Water limits forest ecosystems in the western US

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

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Abstract

Much of the western US is projected to become warmer and drier over the coming century, underscoring the need to understand how climate influences terrestrial ecosystems in this region. 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 climatic 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 based on the difference between precipitation and reference evapotranspiration summed from October-September (i.e., water-year) and then averaged annually from 1985-2014 (CMI\(_{\text{wy}}\)). Median NPP, BIO, and CRT computed at 10 cm yr\(^{-1}\) intervals along the CMI\(_{\text{wy}}\) gradient increased monotonically with increasing CMI\(_{\text{wy}}\) 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 Mg C ha\(^{-1}\) 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 indicate that mature forests in this region were widely sensitive to changes in water availability, suggesting that projected climatic change over the coming century could reduce NPP, BIO, and CRT in many parts of this region, particularly the Southwest, with resulting impacts on ecosystem services.
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1 Introduction

Climatic water availability strongly affects the distribution of plants on Earth’s land surface (Holdridge, 1947; Major, 1963) and the resulting structure and function of terrestrial ecosystems (Schuur, 2003; Churkina and Running, 1998; Law et al., 2002). For instance, productivity of desert (Whittaker and Niering, 1975), grassland (Yang et al., 2008) and forest (Schuur, 2003; Law et al., 2002; Berner and Law, 2015) ecosystems varies along spatial gradients in climatic water availability. Climatic water availability is projected to change in many parts of the world over the coming century in response to atmospheric warming from sustained anthropogenic greenhouse gas emissions (Dai, 2013; Collins et al., 2013; Walsh et al., 2014).

Rising atmospheric temperatures increase evaporative demand (Hobbins et al., 2012) and the probability that periods with anomalously low precipitation co-occur with anomalously high temperatures, which increases the frequency and severity of drought (Diffenbaugh et al., 2015).

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.

Atmospheric warming in the western United States has increased the risk of drought and continued warming over the coming century could reduce water availability in much of the region (Diffenbaugh et al., 2015; Kunkel et al., 2013; Williams et al., 2012). Regional mean annual temperatures increased 0.8-1.1°C from 1895 to 2011, while concomitant changes in precipitation were more variable (Kunkel et al., 2013; Mote et al., 2014). Coincident with regional warming there was an increase in area annually affected by drought (Cook et al., 2004) and an increase in drought frequency (McCabe et al., 2004). The 2000-2004 drought was the most severe drought to have occurred in the region during the past 800 years (Schwalm et al.,...
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In 2013-2015, much of the western US experienced record low soil moisture and mountain snowpack along with persistent high temperatures that exacerbated the multi-year drought (Singh et al., 2016; Diffenbaugh et al., 2015). Climate models project mean annual temperatures could further increase ~3.8-5.5°C by the end of the 21st century under a high greenhouse gas emission scenario (RCP 8.5; Walsh et al., 2014; Kunkel et al., 2013). Models also suggest that mean annual precipitation might increase ~10% in the northern part of the region, though change little in the southern parts under the same high-emissions scenario; however, these projections are more uncertain than projected changes in temperature (Walsh et al., 2014; Kunkel et al., 2013). The recent severe droughts and projected increases in regional atmospheric temperatures potentially foreshadow a shift towards hotter, drier conditions in much of the region over the coming century (Collins et al., 2013; Dai, 2013; Williams et al., 2012; Schwalm et al., 2012).

Changes in ecosystem structure and function along spatial climatic gradients can provide insight into long-term ecosystem response to climatic change (Jin and Goulden, 2014; Biederman et al., 2016; Berner et al., 2013). Mean annual precipitation varies over 500 cm yr⁻¹ across the western US (Daly et al., 2008) contributing to a range of ecosystems from dry desert shrublands to coastal temperate rainforests (Franklin and Dyrness, 1988; Waring and Franklin, 1979) where live tree biomass (BIO) attains levels thought to be exceeded only be primary Eucalyptus regnans forests in southern Australia (Keith et al., 2009; Waring and Franklin, 1979). Field studies carried in this region found that BIO and/or net primary productivity (NPP) tended to increase as conditions became wetter (Huxman et al., 2004; Knapp and Smith, 2001; Webb et al., 1983; Berner and Law, 2015; Whittaker and Niering, 1975; Gholz, 1982); however, each study was based on fewer than 20 field sites selected using a set of criteria (e.g., mature forest near a
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road). Several of these earlier studies also indicated that mean carbon residence time
(CRT=BIO/NPP) in live aboveground biomass (AGB) increased several fold between the driest
and wettest plant communities (Webb et al., 1983; Whittaker and Niering, 1975; Gholz, 1982),
which is potentially related to differences in disturbance regimes and carbon allocation (Girardin
et al., 2010). These studies illustrate that ecosystem structure and function are strongly
influenced by water availability in parts of the western US; however, additional efforts are
needed to assess forest response to variation in water availability at larger scales across this
region.

Our objective in this study was to explore how forest structure and function changed
along spatial gradients in climatic water availability in the western US. We hypothesized that
tree NPP, BIO, and CRT in mature stands (>100 years old) are constrained by water availability
in this region. We thus anticipated that NPP, BIO, and CRT would increase as climate became
wetter (or, conversely, decrease as climate became drier). 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 that included three national biomass maps and NPP derived from the Moderate
Resolution Imaging Spectroradiometer (MODIS). Tree NPP, BIO, and CRT were based on
above- and below-ground components. We quantified water availability using a climate moisture
index (CMI) that accounted for the cumulative difference between precipitation (P) and reference
evapotranspiration (ET0) over the approximate seasonal cycle of soil water recharge and draw-
down (October-September; i.e., water year).
2 Materials and methods

2.1 Data sets and preprocessing

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

We used field measurements to estimate BIO (BIO_{field}; Mg C ha\(^{-1}\)), NPP (NPP_{field}; Mg C ha\(^{-1}\) yr\(^{-1}\)), and CRT (CRT_{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 from 2001 to 2006 and comprise a representative sample of forest lands in the region. 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 on survey plots using increment cores (Van Tuyl et al., 2005). BIO_{field} and NPP_{field} were computed for each site as part of a prior study (Hudiburg et al., 2011). BIO_{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, along with estimates of fine root mass derived from a relationship with leaf area index (LAI; m\(^{2}\) leaf m\(^{-2}\) ground). NPP_{field} was estimated based on changes in above- and below-ground woody biomass over a 10-year interval plus annual foliage and fine root turnover. See Hudiburg et al. (2011) for additional details. Carbon residence time is a key ecosystem characteristic that describes the average duration, in years, that a carbon molecule will remain in a specific pool (e.g., live biomass; Waring and Running, 2007). We computed CRT_{field} in live tree biomass as the ratio of BIO_{field} to NPP_{field} in stands averaging >100 years of age.

2.1.2 Remote sensing estimates of tree biomass, productivity, and carbon residence time
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We used satellite remote sensing and ancillary data sets to estimate BIO (BIO\textsubscript{sat}), NPP (NPP\textsubscript{sat}), and CRT (CRT\textsubscript{sat}) across mature forests in the western US. BIO\textsubscript{sat} included the same component carbon pools as BIO\textsubscript{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; Wilson et al., 2013; Kellndorfer et al., 2012). 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; Kellndorfer 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 computed the ensemble average. We used the ensemble average in the subsequent analysis given previous work showing that the ensemble average agreed more closely with state-level estimates of tree aboveground carbon stocks derived from forest inventories than any of the individual maps (Berner et al., in review).

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 (Smith et al., 2006; Berner and Law, 2016). 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.
Water limits forest ecosystems in the western US 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 computed 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 and Law, 2016). We then estimated BIO\(_{sat}\) for each 250-m resolution pixel by summing the above- and below-ground 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 global terrestrial NPP each year at 1-km resolution by incorporating estimates of LAI, absorbed photosynthetically active radiation, and land cover derived from MODIS with plant physiological characteristics and climate data (Running et al., 2004; Zhao et al., 2010). The model predicts annual NPP as the cumulative difference between daily gross primary productivity and daily to annual plant respiration. These estimates thus reflect NPP allocated both above- and below-ground. We obtained annual NPP estimates from 2000 to 2014 for the western US, reprojected the data onto an equal area grid, and then averaged 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
Water limits forest ecosystems in the western US where stand age was at least 100 years. The map of stand age reflected conditions c. 2006 and was produced by Pan et al. (2011) 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\textsubscript{sat} assuming homogenous land cover and stand age within each 1-km pixel. We then average aggregated BIO\textsubscript{sat} from 250-m to 1-km resolution and computed CRT\textsubscript{sat} as the ratio of BIO\textsubscript{sat} to NPP\textsubscript{sat}.

**2.1.3 Climate date 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 \( \text{ET}_0 \) (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 (CMI\textsubscript{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 \( \text{ET}_0 \) 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 ($\gamma$) and the slope of the vapor pressure curve ($\Delta$). We quantified $R_n$ and $U$ using monthly climatologies from the North American Land Data Assimilation System-2 (NALDAS-2) 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). After computing $CMI_{wy}$, 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.

2.2 Analysis

We quantified the response of forest NPP, BIO, and CRT to changes in $CMI_{wy}$ across both WAORCA and the broader western US. We specifically focused on areas where $CMI_{wy}$ 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$^{-1}$ non-overlapping bins and then summarized forest characteristics in each bin by computing the median, along with the 10$^{th}$, 25$^{th}$, 75$^{th}$ and 90$^{th}$ 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 $CMI_{wy}$ across the ecoclimatic gradient using nonparametric Spearman’s rank correlation. This test yields a coefficient ($r_s$) between -1 and +1, where a value
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... 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 have first been ranked. We assessed the association between forest characteristics and CMI\textsubscript{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 extensive on the R packages `raster` (Hijmans and van Etten, 2013) and `dplyr` (Wickham and Francois, 2015).

### 2.3 Uncertainty

We minimize uncertainty in our analysis by incorporating satellite and field data sets, as well as by examining the sensitivity of CMI\textsubscript{wy} to methods used to estimate ET\textsubscript{0}. Specifically, we characterized forest BIO using three satellite-derived maps and field inventories. We similarly characterized forest NPP using both satellite and field inventory data sets. This approach combines the strengths of spatially continuous satellite-based model output with the rigor of spatially-limited, field-based inventory measurements. Additionally, we computed CMI\textsubscript{wy} based on ET\textsubscript{0} derived using both the FAO-56 (Allen et al., 1998) and modified-Hargreaves (Hargreaves and Samani, 1985; Droogers and Allen, 2002) methods. This comparison revealed that our results were robust to differences in methods (results not shown) and thus we focused on CMI\textsubscript{wy} computed using the FAO-56 method.
Results

Average annual climatic water availability varied widely across both WAORCA and the broader western US from 1985-2014 (Fig. 1a, b). The CMI$_{wyr}$ ranged from around -400 cm yr$^{-1}$ in southern California and Arizona to over 400 cm yr$^{-1}$ in the coastal mountain ranges in northwestern Washington and Oregon. Forests mapped by MODIS occurred in areas where CMI$_{wyr}$ 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 (±1 SD) CMI$_{wyr}$ in forested areas was -40±80 cm yr$^{-1}$. The Coast Range and Cascade Mountains in Washington and Oregon were the wettest areas, with CMI$_{wyr}$ generally >100 cm yr$^{-1}$. Water availability decreased rapidly in the rain shadows east of the Cascades and Sierra Nevada, giving rise to very steep CMI$_{wyr}$ gradients. For instance, annual CMI$_{wyr}$ in northern Oregon decreased nearly 350 cm over ~30 km between high-elevation forests in the Cascades and low-elevation woodlands in the eastern foothills of the Cascades. The range in CMI$_{wyr}$ encountered along this gradient in the Cascades almost spanned the full range in CMI$_{wyr}$ 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$_{wyr}$ (Fig. 1, 2, Table 2). We focused on forests in areas where CMI$_{wyr}$ 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 NPP$_{field}$, BIO$_{field}$, and CRT$_{field}$ all exhibited a strong, positive association with CMI$_{wyr}$ ($r_s=0.93$-0.96, $p<0.001$).
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Median NPP_{field} increased 155% between the driest and wettest 5% of sites in WAORCA (Fig. 2a), while median BIO_{field} and CRT_{field} increased 997% and 358%, respectively, between these sites (Fig. 2b, c; Table 2). The relationship in each case was slightly curvilinear. There were also strong, positive relationships among median NPP_{field}, BIO_{field}, and CRT_{field} along the WAORCA ecoclimatic 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. 1b, c, d; Table 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. 2d, Table 2). Similarly, median BIO_{sat} and CRT_{sat} increased 410% and 160%, respectively, between the driest and wettest areas (Fig. 2e, f, Table 2). The response of median NPP_{sat}, BIO_{sat}, and CRT_{sat} to increased CMI_{wy} was more curvilinear than the responses observed in the field measurements, with the satellite data sets plateauing in areas where annual CMI_{wy} was above ~100 cm. Furthermore, while magnitude of NPP_{sat} and NPP_{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 BIO_{field} and CRT_{field}. There were again strong relationships among median NPP_{sat}, BIO_{sat}, and CRT_{sat} along the western US ecoclimatic gradient (r_s=0.93-0.97, p<0.001).

4 Discussion and conclusions

4.1 Climate moisture index
Climatic water availability exerted a strong influence on NPP, BIO, and CRT among mature forests in the western US. We chose to quantify climatic water availability using an index that accounted for both precipitation and energy-mediated ET₀, 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 short-comings. 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 CMIₓy; 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 and Dawson, 2010). This potentially explains why there were areas with low CMIₓy along the central and northern coast of California that supported forests with higher NPP and BIO than other forests with similar CMIₓy. 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 run-off increases with precipitation (Sanford and Selnick, 2013). Despite its relative simplicity, prior studies showed that CMI was a useful index for explaining interannual variability in fire activity in the southwest 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 and Law, 2015). Several studies also found that the index, or its inverse (i.e. ET₀ - P), explained substantial spatial variability in mature forest gross photosynthesis (Law et al., 2002), productivity and biomass across a range of ecosystems.
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(Berner and Law, 2015; Webb et al., 1983; Hogg et al., 2008). Our current study further demonstrates that CMI is a useful, empirical index for assessing climatic constraints on forest ecosystems at large spatial scales.

4.2 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 (Webb et al., 1983; Whittaker and Niering, 1975; Gholz, 1982; Berner and Law, 2015). Our current study demonstrates a robust relationship between mature forest NPP and climatic water availability using field measurements from nearly 2,000 inventory plots along with satellite remote sensing data sets covering ~18 Mha. The NPP-CMI$_{wy}$ relationship was similar when NPP was assessed using field measurements from across WAORCA or using MODIS covering the western US, though MODIS showed NPP leveling off in the wettest areas (CMI$_{wy}$ $\approx$ 100-200 cm yr$^{-1}$), whereas this was less evident in the field measurements. A recent remote sensing analysis of California used absorbed photosynthetically-active radiation (APAR) derived from MODIS as an index of gross primary productivity and found that APAR increased asymptotically with increasing mean annual precipitation across vegetation communities (Jin and Goulden, 2014). Forests—occupying the wettest areas and having the highest APAR—exhibited the smallest increase in APAR per unit increase in precipitation of any vegetation community whether assessed along a
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spatial or a temporal gradient, suggesting that forests were less sensitive to changes in precipitation than other vegetation communities (Jin and Goulden, 2014). The lack of asymptotic response in our field measurements together with the asymptotic response of both MODIS NPP and APAR suggests that climate impact assessments based on MODIS could underestimate the sensitivity of NPP to changes in water availability in wet, densely forested area.

Mechanistically, the strong NPP-CMIWy 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 (Waring, 1983; Schroeder et al., 1982), 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) that 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 CMIWy in the wettest areas is likely due to low temperatures constraining productivity at high-elevations (Nakawatase and 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 climatic water availability emerges as a key environmental constraint in the western US.
4.3 Tree carbon stocks

Mature forest BIO increased notably with increasing $\text{CMI}_{\text{wy}}$ across both WAORCA and the broader western US, reflecting underlying shifts in NPP and, likely, tree mortality due to 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 time scales (Olson, 1963). Hence, the increase in NPP with increasing $\text{CMI}_{\text{wy}}$ explains some of the concomitant increase in BIO. We suspect that as conditions became wetter there was also a decline in the proportion of BIO lost to annual mortality from natural disturbances. Several recent studies found that tree 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 (Berner et al., in review; Hicke et al., 2013). Furthermore, the field and satellite data sets also incidentally revealed there was an increase in the median age of stands over 100 years as conditions became wetter, with median stand age ~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 lower rates of mortality from natural disturbance.

The observed increase in mature forest BIO with increasing climatic water availability was generally consistent with prior field studies from this region, yet our study demonstrates this response over a much broader ecoclimatic 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 LTER sites spread across the conterminous US
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(Webb et al., 1983) and at sites in Oregon (Berner and 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 ≈ 950 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 and Franklin, 1979), which is thought to be exceeded only by the >3,000 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 (~377 Mg C ha\(^{-1}\)) was over twice that of high-biomass stands in wet tropical forests (~179 Mg C ha\(^{-1}\)) and nearly six times that of high-biomass stands in wet boreal forests (~64 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\(_{\text{wy}}\), yet the satellite data set showed less of an increase than the field measurements. Median forest BIO\(_{\text{field}}\) increased nearly 1,000% between the dry woodlands and coastal temperate rainforests in WAORCA, yet the increase in BIO\(_{\text{sat}}\) with increasing CMI\(_{\text{wy}}\) was less pronounced (410% increase) when assessed across the western US. Furthermore, median BIO\(_{\text{sat}}\) plateaued around 175 Mg C ha\(^{-1}\) in areas where CMI\(_{\text{wy}}\) was ~100-200 cm yr\(^{-1}\). The response of BIO to increasing CMI\(_{\text{wy}}\) was likely more muted when assessed using the satellite-derived maps than the field measurements for several reasons. 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
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footprint relative to that of a field plot, which thus averages BIO over a larger area, reducing peak values. Additionally, the maps are largely derived from optical, multi-spectral satellite imagery that is not very sensitive to variation in BIO in high-biomass forests. 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 and Dubayah, 2011). Nevertheless, current BIO maps (e.g., Wilson et al., 2013; Kellndorfer et al., 2012) proved a valuable tool for ecologic and natural resource assessments (Goetz et al., 2014; Krankina et al., 2014; Berner et al., in review).

4.4 Carbon residence time in tree biomass

Median CRT\textsubscript{field} increased persistently with CMI\textsubscript{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 ecoclimatic gradient. A prior study focused on 11 LTERS spread across the conterminous US found that CRT increased from \~2 years in a desert shrubland to \~73 years in 450-years old Douglas-fir stand at the Andrews LTER in the Oregon Cascade Mountains (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 averaged 79\pm23 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 Arizona Santa Catalina Mountains (Whittaker and Niering, 1975) and across nine mature stands in a range of forest types in Oregon (Gholz, 1982). Although this pattern has been documented in several instances, the underlying mechanisms remain unclear.
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We speculate that the increase in CRT with increased water availability was potentially associated with underlying changes in NPP allocation and BIO mortality rates. Trees invest a larger proportion of NPP into aboveground tissue production as conditions become wetter and competition for light intensifies (Runyon et al., 1994; Law et al., 2003). 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 the CRT in belowground tissues. Thus, a shift in NPP allocation toward longer-lived aboveground tissues likely contributed to the observed increase in CRT as conditions become wetter, as might changes in BIO mortality rates along this hydraulic gradient. Recent BIO mortality rates due to disturbance by wildfires and bark beetles tended to be considerably lower in the wettest parts of the western US than in drier parts of the region (Berner et al., in review). The incidental observation that mature stands tended to be older in the wetter areas is consistent with these areas experiencing lower morality rates from natural disturbances. Our study demonstrates that CRT in live tree biomass was strongly influenced by water availability, yet additional efforts are needed to elucidate underlying mechanism affecting 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).

4.5 Climate change implications

Forest NPP, BIO, and CRT in mature stands increased with CMI_WY across WAORCA and the broader western US, underscoring that climatic water availability is a major abiotic constraint on several keys aspects of ecosystem structure and function in forests ranging from dry woodlands...
Water limits forest ecosystems in the western US to coastal temperate rainforests. What do these findings mean in the context of regional climate change? Although future changes in precipitation are uncertain, climate models widely project extensive regional warming over the coming century in response to high rates of greenhouse gas emissions, which could lead to drier conditions as higher temperatures increase atmospheric evaporation demand (Walsh et al., 2014; Collins et al., 2013; Dai, 2013). For instance, simulations based on the sophisticated Variable Infiltration Capacity (VIC) hydraulic model and a high-emission scenario (A2) suggest that soil moisture could decline ~1-15% in many parts of the region by the end of the 21st century, with drying particularly acute in the Southwest (Walsh et al., 2014). Similarly, a large ensemble of climate models indicate that soil moisture could decline 3-12% throughout the region over this century (Dai, 2013). In fact, projections of regional drying are widespread, particularly for the Southwest (e.g., Williams et al., 2012; Schwalm et al., 2012; Burke et al., 2006; Seager and Vecchi, 2010; Dai, 2011; Collins et al., 2013).

Increased atmospheric CO$_2$ and warming in the Northwest could enhance tree productivity in some areas by (1) increasing water use efficiency (WUE) through CO$_2$ fertilization and (2) enhancing spring photosynthesis (Ruehr et al., 2014; Hudiburg et al., 2013; Kang et al., 2014; Soulé and Knapp, 2015). On the other hand, many tree species have narrow hydraulic safety margins (Choat et al., 2012) and warming-induced declines in tree growth have occurred in other regions despite increased WUE (Andreu-Hayles et al., 2011; Peñuelas et al., 2011; Lévesque et al., 2014). It is unlikely that increased WUE and other physiological adjustments will fully compensate for impacts of rapid future warming on tree physiology (Allen et al., 2015), especially in the Southwest where hotter and drier conditions are already suppressing tree productivity and increasing tree mortality in some areas (Dennison et al., 2014; Creedon et al., 2014; Williams et al., 2012; Anderegg et al., 2015; McDowell et al., 2015).
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The strong NPP-CMI<sub>wy</sub>, BIO-CMI<sub>wy</sub>, and CRT-CMI<sub>wy</sub> associations that we observed in the western US suggest that future reductions in water availability will likely reduce NPP, BIO, and CRT in mature forests, particularly those in the driest areas.

4.6 Conclusions

Forests in the western US range from dry woodlands to temperate rainforests, an ecological gradient that nearly spans the global range in tree biomass and that largely reflects spatial variation in climatic water availability. In this study, we quantified changes in tree productivity, live biomass, and carbon residence time along spatial gradients in climatic 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 climatic water availability, which was 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 likely due to the increased productivity and stand age, along with a decreased proportion of live biomass lost to annual mortality. Forest productivity and biomass derived from field- and satellite-measurements exhibited broadly similar sensitivities to changes in climatic 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 carbon residence time with increasing water availability suggests that efforts to increase terrestrial carbon storage as a tool to...
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combat climate change will be most effective in the wettest areas. Furthermore, the observed change in carbon residence time could provide a benchmark for evaluating the performance of global vegetation models, in which carbon residence time is a principle source of uncertainty in future projections of the global carbon cycle. Overall, our results indicate that tree productivity, live biomass, and carbon residence time in mature stands are widely sensitive to changes in climatic water availability in the western US, suggesting that projected warming and drying over the coming century due to business-as-usual greenhouse gas emissions could have important impacts on ecosystem structure, function, and services in many parts of this region.

Author contributions

L.T.B. designed the study, analyzed the data, and prepared the manuscript with contributions from B.E.L. and T.W.H., who both also contributed data sets to this effort.

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Tables

Table 1. Summary of 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 across both WAORCA and the broader western US. These forest characteristics were quantified for WAORCA using field measurements from 1,953 sites and for the western US 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 CRT=BIO/NPP. It is also known as the biomass accumulation ratio. These carbon stocks and fluxes combine above- and below-ground components.

<table>
<thead>
<tr>
<th>Domain</th>
<th>Variable</th>
<th>Units</th>
<th>Time span</th>
<th>Mean (SD)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAORCA</td>
<td>NPP(_{field})</td>
<td>Mg C ha(^{-1}) yr(^{-1})</td>
<td>2001-2006</td>
<td>4.3 (2.5)</td>
<td>0.6 – 20.9</td>
</tr>
<tr>
<td></td>
<td>BIO(_{field})</td>
<td>Mg C ha(^{-1})</td>
<td>2001-2006</td>
<td>158 (135)</td>
<td>2 – 947</td>
</tr>
<tr>
<td></td>
<td>CRT(_{field})</td>
<td>year</td>
<td>2001-2006</td>
<td>33 (19)</td>
<td>2 – 137</td>
</tr>
<tr>
<td>Western US</td>
<td>NPP(_{sat})</td>
<td>Mg C ha(^{-1}) yr(^{-1})</td>
<td>2000-2014</td>
<td>5.3 (2.0)</td>
<td>0.1 – 227</td>
</tr>
<tr>
<td></td>
<td>BIO(_{sat})</td>
<td>Mg C ha(^{-1})</td>
<td>2000-2008</td>
<td>83 (54)</td>
<td>2 – 669</td>
</tr>
<tr>
<td></td>
<td>CRT(_{sat})</td>
<td>year</td>
<td>2000-2008</td>
<td>15 (9)</td>
<td>2 – 1390</td>
</tr>
</tbody>
</table>
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Table 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\(_{\text{wy}}\); 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\(_{\text{wy}}\) was between -200 cm yr\(^{-1}\) and 200 cm yr\(^{-1}\). Summaries include (1) median forest characteristic in the driest 5% and wettest 95% of sites/pixels; (2) the corresponding change; (3) and the Spearman correlation (\(r_s\)) between CMI\(_{\text{wy}}\) and the median forest characteristic computed at 10 cm yr\(^{-1}\) CMI\(_{\text{wy}}\) intervals. All correlations were statistically significant at \(\alpha < 0.001\).

<table>
<thead>
<tr>
<th>Domain</th>
<th>Variable</th>
<th>Units</th>
<th>Median of…</th>
<th>Change…</th>
<th>CMI(_{\text{wy}}) cor.</th>
<th>Domain</th>
<th>Variable</th>
<th>Units</th>
<th>Median of…</th>
<th>Change…</th>
<th>CMI(_{\text{wy}}) cor.</th>
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</thead>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Driest 5%</td>
<td>Wettest 95%</td>
<td>Abs.</td>
<td>%</td>
<td>rs</td>
<td></td>
<td>Driest 5%</td>
<td>Wettest 95%</td>
<td>Abs.</td>
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<tr>
<td>WAORCA</td>
<td>NPP(_{\text{field}})</td>
<td>Mg C ha(^{-1}) yr(^{-1})</td>
<td>2.2</td>
<td>5.6</td>
<td>3.4</td>
<td>155</td>
<td>0.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BIO(_{\text{field}})</td>
<td>Mg C ha(^{-1})</td>
<td>26</td>
<td>281</td>
<td>255</td>
<td>997</td>
<td>0.96</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>CRT(_{\text{field}})</td>
<td>year</td>
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<td>49</td>
<td>38</td>
<td>358</td>
<td>0.96</td>
<td></td>
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<tr>
<td>Western US</td>
<td>NPP(_{\text{sat}})</td>
<td>Mg C ha(^{-1}) yr(^{-1})</td>
<td>3.4</td>
<td>6.7</td>
<td>3.3</td>
<td>97</td>
<td>0.93</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>BIO(_{\text{sat}})</td>
<td>Mg C ha(^{-1})</td>
<td>32</td>
<td>165</td>
<td>133</td>
<td>410</td>
<td>0.97</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>CRT(_{\text{sat}})</td>
<td>year</td>
<td>10</td>
<td>26</td>
<td>16</td>
<td>160</td>
<td>0.99</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
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Figure 1. Mean climatic moisture index ($CM_{\text{wy}}$; 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 US. (a) BIO derived from field measurements ($BIO_{\text{field}}$) at mature sites (>100 years) in WAORCA. For visual clarity only 20% of the 1,953 sites are depicted. (b) $CM_{\text{wy}}$ 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 ($NPP_{\text{sat}}$). (d) BIO was quantified using satellite-derived estimates of carbon stocks ($BIO_{\text{sat}}$).
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Figure 2. Tree net primary productivity (NPP; Mg C ha\(^{-1}\) yr\(^{-1}\)), live biomass (BIO; Mg C ha\(^{-1}\)), and carbon residence time (CRT; years) increased with increasing climatic water availability across both WAORCA (a-c) and the broader western US (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 US (d-f). NPP\(_{\text{sat}}\) was characterized using MODIS data averaged annual from 2000 to 2014. BIO\(_{\text{sat}}\) was quantified based on an ensemble of aboveground biomass maps plus estimates of coarse root, fine root, and foliage biomass. CRT was computed for each field plot and pixel as BIO / NPP. Water availability was quantified using a climate moisture index (CMI= P-ET\(_{0}\)) summed over the water year (October-September) and then averaged from 1985-2014 (CMI\(_{\text{wy}}\)). The region was partitioned into 10 cm yr\(^{-1}\) (non-overlapping) CMI\(_{\text{wy}}\) bins, pixels/plots were allocated to bins, and then forest characteristics were summarized within each bin. In each panel, the bold line
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denotes the median, dark gray band the 25-75th percentiles, and light gray band the 10-90th percentiles. Note the different y-axis scales between (b) and (e), as well as (c) and (f).