studies (Gholz, 1982, Grier & Running, 1977), illustrated that average water availability is a key determinant of forest structure and function in the Cascade Mountains.

Our tree-ring analysis revealed that tree radial growth became increasingly decoupled from interannual fluctuations in water availability as sites became wetter, yet trees at all sites were vulnerable to persistent drought. Radial growth of individual western juniper responded more strongly and uniformly to interannual fluctuations in water availability than ponderosa pine or grand fir in progressively wetter areas. Nevertheless, radial growth declined among all three species during a persistently dry decade (1985-1994), with declines in growth particularly severe among grand fir. Western juniper and ponderosa pine in Southern Oregon also experienced reduced growth during this period (Knutson & Pyke, 2008). Multi-year drawdown of soil water due to insufficient recharge might have triggered the growth declines; which in the case of grand fir and, to a lesser extent, ponderosa pine, were further exacerbated by insect attack. Radial growth also declined among western juniper and ponderosa pine during the early 2000s due to severe drought, which also suppressed forest productivity more broadly across the western US (Schwalm *et al.*, 2012).

Tree morphology changed notably between the driest and wettest sites, reflecting tree adaptations to reduced hydrologic stress and increased competition for light. As conditions became wetter there was a decline in stem wood density, along with increases in both maximum tree height and the ratio of leaf area to sapwood area. For instance, western juniper had high stem wood density, short stature, and limited leaf area per unit of sapwood area (LA:SA), which helped trees endure or minimize hydraulic stress (e.g., low xylem water potential) under very dry conditions (Chave *et al.*, 2009, Whitehead *et al.*, 1984). Conversely, grand fir had relatively low stem wood density, reached three times the maximum height of juniper and also had four times as much LA:SA, suggesting that these trees invested more resources into competition for light as hydrologic stress declined. These differences in tree morphology together with our forest inventory analysis highlight trade-offs associated with investment in stress tolerance versus competitive ability in productive environments (Grime, 2001, Reich, 2014). Altogether, this study demonstrated the sensitivity of forest carbon cycling to changes in water availability in the eastern Cascades and also illustrated several important tree morphological responses to shifts in water availability (Berner & Law, 2015).

Summary of Chapter 3

The second study (Chapter 3) built on elements of our first study by investigating how forest carbon cycling responded to variation in long-term average water availability across the western United States (Berner *et al.*, 2017). Specifically, we quantified how (aboveground + belowground) tree net primary productivity (NPP), live biomass (BIO), and carbon residence time in live biomass (CRT) varied with respect to CMI_{wy} across mature forests in Washington, Oregon, and California (WAORCA), as well as in the broader western United States. We used forest inventory measurements from 1,953 mature stands (>100 years) in WAORCA (Hudiburg *et al.*, 2011), along with satellite and climate data sets covering ~18 Mha of mature forest in the western United States (e.g., Daly *et al.*, 2008, Kellndorfer *et al.*, 2012, Zhao *et al.*, 2010). Both study areas encompassed forests ranging from dry woodlands to coastal temperate rainforests, where tree biomass is among the highest found anywhere in the world (Hudiburg *et al.*, 2009, Keith *et al.*, 2009)

Our multi-method, multi-scale analysis revealed that tree NPP, BIO, and CRT increased persistently and nonlinearly with CMI_{wy} across both WAORCA and the broader western United States. Tree NPP, BIO, and CRT peaked among wet, coastal forests in WAORCA where CMI_{wy} exceeded 100 cm yr^{-1} , such as in parts of the Olympic, Coastal, Cascade, and Klamath Mountains. Field measurements from WAORCA showed that median NPP increased from 2.2 to 5.6 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ between the driest and wettest 5% of sites, while BIO increased from 26 to 281 Mg C ha^{-1} and CRT increased from 11 to 49 years. Satellite remote sensing revealed similar changes over the western United States, though unlike the field measurements both BIO and NPP derived from satellites tended to plateau in the wettest areas. There were also strong positive relationships among NPP, BIO, and CRT along both hydrologic gradients.

The pronounced increase in tree NPP, BIO, and CRT between the driest and wettest areas illustrate gradual adjustment of ecosystem structure and function to long-term variation in water availability. Tree NPP increased with average water availability in part because forests can support more leaf area as climate becomes wetter (Berner & Law, 2015, Yan *et al.*, 2016), which increases the amount of photosynthate available to fuel NPP unless photosynthesis becomes limited by other resources (e.g., nitrogen) or climate conditions (e.g., low temperature, cloud cover). A combination of higher NPP and longer CRT then contributed to more rapid build-up of BIO in progressively wetter forests. Longer CRT in wetter areas is potentially associated with a greater proportion of NPP being allocated to

longer-lived stem wood rather than shorter-lived coarse and fine roots. These whole tree estimates of CRT were computed from BIO and NPP summed across all tree components (i.e., stem, branches, bark, leaves, roots), yet CRT varies widely among individual components. For instance, CRT in coarse roots is 10-20 years, whereas CRT of wood is around 100 years (Zhou & Luo, 2008). Carbon sequestration by forests can help mitigate climate change (Canadell & Raupach, 2008) and these results suggest that efforts to increase terrestrial carbon storage should focus on wet areas with high NPP, long CRT, and low rates of tree mortality from fires and bark beetles.

Tree NPP and BIO derived from field- and satellite-measurements exhibited similar responses to increasing water availability, though the satellite data sets tended to plateau in the wettest areas. This highlighted that satellite remote sensing is a valuable tool for monitoring climate impacts on forests, though suggests that additional efforts are needed to better quantify NPP and BIO from satellites in high-NPP, high-BIO forests. Overall, this study showed that average water availability is a key determinant of tree NPP, BIO, and CRT in mature forests across the western United States, underscoring that projected warming and drying over the coming century could lead to extensive shifts in forest carbon cycling (Berner *et al.*, 2017).

Summary of Chapter 4

The third study (Chapter 4) investigated the magnitude and proportion of tree mortality caused by fires, bark beetles, and timber harvest from 2003-2012 across the western United States (Berner *et al.*, in revision). We developed spatially explicit estimates of mean annual tree mortality from fires and beetles using tree aboveground carbon (AGC) stock (Blackard *et al.*, 2008, Kellndorfer *et al.*, 2012, Wilson *et al.*, 2013) and disturbance (Eidenshink *et al.*, 2007, Meddens *et al.*, 2012) data sets derived largely from remote sensing. We then estimated mean annual tree mortality from harvest for each state using data from several US Forest Service reports and ancillary information (Miles & Smith, 2009, Oswalt *et al.*, 2014, Smith *et al.*, 2009). We quantified uncertainty in these estimates by propagating temporal variability and parameter error using a Monte Carlo approach (Harmon *et al.*, 2007).

The analysis indicated that regional tree mortality from timber harvest, bark beetles, and fires ($MORT_{H+B+F}$) together averaged 45.8 ± 16.0 Tg AGC yr^{-1} (1.10 ± 0.38 % yr^{-1}), with harvest accounting for the largest percentage (50%), followed by beetles (32%), and then fires (18%). Our estimates of regional tree mortality from these three forms of disturbance

were similar to estimates of tree mortality from all (undifferentiated) forms of disturbance previously derived from Landsat imagery (Powell *et al.*, 2014). Estimates from these independent approaches differed by $\pm 5\%$ during 2003 and 2004 (only years of overlap). This suggested that timber harvest, bark beetles, and fires were the primary causes of disturbance-induced tree mortality during the 2000s in this region. Regional timber harvest declined about 40% since the 1980s (Oswalt *et al.*, 2014) yet still caused more tree mortality than bark beetles or fires during the 2000s, which was a period with extensive beetle and fire activity relative to recent decades (Cohen *et al.*, 2016, Hicke *et al.*, 2015).

Tree mortality from each type of disturbance varied notably across the region. Tree mortality from harvest was concentrated in high-biomass forests found in Washington and Oregon, with harvest in each of these states responsible for $\sim 80\%$ of $MORT_{H+B+F}$. Prior work found that forests in coastal Oregon and northern California could store almost twice as much carbon as they currently store if they were undisturbed (Hudiburg *et al.*, 2009). Furthermore, protecting high-biomass forests from harvest is an important climate change mitigation strategy (Keith *et al.*, 2009) since the carbon debt created by logging high-biomass forests can take centuries to offset (Harmon *et al.*, 1990), yet in the Pacific Northwest only about 20% of high-biomass stands ($AGC > 100 \text{ Mg ha}^{-1}$) are strictly protected from logging (Krankina *et al.*, 2014). Carbon emissions could be reduced in these states by reducing the extent, frequency, or severity of timber harvest.

Tree mortality from beetles occurred widely at low levels across the region, though the most pronounced impacts occurred in Colorado and Montana, where beetles accounted for $\sim 80\%$ of $MORT_{H+B+F}$. A combination of high stand susceptibility, increased beetle pressure from rising air temperatures, and drought-induced reductions in tree defense against beetle attack contributed to tree mortality in these states (Creeden *et al.*, 2014, Hicke & Jenkins, 2008). Tree mortality from fires was concentrated in the Southwest, where forests experienced extremely high air temperatures and severe drought (Diffenbaugh *et al.*, 2015, Williams *et al.*, 2012). Fire burn area and severity in the region do not appear to be strongly affected by recent beetle-killed trees (Hart *et al.*, 2015, Meigs *et al.*, 2015a), suggesting that efforts to reduce fire hazard by removing beetle-killed trees could be counter-productive and increase carbon emission to the atmosphere (Heller, 2017). Furthermore, beetles caused more tree mortality than fires in most areas, indicating that thinning small trees to reduce fire risk could potentially reduce forest resilience to a bark beetle attack (Baker & Williams, 2015). Tree mortality from bark beetles and fires will likely increase during coming decades in parts of the region as anthropogenic GHG emissions drive higher temperatures and increased risk

of drought. Efforts to track climate change impacts, manage natural resources, and meet GHG emission reduction targets will all benefit from better understanding of where, when, and why trees live and die.

Concluding remarks

There is broad scientific consensus that human activities are warming Earth's atmosphere (Cook *et al.*, 2013, IPCC, 2013) and that warming is affecting global forests (Allen *et al.*, 2010, Berner *et al.*, 2013, Nemani *et al.*, 2003, Salzer *et al.*, 2009), yet potential ecosystem impacts of future warming remain uncertain (Allen *et al.*, 2015, Friend *et al.*, 2014). It is crucial to understand how forests will response to climatic change given that these ecosystems currently store a similar amount of carbon as the atmosphere and could amplify or mitigate ongoing climatic change (Houghton, 2013, Pan *et al.*, 2011a). This dissertation demonstrated that water availability is a key environmental constraint on forests in the western US, yet additional efforts are needed to better understand forest carbon cycling and its response to continued warming and drying in the region. Detailed tree physiological measurements (e.g., leaf water potential, tree transpiration) are needed to identify thresholds leading from drought stress to mortality, as well as how thresholds vary among tree species and life stage. Furthermore, additional efforts are needed to improve regional estimates of forest carbon stocks and fluxes derived from satellite observations, particularly in high-biomass forests, and to assess the impacts of fires, insects, and timber harvest on forest carbon dynamics at large scales. Detailed physiological measurements can inform development of mechanistic ecosystems models and model performance can subsequently be evaluated and refined through comparison with observed spatial and temporal variation in forest carbon stocks and fluxes. Mechanistic ecosystem models can then be used to project how management activities and climate change might influence regional forests, thus providing rigorous information to inform forest management. Sustained assessment of forest carbon uptake, storage, and release is needed to guide forest and GHG management in a warming world.

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APPENDICES

Appendix A: Supporting information for Chapter 2

Table A1. Location and forest characteristics of 12 field sites located in the eastern Cascade Mountains, Oregon. Forest characteristics include aboveground live biomass (AGB; kg C m⁻²), annual aboveground net primary productivity (ANPP; kg C m⁻² yr⁻¹), leaf area index (LAI; m² m⁻²), sapwood area, leaf:sapwood area ratio (LA:SA; m² cm⁻²), maximum tree height (H_{max}; m), and ecosystem-average stem wood density (WD; g cm⁻³). Characteristics were averaged ($\pm$ SE) across four subplots per plot. Stand age was calculated as the average age of the oldest 10% of trees. Sites were sampled during the summer of 2014.

Forest type	Plot	Lat.	Long.	Elev. (m)	Stand Age (yrs)	AGB	ANPP	LAI	Sapwood Area	LA:SA	H _{max}	WD
Western juniper	1	44.20	-121.37	1007	148	1.95 $\pm$ 0.73	17 $\pm$ 2	0.24 $\pm$ 0.06	3.8 $\pm$ 1.4	0.06 $\pm$ 0.03	10.6 $\pm$ 1.0	0.48 $\pm$ 0.03
	2	44.25	-121.43	958	537	2.99 $\pm$ 0.87	21 $\pm$ 2	0.37 $\pm$ 0.05	6.4 $\pm$ 1.7	0.06 $\pm$ 0.02	9.9 $\pm$ 0.3	0.44 $\pm$ 0.01
	3	44.30	-121.33	929	253	2.67 $\pm$ 0.86	11 $\pm$ 2	0.09 $\pm$ 0.03	5.2 $\pm$ 1.6	0.02 $\pm$ 0.01	10.5 $\pm$ 0.1	0.47 $\pm$ 0.02
	4 ^a	44.31	-121.33	908	32	0.21 $\pm$ 0.04	16 $\pm$ 3	0.32 $\pm$ 0.04	1.2 $\pm$ 0.3	0.27 $\pm$ 0.07	5.7 $\pm$ 0.7	0.52 $\pm$ 0.02
	5	44.26	-121.34	975	119	2.58 $\pm$ 0.49	19 $\pm$ 2	0.35 $\pm$ 0.09	5.9 $\pm$ 1.0	0.06 $\pm$ 0.02	11.2 $\pm$ 0.8	0.49 $\pm$ 0.02
Ponderosa pine	1	44.33	-121.67	1124	327	16.51 $\pm$ 2.73	145 $\pm$ 16	1.41 $\pm$ 0.17	20.3 $\pm$ 2.8	0.07 $\pm$ 0.01	35.4 $\pm$ 0.5	0.46 $\pm$ 0.01
	2	44.34	-121.57	978	190	7.26 $\pm$ 1.47	125 $\pm$ 25	1.63 $\pm$ 0.09	16.3 $\pm$ 3.6	0.10 $\pm$ 0.02	26.2 $\pm$ 1.0	0.42 $\pm$ 0.01
	3	44.26	-121.65	1315	280	10.03 $\pm$ 1.27	262 $\pm$ 8	2.58 $\pm$ 0.19	18.4 $\pm$ 0.4	0.14 $\pm$ 0.01	27.1 $\pm$ 3.0	0.45 $\pm$ 0.01
	4 ^a	44.32	-121.61	996	23	0.72 $\pm$ 0.06	77 $\pm$ 7	1.21 $\pm$ 0.09	3.9 $\pm$ 0.5	0.31 $\pm$ 0.04	8.43 $\pm$ 0.3	0.43 $\pm$ 0.01
	5	44.45	-121.56	1254	106	8.74 $\pm$ 0.68	210 $\pm$ 23	2.04 $\pm$ 0.21	20.3 $\pm$ 1.6	0.10 $\pm$ 0.01	22.9 $\pm$ 0.7	0.44 $\pm$ 0.01
Grand fir	1	44.23	-121.67	1560	114	8.82 $\pm$ 1.64	205 $\pm$ 12	5.19 $\pm$ 0.29	19.3 $\pm$ 1.8	0.27 $\pm$ 0.03	25.6 $\pm$ 3.1	0.39 $\pm$ 0.02
	2	44.24	-121.68	1519	194	21.60 $\pm$ 2.47	311 $\pm$ 60	6.15 $\pm$ 1.12	31.4 $\pm$ 2.9	0.20 $\pm$ 0.04	35.0 $\pm$ 1.7	0.39 $\pm$ 0.02
	3 ^a	44.30	-121.76	1429	46	11.30 $\pm$ 2.94	342 $\pm$ 83	5.39 $\pm$ 1.03	22.1 $\pm$ 3.4	0.24 $\pm$ 0.06	25.6 $\pm$ 2.84	0.41 $\pm$ 0.01
	4	44.30	-121.70	1208	82	10.46 $\pm$ 0.68	190 $\pm$ 34	2.67 $\pm$ 0.16	14.5 $\pm$ 1.8	0.18 $\pm$ 0.03	35.2 $\pm$ 2.4	0.42 $\pm$ 0.01
	5	44.37	-121.76	1292	182	16.89 $\pm$ 2.13	247 $\pm$ 18	4.16 $\pm$ 0.04	20.8 $\pm$ 2.4	0.20 $\pm$ 0.02	38.5 $\pm$ 1.4	0.42 $\pm$ 0.01

^a Young stands not included in the analysis.

Table A2. Equations relating sapwood area (SA; cm²) to diameter at breast height (DBH; cm) for three conifer species in the eastern Cascade Mountains, Oregon. Equations are of the form $SA = aDBH^b$, where a and b are fitted coefficients.

Species	a	a (SE)	b	b (SE)	r ²	DF	RMSE (cm ²)
western juniper	2.303	1.028	1.382	0.113	0.76	2,54	29.96
ponderosa pine	2.428	0.736	1.587	0.071	0.92	2,63	49.39
grand fir	1.153	0.517	1.676	0.113	0.85	2,49	34.69

Table A3. Equations relating tree height (H; m) to diameter at breast height (DBH; cm) for three conifer species in the eastern Cascade Mountains, Oregon. Equations are of the form

$H = 1.3 + e^{a + \frac{b}{DBH + c}}$, where a , b , and c are fitted coefficients.

Species	a	a (SE)	b	b (SE)	c	c (SE)	r ²	RMSE (m)	n
western juniper	2.214	0.052	-14.095	2.502	2.138	1.621	0.66	1.55	225
ponderosa pine	4.015	0.054	-50.696	5.154	7.738	2.253	0.86	3.12	378
grand fir	4.081	0.079	-49.431	6.333	8.495	2.327	0.87	3.21	340

Table A4. Average (± 1 SD) water-year climate conditions from 1964 to 2013 for sites dominated by western juniper, ponderosa pine, and grand fir in the eastern Cascade Mountains, Oregon. The growing-year extended from October of year $t-1$ through September of year t . Climate variable include average daily temperature ($T_{\overline{wy}}$), precipitation ($PPT_{\overline{wy}}$), reference evapotranspiration ($ET_{\overline{wy}}$) and climate moisture index ($CMI_{\overline{wy}} = PPT_{\overline{wy}} - ET_{\overline{wy}}$) calculated from monthly PRISM climate data (Daly et al. 2008).

Forest type	Plot	$T_{\overline{wy}}$ (° C)	$PPT_{\overline{wy}}$ (mm yr ⁻¹)	$ET_{\overline{wy}}$ (mm yr ⁻¹)	$CMI_{\overline{wy}}$ (mm yr ⁻¹)
western juniper	1	8.3±0.8	290±70	1530±70	-1240±120
	2	8.0±0.8	330±80	1530±70	-1200±130
	3	8.6±0.8	240±60	1570±70	-1330±110
	5	8.4±0.8	280±70	1510±60	-1240±120
ponderosa pine	1	7.0±0.7	630±150	1470±70	-840±200
	2	7.7±0.8	430±110	1570±70	-1140±160
	3	6.0±0.7	760±190	1200±60	-430±230
	5	6.9±0.7	610±150	1190±60	-580±190
grand fir	1	6.7±0.8	650±170	1290±60	-640±210
	2	5.6±0.7	960±220	1150±60	-190±260
	4	6.3±0.7	920±210	1250±70	-330±250
	5	6.5±0.7	1260±250	1210±70	50±290

Table A5. Summary of tree-ring width index (RWI) correlations with a variety of climate variables for western juniper, ponderosa pine, and grand fir three tree species in the eastern Cascade Mountains, Oregon. Correlations between RWI and the climate variables were computed for each individual tree (n=216), with climate data averaged (temperature-related variables) or summed (water-related variable) monthly at 1- to 36-month lags. The climate response for each tree was then summarized based on the average of the top 5% of correlations, regardless of the temporal response window. The climate response for each species was then evaluated both in terms of the percent of trees that exhibited a significant ($P < 0.05$) positive or negative correlation with the climate variable of interest and as the average strength of the correlation.

Climate variable	Units	Species	% of trees with sig. RWI-climate correlation				RWI-climate correlation (r)								
			1964 to 2013		1994 to 2013		1964 to 2013			1994 to 2013			mean	SD	P
			negative	positive	negative	positive									
T_{avg}	°C	juniper	33.36	5.94	28.00	8.10	-0.21	0.13	0.19	-0.25	0.17	0.23			
		pine	24.89	5.59	19.95	4.30	-0.16	0.15	0.32	-0.20	0.19	0.33			
		fir	18.11	9.23	10.81	5.55	-0.11	0.14	0.34	-0.06	0.18	0.43			
T_{max}	°C	juniper	72.05	3.6	61.17	1.80	-0.33	0.13	0.10	-0.36	0.18	0.12			
		pine	35.21	4.55	29.00	2.76	-0.2	0.16	0.26	-0.24	0.20	0.27			
		fir	19.55	5.16	12.10	5.50	-0.14	0.14	0.32	-0.12	0.19	0.41			
T_{min}	°C	juniper	6.76	49.91	4.56	42.24	0.26	0.14	0.16	0.32	0.19	0.18			
		pine	9.48	12.69	7.20	13.50	0.06	0.14	0.43	0.14	0.20	0.40			
		fir	10.5	12.64	7.07	9.90	0.04	0.14	0.40	0.10	0.19	0.44			
VPD	kPa	juniper	87.45	3.75	78.68	3.64	-0.41	0.15	0.07	-0.45	0.19	0.08			
		pine	46.68	4	37.33	2.22	-0.23	0.17	0.23	-0.26	0.20	0.25			
		fir	29.41	4.06	18.39	4.82	-0.18	0.15	0.28	-0.16	0.21	0.35			
Freeze	days	juniper	45.79	4.33	40.36	2.75	-0.25	0.13	0.16	-0.32	0.18	0.18			
		pine	14.28	9.1	14.20	6.86	-0.07	0.15	0.41	-0.14	0.20	0.39			
		fir	12.67	14.9	8.86	8.91	0.03	0.14	0.39	-0.08	0.19	0.45			
CMI	mm	juniper	2.62	90.59	2.09	89.24	0.52	0.18	0.05	0.56	0.20	0.05			
		pine	4.14	50.86	2.00	39.84	0.27	0.21	0.23	0.28	0.21	0.24			
		fir	6.86	11.62	6.25	9.84	0.11	0.13	0.40	0.05	0.22	0.42			
Deficit	mm	juniper	89.24	3.56	87.95	1.58	-0.46	0.16	0.06	-0.52	0.20	0.07			
		pine	52.67	4	43.37	2.60	-0.26	0.17	0.19	-0.30	0.20	0.21			
		fir	13	7.33	8.45	6.70	-0.11	0.13	0.39	-0.11	0.19	0.41			
SPEI	unitless	juniper	3.83	90.94	2.56	89.31	0.53	0.18	0.05	0.57	0.20	0.05			
		pine	4.44	51.38	2.14	40.94	0.25	0.2	0.20	0.28	0.21	0.22			
		fir	5.86	10.6	6.31	8.78	0.11	0.12	0.44	0.05	0.21	0.42			

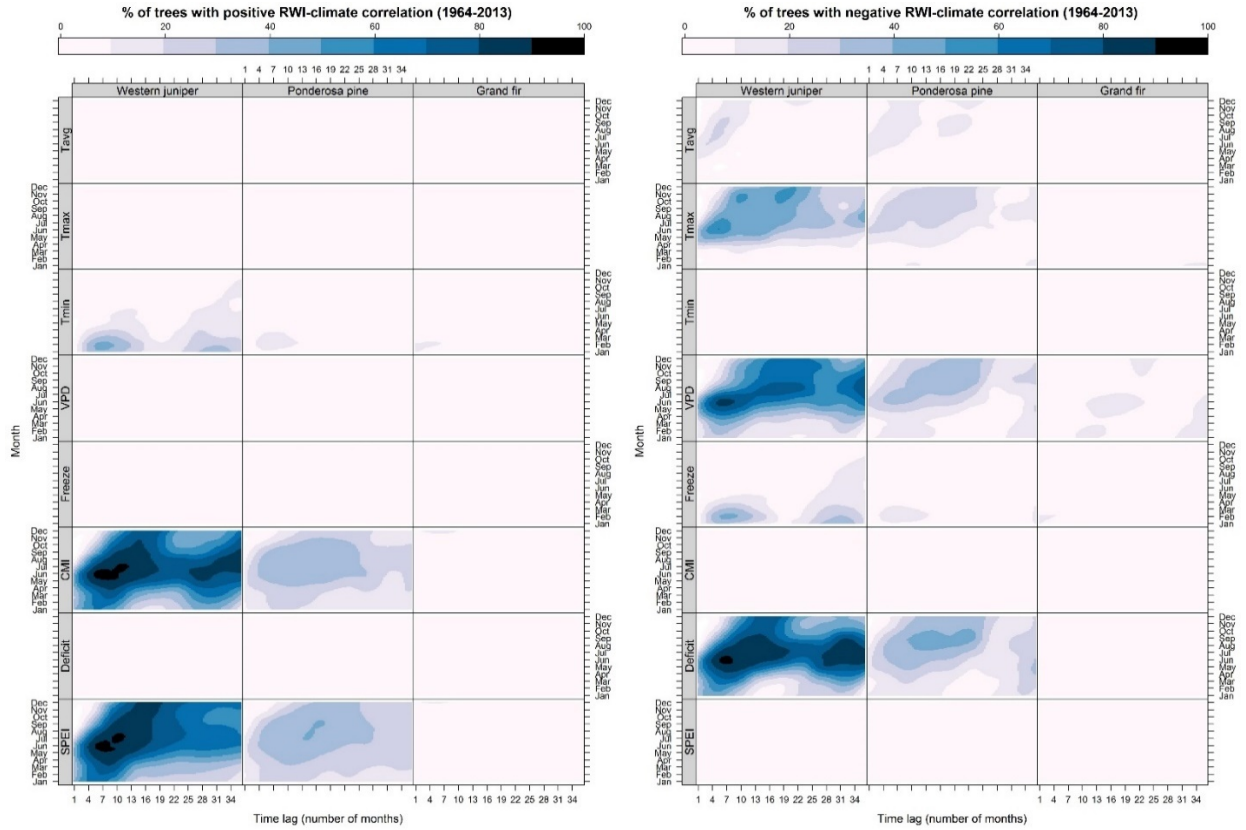


Figure A1. Proportion of trees with a significant positive (left panel) or negative (right panel) correlation between annual ring-width indices (RWI) and a variety of climate variables calculated for each month at time lags extending from 1 to 36 months. Correlations were computed for each tree ($n=216$) using growth and climate data from 1964 to 2013, with climate data averaged for temperature-related variables and summed for water-related variables.

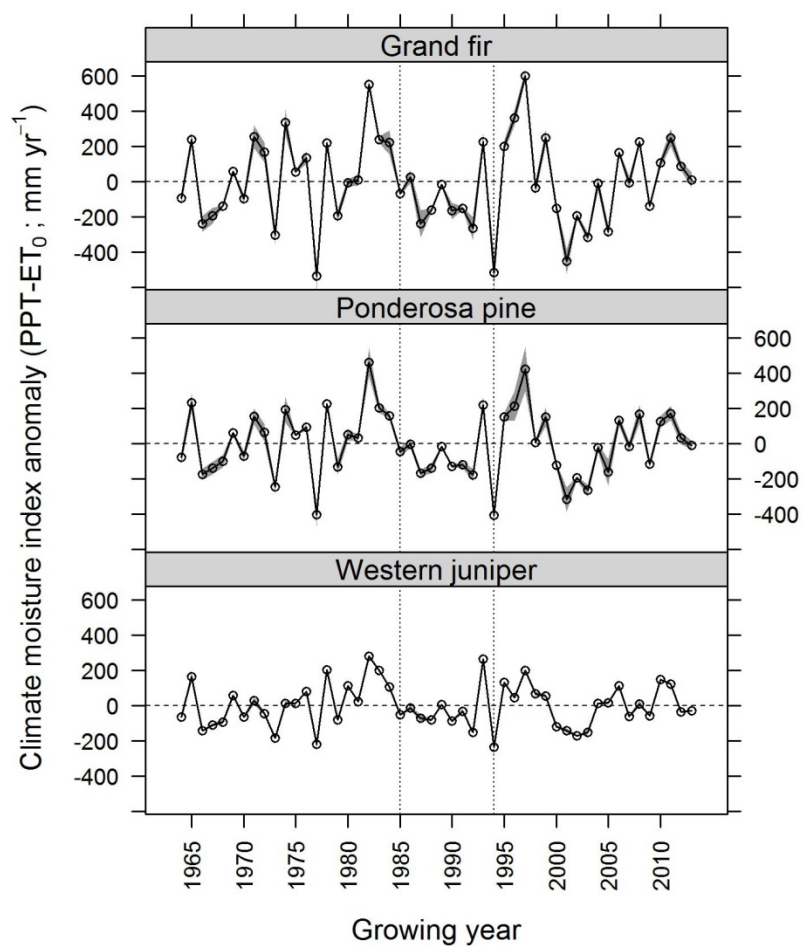


Figure A2. Water year climate moisture index anomalies from 1964 to 2013 for three forest types in the eastern Cascade Mountains, Oregon

Appendix B: Supporting information for Chapter 3

Table B1. Carbon in live tree biomass for states in the western United States. Tree biomass was derived from remote sensing estimates of tree aboveground biomass (AGB) and MODIS leaf area index (LAI) at 250 m spatial resolution, along with allometric equations for estimating coarse and fine root biomass from AGB and LAI, respectively. Forest area was based on areas commonly mapped as forest by three separated AGB data set (Blackard *et al.* 2008; Kellndorfer *et al.* 2012; Wilson *et al.* 2013).

State	Carbon in live tree biomass			Forest area (Mha)
	Average (Mg C ha ⁻¹)	SD (Mg C ha ⁻¹)	Total (Tg C)	
AZ	25.6	18.7	145	5.68
CA	100.4	52.7	1089	10.85
CO	41.9	21.6	341	8.13
ID	57.0	24.1	484	8.50
MT	54.1	19.8	464	8.58
NM	28.2	17.4	162	5.74
NV	19.1	10.9	59	3.11
OR	103.4	61.6	1165	11.26
UT	26.4	14.5	148	5.59
WA	110.2	61.0	1018	9.24
WY	46.7	18.7	163	3.48

Table B2. Carbon in live tree biomass for ecoregions in the western United States. Tree biomass was derived from remote sensing estimates of tree aboveground biomass (AGB) and MODIS leaf area index (LAI) at 250 m spatial resolution, along with allometric equations for estimating coarse and fine root biomass from AGB and LAI, respectively. Forest area was based on areas commonly mapped as forest by three separated AGB data set (Blackard *et al.* 2008; Kelldorfer *et al.* 2012; Wilson *et al.* 2013).

Ecoregion	Live tree biomass			Forest area (Mha)
	Average (Mg C ha ⁻¹)	SD (Mg C ha ⁻¹)	Total (Tg C)	
AZNMM	28.7	18.4	197	6.89
AZNMP	14.2	7.0	23	1.61
BM	55.5	22.4	188	3.39
CBR	17.9	7.1	71	3.95
CCFCM	60.0	33.8	44	0.74
CCV	24.2	10.6	0	0.00
CD	14.7	7.3	0	0.03
CM	139.2	57.6	754	5.41
CNR	51.9	17.5	78	1.50
COLPL	37.2	19.7	7	0.20
COP	19.8	8.4	68	3.43
CR	143.7	56.9	656	4.57
ECSF	56.0	32.6	189	3.38
HP	17.2	5.7	0	0.02
IB	53.8	21.7	252	4.68
KMCCR	123.1	45.0	493	4.00
MA	18.9	14.7	10	0.54
MBR	17.9	9.8	4	0.22
MR	49.7	17.1	372	7.48
NBR	27.6	11.6	11	0.41
NC	122.2	59.9	311	2.54
NR	65.7	22.9	445	6.78
NWGLP	26.9	11.4	0	0.01
NWGP	22.6	11.3	10	0.45
PL	104.5	43.0	94	0.90
SBR	5.5	3.7	0	0.00
SCM	54.4	22.7	21	0.38
SCNBC	54.7	22.3	0	0.00
SN	99.9	47.2	393	3.93
SR	44.8	20.4	407	9.09
SRP	32.0	13.2	1	0.02
SWT	14.3	7.6	6	0.39
WB	20.4	10.7	3	0.14
WUM	34.3	15.0	96	2.79
WV	117.3	40.8	34	0.29

Table B3. Forest net primary productivity for states in the western United States. Forest net primary productivity was derived from the MODIS productivity dataset averaged 2000-2014 and was masked to areas mapped by MODIS as forest or woodlands.

State	MODIS Net Primary Productivity (2000-2014)			Forest and woodland area (Mha)
	Average (Mg C ha ⁻¹ yr ⁻¹)	SD (Mg C ha ⁻¹ yr ⁻¹)	Total (Tg C yr ⁻¹)	
AZ	2.55	0.95	8	3.3
CA	7.43	3.31	110	15.04
CO	4.15	1.15	24	5.88
ID	4.45	1.26	37	8.31
MT	4.86	1.1	41	8.53
NM	3.83	1.28	11	2.99
NV	1.93	0.78	3	1.84
OR	6.97	2.48	82	11.79
UT	2.63	0.82	7	2.75
WA	6.61	2.14	64	9.8
WY	3.64	1.06	11	3.09

Table B4. Forest net primary productivity for ecoregions in the western United States. Forest net primary productivity was derived from the MODIS productivity dataset averaged 2000-2014 and was masked to areas mapped by MODIS as forest or woodlands.

State	MODIS Net Primary Productivity (2000-2014)			Forest and woodland area (Mha)
	Average (Mg C ha ⁻¹ yr ⁻¹)	SD (Mg C ha ⁻¹ yr ⁻¹)	Total (Tg C yr ⁻¹)	
AZNMM	2.91	0.93	12	4.05
AZNMP	2.17	0.82	1	0.32
BM	4.64	1.12	14	3.10
CBR	1.98	0.73	4	2.30
CCFCM	7.84	2.97	29	3.82
CCV	5.30	1.30	3	0.49
CD	1.68	0.65	0	0.04
CM	6.84	1.30	37	5.45
CNR	4.74	1.12	6	1.38
COLPL	3.28	1.18	1	0.41
COP	2.62	0.82	3	1.12
CR	10.38	2.59	53	5.09
ECSF	5.28	1.36	15	2.94
HP	2.92	0.72	0	0.06
IB	4.25	1.08	18	4.26
KMCCR	9.22	2.01	41	4.44
MA	1.65	0.71	0	0.29
MBR	1.42	0.74	0	0.20
MR	4.17	1.16	29	7.13
NBR	2.30	0.77	1	0.62
NC	5.23	1.55	12	2.37
NR	5.55	0.68	37	6.83
NWGLP	3.49	0.85	0	0.06
NWGP	3.48	0.88	1	0.39
PL	8.14	1.58	10	1.35
SBR	1.48	0.78	0	0.11
SCM	7.50	2.18	6	0.78
SCNBC	8.61	2.84	2	0.24
SN	4.80	1.44	17	3.60
SR	4.38	1.08	31	7.05
SRP	2.47	1.11	1	0.23
SWT	3.00	0.95	0	0.13
WB	2.64	0.86	1	0.29
WUM	2.87	0.81	5	1.65
WV	8.44	1.27	6	0.72

Appendix C: Supporting information for Chapter 4

Table C1. Percentage of live tree biomass typically killed by low, moderate, and high severity fire in the western United States. We derived these summaries from 116 estimates collated from 29 regional field studies by Ghimire et al. (2012). These field studies included extensive sampling in California, Arizona, and Oregon, as well as sampling in Colorado, Montana, Wyoming, Idaho, Washington, and South Dakota.

Forest type	Burn Severity	Mortality (%)		
		Mean	SE	N
Angiosperm	Low	29	15	5
	Moderate	66	7	9
	High	94	7	2
Gymnosperm	Low	22	3	30
	Moderate	45	3	53
	High	91	2	13

Table C2. Tree aboveground carbon stocks (AGC; Tg AGC) and mean annual tree mortality from fires, bark beetles, and timber harvest on forestland from 2003-2012 for each state in the western United States. Tree mortality was quantified as the amount of AGC stored in tree biomass killed by disturbance. Tree mortality is summarized in terms of absolute mortality (Tg AGC yr⁻¹), mortality rate (i.e., % of statewide AGC in tree biomass killed each year), and percentage of total mortality from harvest, beetles, and fire caused by each type of disturbance (%). Tree mortality from bark beetles and fires was derived using remote sensing, whereas harvest was derived from USFS forest resource reports.

State	Tree carbon stock Tg AGC	Disturbance	Tree mortality		
			Tg AGC yr ⁻¹	% yr ⁻¹	%
AZ	111±3	harvest	0.14±0.04	0.13±0.04	12
		beetles	0.45±0.75	0.40±0.67	37
		fire	0.61±0.55	0.55±0.49	51
		total	1.20±1.34	1.08±1.20	100
CA	868±27	harvest	3.32±0.34	0.38±0.04	44
		beetles	1.65±0.95	0.19±0.11	22
		fire	2.60±2.14	0.30±0.25	34
		total	7.56±3.43	0.87±0.40	100
CO	262±6	harvest	0.11±0.03	0.04±0.01	3
		beetles	2.94±1.17	1.12±0.45	93
		fire	0.09±0.08	0.04±0.03	3
		total	3.14±1.29	1.20±0.49	100
ID	384±10	harvest	2.57±0.42	0.67±0.11	43
		beetles	1.85±0.77	0.48±0.20	31
		fire	1.56±1.34	0.41±0.35	26
		total	5.97±2.53	1.56±0.66	100
MT	364±8	harvest	1.45±0.25	0.40±0.07	27
		beetles	2.82±1.65	0.77±0.45	53
		fire	1.09±0.88	0.30±0.24	20
		total	5.35±2.77	1.47±0.76	100
NM	123±4	harvest	0.07±0.01	0.06±0.01	9
		beetles	0.29±0.24	0.23±0.19	37
		fire	0.43±0.28	0.35±0.23	55
		total	0.79±0.53	0.64±0.43	100
NV	43±1	harvest	0.11±0.03	0.26±0.07	50
		beetles	0.07±0.08	0.16±0.18	31
		fire	0.04±0.03	0.09±0.06	19
		total	0.22±0.13	0.51±0.31	100
OR	939±29	harvest	8.07±1.00	0.86±0.11	83
		beetles	0.90±0.25	0.10±0.03	9
		fire	0.76±0.25	0.08±0.03	8
		total	9.73±1.51	1.04±0.16	100
UT	109±3	harvest	0.07±0.02	0.06±0.02	10
		beetles	0.43±0.18	0.39±0.16	62

WA	826±24	fire	0.19±0.10	0.17±0.09	28
		total	0.69±0.30	0.63±0.27	100
		harvest	7.02±0.64	0.85±0.08	76
		beetles	1.64±0.45	0.20±0.05	18
WY	131±4	fire	0.52±0.38	0.06±0.05	6
		total	9.18±1.47	1.11±0.18	100
		harvest	0.1±0.020	0.08±0.02	5
		beetles	1.54±0.51	1.18±0.39	80
Regional	4160±119	fire	0.29±0.17	0.22±0.13	15
		total	1.92±0.71	1.47±0.54	100
		harvest	23.03±2.80	0.55±0.07	50
		beetles	14.56±6.99	0.35±0.17	32
		fire	8.18±6.21	0.20±0.15	18
		total	45.77±16.00	1.10±0.38	100