Author responses to referee comments

Manuscript ID: bg-2016-419

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

Authors: Logan T. Berner, Beverly E. Law, and Tara W. Hudiburg

Anonymous Referee #1

General Comments:

This is a very interesting paper that uses forest inventory and satellite data to evaluate the influence of mean annual moisture balance on forest productivity and biomass across the western US with a particular focus on California, Oregon, and Washington. While it is no surprise that productivity and biomass in this region are affected by water availability, this paper provides the most thorough quantification of this influence to date and represents a fantastic use of US Forest Service survey data. This thorough quantification leads to the conclusion that water balance has not just an important influence on forest carbon in the western US, but that it is instead THE dominant driver in this region, with a strong and reliable effect on both biomass and productivity, which translates to a strong and reliable effect on carbon residence time. This information has clear implications for future forest carbon dynamics in a warmer world with altered precipitation regimes, which is importance since dynamic vegetation models are still in need of substantial improvement before their representations of future shifts in forest demographics across regions as large and complex as the western US are taken seriously. I recommend publication after some minor points below are addressed.

RESPONSE: Thank you for your feedback on our manuscript. Your comments were very helpful in preparing a revised version of our manuscript. We made the minor revisions that you suggested, as detailed below.

Specific Comments:

L79: The Singh et al. study is a great one but the focus is not on the impact of recent warm temperatures on west coast drought, but rather on an observed increase in the frequency of east-west dipole years when the western US is anomalously warm and the eastern US is anomalously cool. There have been many papers that more compellingly evaluate the role of temperature in exacerbating recent drought conditions on the west coast, particularly CA, than either of the references provided here:

AghaKouchak, A., L. Cheng, O. Mazdiyasni, A. Farahmand (2014), Global warming and changes in risk of concurrent climate extremes: Insights from the 2014 California drought, Geophysical Research Letters, 41(24), 8847-8852, doi:10.1002/2014GL062308.

Griffin, D., K. J. Anchukaitis (2014), How unusual is the 2012–2014 California drought? Geophysical Research Letters, 41(24), 9017-9023, doi:10.1002/2014GL062433.

Mao, Y., B. Nijssen, D. P. Lettenmaier (2015), Is climate change implicated in the 2013- 2014 California drought? A hydrologic perspective, Geophysical Research Letters, 42(8), 2805-2813, doi:10.1002/2015GL063456.

Mote, P. W., D. E. Rupp, S. Li, D. J. Sharp, F. Otto, P. F. Uhe, M. Xiao, D. P. Lettenmaier, H. Cullen, M. R. Allen (2016), Perspectives on the causes of exceptionally low 2015 snowpack in the western United States, Geophysical Research Letters, 10.1002/2016GL069965, In press, doi:10.1002/2016GL069965.

Shukla, S., M. Safeeq, A. AghaKouchak, K. Guan, C. Funk (2015), Temperature impacts on the water year 2014 drought in California, Geophysical Research Letters, 42(11), 4384-4393, doi:10.1002/2015GL063666.

Williams, A. P., R. Seager, J. T. Abatzoglou, B. I. Cook, J. E. Smerdon, E. R. Cook (2015), Contribution of anthropogenic warming to California drought during 2012-2014, Geophysical Research Letters, 42(16), 6819-6828, doi:10.1002/2015GL064924.

RESPONSE: Thank you for guiding us towards several more appropriate references. We removed the citation to Singh et al. (2016) found several of the suggested citations to be more appropriate (e.g., Mote et al. 2016; AghaKouchak et al. 2014).

L132-136: The allometric equations and LAI-vs-root relationship should be cited, particularly for the diverse (non-forestry) readership of this journal.

RESPONSE: We added the appropriate citations for the allometric equations (Means et al. 1994; Law et al. 2001) and equation for estimating root biomass from leaf area index (Van Tuyl et al. 2005).

L140: I don't think it's necessary to specify that stands of >100 years of age are considered here since it was already stated that only stands of this age group were considered in the analysis.

RESPONSE: Suggestion adopted.

L177-194: The circularity involved in using the MODIS NPP product, which incorporates climate data, to evaluate the relationship between NPP and climate needs to be acknowledged.

RESPONSE: We agree that the circularity should be acknowledged and added the following sentence to the methods (section 2.1.2):

> We acknowledge a degree of circularity in relating NPP_{sat} to CMI given that both computations incorporate temperature data, specifically, temperature-effects on VPD.

L341-344: Is this artifact due to saturation of satellite-derived NDVI/LAI in densely vegetated areas? It seems like the likely reason for the false plateauing in the satellite obs could be stated.

RESPONSE: It is possible that the apparent saturation of MODIS NPP in the wettest areas was related to MODIS becoming less sensitive to variation in FPAR in densely vegetated areas. We modified part of the text to read (starting on line 337):

> The NPP-$\mathrm{CMI}_{\overline{wy}}$ 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 ($\mathrm{CMI}_{\overline{wy}} \approx$ 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 $\mathrm{CMI}_{\overline{wy}}$ 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)….

L459-460: The projected soil moisture trends in Dai (2013) are for just 0-10 cm. For model projections of the more important 1-2 m layer, Cook et al. (2015) is a good reference, at least for CA and the Southwest. Cook, B. I., T. R. Ault, J. E. Smerdon (2015), Unprecedented 21st century drought risk in the American Southwest and Central Plains, Science Advances, 1(1), e1400082, doi:10.1126/sciadv.1400082.

RESPONSE: Thank you for the suggestion. We incorporated this reference into our discussion.

L469-472: But isn't it under hotter/drier conditions where, all else held equal, vegetation stands to benefit the most from increased CO2. The argument that recent drought-driven declines in productivity in the Southwest is evidence for a lack of a CO2 effect is an incomplete argument, as it could be counter-argued that the recent drought period has been particularly intense and that the consequences would have been more severe without CO2 fertilization. There is still much that is unknown about CO2 fertilization, the forests that will benefit from it, and how these benefits will manifest, but just as it is unwise to argue that CO2 fertilization will definitely allow semi-arid forests to become more productive in a warmer world, it is also unwise to imply without a thorough evaluation of evidence that CO2 fertilization will not have any effect on the future relationship between CMI and NPP, BIO, or CRT.

RESPONSE: Following this comment and feedback from Reviewer 2, we chose to remove the ‘Climate change implications’ section and replace it with a section called ‘Predicting ecosystem response to environmental change’ that reads (starting on line 475):

> 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 (Walsh et al., 2014;Dai, 2013;Cook et al., 2015). 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 ecoclimatic 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 (Wilcox et al., 2016;Jin and Goulden, 2014). Near-term effects of climate variability depend on the physiological characteristics of species in the extant plant community, yet ecoclimatic relationships derived from spatial data reflect gradual adjustment of community composition and population size to climate over long periods of time (Wilcox et al., 2016;Jin and Goulden, 2014). Furthermore, ecoclimatic models derived from spatial data cannot account for other ecophysiological impacts of environmental change, such as (1) enhanced plant water use efficiency from CO_2 fertilization (Soulé and Knapp, 2015); (2) increased likelihood of tree mortality due to hotter drought (Adams et al., 2009); or (3) novel changes in disturbance regimes (Hicke et al., 2006;Dale et al., 2001). 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 (Law, 2014;Hudiburg et al., 2013). Although spatial models may not be suitable for near-term projection of ecosystems 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 forestlands.

Technical Corrections:

L39 & 41: CMI should be defined on L39, therefore allowing the definition of CMIwy on L41 to make more sense.

RESPONSE: Suggestion adopted.

L94: Should “be” be “by”?

RESPONSE: Yes, thank you.

L112: The specification of the converse hypothesis is unnecessary.

RESPONSE: The converse hypothesis has been removed.

L125: Should “using” be “used”?

RESPONSE: Yes, thank you.

L237: Should “extensive” be “extensively”?

RESPONSE: Yes, thank you.

L443: “elucidate underlying mechanism” may be missing a word or letter.

RESPONSE: We changed the sentence to read, “…additional efforts are needed to determine the underlying mechanism by which changes in water availability affect CRT.”

L847 (Fig 2 caption): Should “annual” be “annually”?

RESPONSE: Yes, thank you.

Anonymous Referee #2

This is a nice study demonstrating the regional relationship between water availability and productivity, C stocks and residence time in forests of the western US. An impressive data set based on both forest inventory and satellite data were used to establish these relationships. I am not a specialist in estimating forest NPP or C dynamics, but the methods used and assumptions made seem reasonable and the authors are experts in these ecosystems.

Their results indicate that mature forests in the western US were strongly sensitive (across spatial gradients) to changes in water availability. This is not a surprising result, but the scale and scope of this analysis makes this a publishable study. Where I take issue is the inference drawn from this analysis. The authors conclude that their analysis suggests that projected climatic change over the coming century could reduce productivity, biomass and carbon residence time in many parts of this region. Indeed, they justify their study by noting that “Changes in ecosystem structure and function along spatial climatic gradients can provide insight into long-term ecosystem response to climatic change”. While this makes sense in the broadest terms, using spatial relationships (based on average values derived from long-term data) to make predictions about temporal changes in (or the differential sensitivity of) ecosystems to a climate change is risky at best.

We have long known that large scale spatial relationships between NPP and precipitation (or water availability) have a slope that is determined by combined changes in water availability, biogeochemistry and the plant community. But the temporal dynamics over which each of these factors will change in the future will vary dramatically. . .from decades to centuries to even millennia. Thus, spatial models of NPP vs. water are not good predictors of expected temporal dynamics in ecosystems...particularly in forests that have long-lived trees and where communities may turnover very slowly (hundreds of years?). Please see the three references below. Combined, they do a nice job of covering many of the well-known problems inherent in substituting spatial models for temporal models when projecting a future with directional and chronic climate change.

Thus, while I am in favor of publishing this analysis, the conclusions drawn that “projected warming and drying over the coming century. . .could have important impacts on ecosystem structure, function, and services. . .” are really not that noteworthy. Nonetheless, a well-done confirmatory message is much better than much of the introduction and discussion which repeatedly references “sensitivities to changes in water availability” in the context of climate change. As presented, the implication that there is climate change relevance in this analysis is really quite misleading. . .given that spatial sensitivity does not equate to temporal sensitivity – except perhaps for sign. This is true under today’s environment, and spatial relationships such as those derived here will likely be even poorer surrogates for predicting the future as the varying time scales of change (climate vs forest community turnover vs. biogeochemistry) lead to novel functional relationships.

Thus, at the very least the authors should point out the limitations of their analysis and approach with regard to its relevance to future temporal C dynamics. Specifically, because the slopes (sensitivity) of temporal relationships between NPP and water are almost always less steep than slopes from spatial models, the authors need to recognize that the sensitivity implied by their analysis will likely not be manifest.

Estiarte, M., Vicca, S., Peñuelas, J., Bahn, M., Beier, C., Emmett, B. A., Fay, P. A., Hanson, P. J., Hasibeder, R., and Kigel, J.: Few multi‐year precipitation‐reduction experiments find a shift in the productivity‐precipitation relationship, Global change biology, 2016.

Gaitan et al. 2014. Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. Journal of Ecology 102: 1419- 1428.

Wilcox 2016. Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? Ecology 97: 561-568.

RESPONSE: We appreciate your critique of our manuscript, as well as the references that you suggested. We revised our manuscript to better acknowledge that the ecoclimatic relationships we observed reflect long-term climatic constraints on ecosystem structure and function, which are shaped by gradual shifts in community composition and population size (Jin and Goulden, 2014). Consequently, these ecoclimatic relationships are not sufficient to predict ecosystem response to near-term changes in climate. We re-wrote the introduction, de-emphasizing observed and projected climate change, while emphasizing how this study seeks to confirm earlier observation at a larger scale. Furthermore, we remove the "Climate change implications" section (4.5) from the discussion and replaced it with section called "Predicting ecosystems response to environmental change" that reads (starting on line 475):

"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 (Walsh et al., 2014;Dai, 2013;Cook et al., 2015). 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 ecoclimatic 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 (Wilcox et al., 2016;Jin and Goulden, 2014). Near-term effects of climate variability depend on the physiological characteristics of species in the extant plant community, yet ecoclimatic relationships derived from spatial data reflect gradual adjustment of community composition and population size to climate over long periods of time (Wilcox et al., 2016;Jin and Goulden, 2014). Furthermore, ecoclimatic models derived from spatial data cannot account for other ecophysiological impacts of environmental change, such as (1) enhanced plant water use efficiency from CO_2 fertilization (Soulé and Knapp, 2015); (2) increased likelihood of tree mortality due to hotter drought (Adams et al., 2009); or (3) novel changes in disturbance regimes (Hicke et al., 2006;Dale et al., 2001). 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 (Law, 2014;Hudiburg et al., 2013). Although spatial models may not be suitable for near-term projection of ecosystems 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 forestlands."

We also modified the Summary and Conclusions section to read (starting on line 519):

"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 ecoclimatic 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 CO_2) will require mechanistic ecosystem models, which can be evaluated against ecoclimatic relationships developed using inventory sites from a representative sample of forestlands (e.g., Forest Service inventory sites). Overall, our results indicate long-term 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, underscoring that additional 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."

Anonymous Referee #3

General comments:

In my view, this paper makes an important contribution in quantifying the relationship between forest characteristics (net primary productivity, NPP; live biomass, BIO; mean carbon residence time, CRT) and climatic moisture regimes in the western United States. The analysis is strengthened by the inclusion of two fundamentally different data sources and methods, including forest inventory measurements from 3 states (WA, OR and CA) and satellite-based estimates across an even larger area (11 western states). The results are striking as both methods show that forest characteristics in this region are governed primarily by spatial gradients in climatic moisture regimes (as represented by a simple climate moisture index, CMI_wy). Although this general conclusion is not new, the work provides valuable quantitative estimates of forest-climate relationships that are likely to be useful in improving models of forest responses to the climatic drying that is already evident in this region. Overall, the paper is clearly presented and the methods seem appropriate, given the major challenges of spatial scaling in this mountainous and climatically diverse region.

My main questions relate to a) the justification for including only mature stands > 100 years, and b) unstated assumptions and potential sources of error in estimating CRT (see specific points, below).

RESPONSE: Thank you for providing valuable comments on our manuscript. In the revised manuscript we provide (1) better justification for focusing on mature stands and (2) a more thorough discussion of the assumptions and limitations associated with computing CRT as BIO/NPP. We describe these revisions in greater detail below.

Specific comments:

L110 What is the justification for restricting the analysis to mature stands older than 100 years? Is this age considered to be a threshold, beyond which the variables BIO, NPP and/or CRT remain constant over time?

RESPONSE: We focused on mature stands (>100 years) because inventory plots in this region showed that tree BIO and NPP tended to increase rapidly with stand age during the first century and then change more gradually during subsequent years (Hudiburg et al., 2009). In essence, we assume that BIO and NPP have hit much of their 'climatic potential' after 100 years. Several prior studies similarly focused on mature stands that were at least 100 years old (Gholz, 1982;Whittaker and Niering, 1975;Webb et al., 1983). Furthermore, computing CRT as BIO/NPP assumes (as discussed below) that BIO is stable through time, which is an assumption met more closely by examining older stands. We did perform the analysis using all forestland, regardless of stand age, and found very similar results (albeit with lower BIO and CRT). We added the following text to the introduction (starting on line 76):

"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 (Webb et al., 1983;Berner and Law, 2015;Whittaker and Niering, 1975;Gholz, 1982). 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.'"

We also added the following text to the introduction directly before stating our hypotheses (starting on line 112):

"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, though we acknowledge that BIO tends to gradually increase and NPP remains stable or gradually declines during subsequent centuries (Hudiburg et al., 2009)."

L127-128: Do these inventory sites represent forests across the full range of elevations in this region? If they exclude sampling of unproductive forests in climatically cold, wet sites near the upper timberline then I'm wondering if this could explain the observed differences in response to CMI for inventory sites versus satellite-derived estimates (Fig. 2).

RESPONSE: An astute question. The Forest Service inventory sites are spread among areas > 1 acre (0.40 ha) that have at least 10% tree cover (Bechtold and Patterson, 2005). The sites do occur in cold, wet, high-elevation areas so long as those requirements are met. We compared the average (SD) elevation of inventory sites and MODIS forest pixels (stands > 100 years) at each step along the CMIwy gradient and found that inventory sites and MODIS forest had very similar elevational distribution across WAORCA. A paired t-test found no significant difference in average elevation between inventory sites and MODIS forest along the CMIwy gradient in WAORCA (P=0.43). The differences between inventory and satellite-derived estimates of BIO and NPP were most apparent in the wettest areas (e.g, CMIwy > 100 cm/yr) that overwhelming occurred in WAORCA (e.g., 98% of MODIS forest with CMIwy > 100 cm/yr was in WAORCA). Consequently, it does not appear that differences between inventory and satellite-derived estimates of BIO and NPP in wet areas can be attributed to the satellite data systematically including cold, high-elevation areas that are were not represented by the inventory sites. We added text in several places to help clarify. We edited part of the methods to read (starting on line 134):

"These 1-ha sites were surveyed by the US Forest Service Forest Inventory and Analysis (FIA) program between 2001 to 2006 and comprise a representative sample of forest lands (tree cover > 10%) in the region (Bechtold and Patterson, 2005). The inventory sites occurred at elevations ranging from 5 m to 3,504 m, with an average (±1SD) elevation of 1429±677 m."

Additionally, we added modified part of the discussion to read (starting on line 336):

"The NPP-$\text{CMI}_{\overline{\text{wy}}}$ relationship was similar when NPP was assessed using field measurements from across WAORCA or using MODIS covering the western US, though MODIS did show NPP leveling off in the wettest parts of WAORCA ($\text{CMI}_{\overline{\text{wy}}} \approx$ 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 $\text{CMI}_{\overline{\text{wy}}}$ 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)."

L138-140: I believe that the equation used for carbon residence time (CRT = BIO / NPP) is based on the assumption that BIO is constant over time (e.g., see equation 1 of Friend et al 2014, reference cited in the MS). If so, then this assumption (and any others) should be stated explicitly. Overall, I'm wondering how much of the variation in the reported estimates of CRT is driven simply by variation in stand age, given that in my experience, older stands tend to exhibit increasing (or stable) values of BIO along with age-related declines in NPP. On a related point, using the above equation, I would expect estimates of CRT to be inflated in forests with anomalously low NPP over the 10-year period of calculation (e.g., during droughts or insect defoliation episodes that are not sufficiently severe to cause a proportional decline in BIO). Again, it would be helpful to at least acknowledge the potential sources of bias in the reported CRT estimates.

RESPONSE: You are correct that calculating mean carbon residence time (CRT) as CRT = BIO/NPP assumes that BIO is constant over time and we agree that this assumption should be explicitly stated and more thoroughly discussed in our manuscript. We added the following text to the introduction to note this assumption (starting on line 91):

"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 and Niering, 1975). Mean carbon residence time (CRT) describes the average duration that a carbon molecule will remain in a specific pool (Waring and Running, 2007) and for CRT in live biomass 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 an wet, old-growth Douglas-fir forest (Webb et al., 1983)."

Older stands did have higher CRT and average stand age did increase moving into wetter areas. Together, these indicate that the CRT-CMIwy relationships we observed did incorporate an age-related effect; however, the age-relate effect appears to be rather small. For instance, let's compare the median CRT between mature (100-200 years) and old (>200 years) stands occupying very dry (CMIwy < -100 cm yr^{-1}) and very wet (CMIwy > 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 very dry areas 80% of stands were mature and 20% were old, whereas in very wet areas 67% of stands were mature and 33% were old. Furthermore, CRT-CMIwy relationships constructed using mature and old were quite similar, diverging slightly in the wettest areas. These comparisons illustrate CRT is affected by stand age, but that the age effect is quite small relative to the climate effect. We edited the CRT discussion section so that it now begins by addressing uncertainty in our estimates of CRT (starting on line 430):

"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 acknowledge that BIO can gradually increase during subsequent centuries (Hudiburg et al., 2009), which would lead us to underestimated CRT. Conversely, drought and insect-induced defoliation in the early 2000s could have suppressed NPP (Berner and Law, 2015;Schwalm et al., 2012) without a proportional reduction in BIO, which could have inflated our estimates of CRT in some areas."

We then revised the text to include a discussion of the age-related effect (starting on line 457):

"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-$\mathrm{CMI}_{\overline{wy}}$ 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 ($\mathrm{CMI}_{\overline{wy}} < -100$ cm yr^{-1}) and very wet ($\mathrm{CMI}_{\overline{wy}} > 100$ 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 a climate zone. Our study demonstrates that CRT in live tree biomass was strongly influenced by water availability, yet 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)."

L396-400: The discussion includes reporting of the large percentage difference in BIO across the climatic moisture gradient (CMI_wy) using the two methods (from Fig. 2) but I expect that the percentage difference would be even greater than this if dry, naturally unforested areas (with zero forest BIO and NPP) were included in the analysis. In this respect, it would be interesting to see how %forest cover varies as a function of the binned values of CMI_wy across this region. I recognize that such an analysis would go beyond the scope of this paper, but it could provide an interesting additional indicator of how forest NPP and carbon stocks may respond over the long term under the projected (and ongoing) climatic drying, i.e., drought-related loss of forest cover in addition to drought-related decreases in BIO, NPP and CRT in those sites that continue to remain forested.

RESPONSE: We appreciate the suggestion and believe that it would be interesting to investigate how forest cover changes with CMIwy over this region; however, we believe this addition is beyond the scope of our current study.

Anonymous Referee #4

General comments:

This is a thorough, straightforward study using both field and satellite measurements to estimate forest productivity and carbon cycling along a spatial moisture index across the western US. The goals of the study were outlined well, and made use of two datasets that if assimilated properly, can reveal ecological trends and relationships that cross spatial scales. The results revealed, unsurprisingly, that as moisture index increased, so did both productivity and biomass; however this study is one of the more thorough I have seen in both its spatial and methodological scale. The results suggest that climatic moisture availability is perhaps the most fundamental environmental control of forests in the Western US, and that the forest communities are extremely sensitive to this across large spatial scales. I feel this study is well conceived and publishable, but needs more explanation of methods, particularly with regards to data assimilation and validation. You mention in section 2.3 that you 'minimize[d] uncertainty' by using two different data types (field and remotely sensed), but you present no evidence of this. Also, though you present the Spearman coefficient in Table 2, I would have liked to see some cross-domain validation between data types; that is, a simple statistical comparison of how each median variable (NPP, BIO, CRT) value compares between field and satellite data.

RESPONSE: We appreciate the reviewer taking the time to comment on our manuscript. In the revised manuscript we removed the comment about ‘minimizing uncertainty by incorporating both field and remote sensing data sets,’ which was not phrased appropriately. In fact, we removed that section (2.3) entirely and incorporated select element into other parts of the manuscript. Following the reviewer’s second comment, we compared field- and satellite-derived estimates of median NPP, BIO, and CRT, which showed that they were strongly correlated. We then added a sentence towards the end of the results section stating that, “Field- and satellite-derived estimates of median NPP, BIO, and CRT were strongly correlated (r_s=0.90-0.95; $p<0.001$).” We address the reviewer’s remaining comments below.

Specific comments:

L52: Mention of ecosystem services seems unnecessary

RESPONSE: We removed the reference to ecosystem services.

L69: Suggest substituting ‘risk’ with ‘frequency’ or ‘occurrence’

RESPONSE: We changes ‘risk’ to ‘occurrence.’

L101: CRT should be defined before acronym is introduced.

RESPONSE: We edited these sentences to read (starting on line 91):

“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 and Niering, 1975). Mean carbon residence time (CRT) describes the average duration that a carbon molecule will remain in a specific pool (Waring and Running, 2007) and for CRT in live biomass can be computed as BIO/NPP assuming that BIO remains constant over time (Friend et al., 2014;Whittaker, 1961).”

L154: This sentence is very unclear. I don't understand what 'ensemble average' is referring to, nor what the 'previous work' revealed.

RESPONSE: We changed the two sentences to read (starting on line 161):

"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 AGC can vary notably among individual maps (Neeti and Kennedy, 2016)."

L196: Should it be climate 'data' sets?

RESPONSE: Yes, thank you.

L196: Some context should be given for CMI values. What is the typical range? What constitutes extreme values on either end?

RESPONSE: We provide a summary of minimum and maximum CMIwy across the western US, as well as the average CMIwy in forested areas in the results section.

L229: Make sure use of 'Spearman' or 'Spearman's' is consistent

RESPONSE: We edited the manuscript to consistently use *Spearman's* .

L447: Changing natural disturbance regimes should be mentioned in the climate change implications section, given that you discuss it earlier in the context of carbon residence time.

RESPONSE: We ended up replacing the 'Climate change implication' section with a section called 'Predicting ecosystems response to environmental change,' which mentions the importance of changes in disturbance regimes. Part of this section reads (starting on line 485):

"Near-term effects of climate variability depend on the physiological characteristics of species in the extant plant community, yet ecoclimatic relationships derived from spatial data reflect gradual adjustment of community composition and population size to climate over long periods of time (Wilcox et al., 2016;Jin and Goulden, 2014). Furthermore, ecoclimatic models derived from spatial data cannot account for other ecophysiological impacts of environmental change, such as (1) enhanced plant water use efficiency from CO_2 fertilization (Soulé and Knapp, 2015); (2) increased likelihood of tree mortality due to hotter drought (Adams et al., 2009); or (3) novel changes in disturbance regimes (Hicke et al., 2006;Dale et al., 2001). 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 (Law, 2014;Hudiburg et al., 2013)."

Citations

Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., Troch, P. A., and Huxman, T. E.: Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought, Proceedings of the National Academy of Sciences of the United States of America, 106, 7063-7066, 10.1073/pnas.0901438106, 2009.

Bechtold, W., and Patterson, P.: The enhanced forest inventory and analysis program-- national sampling design and estimation procedures, USDA Forest Service General Technical Report SRS-80, Asheville, NC, 98, 2005.

Berner, L. T., and Law, B. E.: Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon, Biogeosciences, 12, 6617-6635, 2015.

Cook, B. I., Ault, T. R., and Smerdon, J. E.: Unprecedented 21st century drought risk in the American Southwest and Central Plains, Science Advances, 1, e1400082, 2015.

Dai, A.: Increasing drought under global warming in observations and models, Nature Climate Change, 3, 52-58, doi: 10.1038/nclimate1633, 2013.

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., and Michael Wotton, B.: Climate Change and Forest Disturbances, BioScience, 51, 723-734, 10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2, 2001.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D. B., Dankers, R., and Falloon, P. D.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO2, Proceedings of the National Academy of Sciences, 111, 3280-3285, 2014.

Gholz, H. L.: Environmental Limits on Aboveground Net Primary Production, Leaf Area, and Biomass in Vegetation Zones of the Pacific Northwest, Ecology, 63, 469-481, 10.2307/1938964, 1982.

Hicke, J. A., Logan, J. A., Powell, J., and Ojima, D. S.: Changing temperatures influence suitability for modeled mountain pine beetle (Dendroctonus ponderosae) outbreaks in the western United States, Journal of Geophysical Research: Biogeosciences (2005–2012), 111, 2006.

Hudiburg, T., Law, B., Turner, D. P., Campbell, J., Donato, D., and Duane, M.: Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage, Ecological Applications, 19, 163-180, 2009.

Hudiburg, T. W., Law, B. E., and Thornton, P. E.: Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests, Biogeosciences, 10, 453-470, 10.5194/bg-10-453-2013, 2013.

Jin, Y., and Goulden, M. L.: Ecological consequences of variation in precipitation: separating short-versus long-term effects using satellite data, Global Ecology and Biogeography, 23, 358-370, 2014.

Law, B. E.: Regional analysis of drought and heat impacts on forests: current and future science directions, Global Change Biology, 20, 3595-3599, 10.1111/gcb.12651, 2014.

Neeti, N., and Kennedy, R.: Comparison of national level biomass maps for conterminous US: understanding pattern and causes of differences, Carbon Balance and Management, 11, 19, 10.1186/s13021-016-0060-y, 2016.

Schwalm, C. R., Williams, C. A., Schaefer, K., Baldocchi, D., Black, T. A., Goldstein, A. H., Law, B. E., Oechel, W. C., and Scott, R. L.: Reduction in carbon uptake during turn of the century drought in western North America, Nature Geoscience, 5, 551-556, 2012.

Soulé, P. T., and Knapp, P. A.: Analyses of intrinsic water-use efficiency indicate performance differences of ponderosa pine and Douglas-fir in response to CO2 enrichment, Journal of Biogeography, 42, 144-155, 2015.

Walsh, J., Wuebbles, D., Hayhoe, K., Kossin, J., Kunkel, K., Stephens, G., Thorne, P., Vose, R., Wehner, M., Willis, J., Anderson, D., Doney, S., Feely, R., Hennon, P., Kharin, V., Knutson, T., Landerer, F., Lenton, T., Kennedy, J., and Somerville, R.: Our Changing Climate, in: Climate Change Impacts in the United States: The Third National Climate Assessment, edited by: Melillo, J. M., Richmond, T. C., and Yohe, G. W., U.S. Global Change Research Program, 19-67, 2014.

Waring, R. H., and Running, S. W.: Forest Ecosystems: Analysis at Multiple Scales, 3rd ed., Elsevier Academic Press, Burlington, MA, 420 pp., 2007.

Webb, W. L., Lauenroth, W. K., Szarek, S. R., and Kinerson, R. S.: Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States, Ecology, 134-151, 1983.

Whittaker, R. H.: Estimation of net primary production of forest and shrub communities, Ecology, 42, 177-180, 1961.

Whittaker, R. H., and Niering, W. A.: Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient, Ecology, 56, 771-790, 1975.

Wilcox, K. R., Blair, J. M., Smith, M. D., and Knapp, A. K.: Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions?, Ecology, 97, 561-568, 2016.

Yan, K., Park, T., Yan, G., Liu, Z., Yang, B., Chen, C., Nemani, R. R., Knyazikhin, Y., and Myneni, R. B.: Evaluation of MODIS LAI/FPAR Product Collection 6. Part 2: Validation and Intercomparison, Remote Sensing, 8, 460, 2016.

List of relevant changes

We made the following changes to our manuscript during the revision process, as described in greater detail in the section above. This list only includes substantive changes, with changes listed in the same order as our responses to the reviewer's comments:

1. We added an acknowledgement regarding the circularity of comparing MODIS NPP against the CMI given that both include the effect of VPD.
2. We added text discussing possible reasons why MODIS NPP could saturate in the wettest areas.
3. We replaced the 'Climate change implications' section in the discussion with a section called 'Predicting ecosystem response to environmental change."
4. We revised our manuscript to better acknowledge that the ecoclimatic relationships we observed reflect long-term climatic constraints on ecosystem structure and function, which are shaped by gradual shifts in community composition and population size (Jin and Goulden, 2014). Consequently, these ecoclimatic relationships are not sufficient to predict ecosystem response

to near-term changes in climate. We re-wrote the introduction, de-emphasizing observed and projected climate change, while emphasizing how this study seeks to confirm earlier observation at a larger scale.

5. We added additional justification for focusing on mature (>100 years) forest.
6. We added clarification about the forest inventory sampling design and discussion as to why difference in NPP between the field and satellite data sets did not reflect differences in sampling extent.
7. We clarified that computing carbon residence time as the ratio of biomass to productivity assumes that both biomass and productivity are not changing through time. We also added text to the discussion illustrating that the changes in CRT that we observed we not due to differences in stand age, but rather climate.
8. We added a comparison of field- and satellite-derived estimates of NPP, BIO, and CRT.

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

Logan T. Berner *[1], Beverly E. Law [1], and Tara W. Hudiburg [2]

[1] Department of Forest Ecosystems and Society
Oregon State University
321 Richardson Hall
Corvallis, Oregon 97331-2212

[2] Department of Forest, Rangeland, and Fire Sciences
University of Idaho
875 Perimeter Drive
Moscow, Idaho 83844-1133

* Corresponding Author:
logan.berner@oregonstate.edu
phone: 702-683-9987
fax: 541-737-5814

Running header:
Water limitations on forests in the western US

Keywords:
~~Ecological gradient, climate~~Bioclimatic gradient, carbon cycle, climate change, climate moisture index, forest inventory, MODIS, satellite remote sensing, biomass

Type of paper:
Primary research article

Formatted: Tab stops: 1.84", Left

Water ~~limits forest ecosystems~~limitations on forests in the western US

Abstract

~~Much of~~ Water availability constrains the ~~western US~~structure and function of terrestrial ecosystems and is projected to ~~become warmer and drier~~change in many parts of the world 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 (CMI) based on the difference between precipitation and reference evapotranspiration summed ~~from~~ over the water-year (October-September~~ (i.e., water-year~~) and then averaged annually from 1985-2014 ($\mathrm{CMI}_{\overline{\mathrm{wy}}}$). Median NPP, BIO, and CRT computed at 10 cm yr^{-1} intervals along the $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ gradient increased monotonically with increasing $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ 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~~illustrate that ~~mature forests in this region were widely sensitive to changes in~~long-term average water availability~~, suggesting that~~ 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 ~~climatic change~~warming and drying 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~~.

Formatted: Tab stops: 1.84", Left

1 Introduction

~~Climatic water~~Water availability strongly ~~affects~~constrains 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 productivity (Schuur, 2003;Law et al., 2002;Berner and Law, 2015)~~ ecosystems varies along spatial gradients in climatic water availability. Climatic water~~ 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 (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., 2012). 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~~The western United States 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)~~ 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~~. 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 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~~ (Keith et al., 2009;Waring and 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 (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 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~~. 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 (Webb et al., 1983;Whittaker and Niering, 1975;Gholz, 1982;Berner and Law, 2015). 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 and 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 and Niering, 1975). Mean carbon residence time (CRT) describes the average duration that a carbon molecule will remain in a specific pool (Waring and Running, 2007) and for CRT in live biomass 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 an 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).

~~These~~Together, these field studies illustrate that ~~ecosystem~~forest structure and function are ~~strongly influenced~~constrained 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.~~these relationships at 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 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 (ET$_0$) over the approximate seasonal cycle of soil water recharge and draw-down (October-September; i.e., water year).~~

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 ($\text{CMI}_{\overline{wy}}$; 1985-2014) as an indicator of long-term water availability (Webb et al., 1983;Hogg and Hurdle, 1995), 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, yet 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., Webb et al., 1983;Berner and Law, 2015;Gholz, 1982), 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 $\text{CMI}_{\overline{wy}}$. Tree NPP, BIO, and CRT were based on above- and below-ground 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.

2 Materials and methods

2.1 Data sets and preprocessing

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

We ~~using~~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.~~Forest Inventory and Analysis (FIA) program between 2001 to 2006 and comprise a representative sample of forest lands (tree cover > 10%) in the region (Bechtold and Patterson, 2005). The inventory sites occurred at elevations ranging from 5 m to 3,504 m, with an average (±1SD) 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 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~~,~~ (Means et al., 1994;Law et al., 2001), along with estimates of fine root mass derived from a relationship with leaf area index (LAI; m^2 leaf m^{-2} ground~~).~~; Van Tuyl et al. 2005). 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 turn-over. 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.~~We then computed CRT$_{field}$ in live tree biomass as the ratio of BIO$_{field}$ to NPP$_{field}$.

2.1.2 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. 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;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).~~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 AGC can vary notably among individual maps (Neeti and 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 (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 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~~ annual NPP ~~each year~~ at 1-km resolution across global terrestrial ecosystems by incorporating estimates of ~~LAI,~~ 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 ~~annual NPP as the cumulative difference between~~ daily gross primary productivity (GPP) based APAR and ~~daily to annual~~ 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 below-ground. 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 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 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_{sat} assuming homogenous land cover and stand age within each 1-km pixel. We then ~~average~~ aggregated BIO_{sat} from 250-m to 1-km resolution and computed CRT_{sat} as the ratio of BIO_{sat} to NPP_{sat}.

2.1.3 Climate ~~date~~ 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).~~ (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 ($\mathrm{CMI}_{\overline{\mathrm{wy}}}$; 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

$$\mathrm{ET_0} = \frac{0.408\Delta\,(\mathrm{R_n} - \mathrm{G}) + \gamma\left(\frac{900}{\mathrm{T} + 273}\right)\mathrm{U}(\mathrm{e_s} - \mathrm{e_a})}{\Delta + \gamma\,(1 + 0.34\,\mathrm{U})}$$

Variables included net incoming radiation ($\mathrm{R_n}$), soil heat flux (G), mean daily temperature (T), wind speed (U), and both saturation ($\mathrm{e_s}$) and actual vapor pressure ($\mathrm{e_a}$), as well as the psychrometric constant (γ) and the slope of the vapor pressure curve (Δ). We quantified $\mathrm{R_n}$ 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, $\mathrm{e_s}$, and $\mathrm{e_a}$ from PRISM temperature data following Zotarelli et al. (2010). We also computed $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ based on ET_0 derived using the modified-Hargreaves approach (Hargreaves and Samani, 1985;Droogers and Allen, 2002) and found that our analysis was robust to differences in methods used to compute ET_0 (results not shown). After computing $\mathrm{CMI}_{\overline{\mathrm{wy}}}$, 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 $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ across both WAORCA and the broader western US. We specifically focused on areas where $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ 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 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 $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ across the ~~ecoclimatic~~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 have first been ranked. We assessed the association between forest characteristics and $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ 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~~extensively 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 $\mathrm{CMI}_{\overline{wy}}$ to methods used to estimate ET_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 $\mathrm{CMI}_{\overline{wy}}$ based on ET_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 $\mathrm{CMI}_{\overline{wy}}$ computed using the FAO-56 method.~~

Formatted: Tab stops: Not at 0.83"

3 Results

Average annual~~ climatic~~ water availability varied widely across both WAORCA and the broader western US from 1985-2014 (Fig. 1a, b). The $\mathrm{CMI}_{\overline{wy}}$ ranged from ~~around -400~~a minimum of -330 cm yr^{-1} in southern California and Arizona to ~~over 400~~a maximum of 490 cm yr^{-1} in the ~~coastal mountain ranges~~Olympic Mountains in northwestern Washington~~ and Oregon~~. Forests mapped by MODIS occurred in areas where $\mathrm{CMI}_{\overline{wy}}$ was between -340 and 490 cm yr^{-1}, though 98% of forest area occurred between -200 and 200 cm y^{-1}, and 72% occurred between -100 and 100 cm yr^{-1}. Average (±1 SD) $\mathrm{CMI}_{\overline{wy}}$ in forested areas was -40±80 cm yr^{-1}. The Coast Range and Cascade Mountains in Washington and Oregon were the wettest areas, with $\mathrm{CMI}_{\overline{wy}}$ 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 $\mathrm{CMI}_{\overline{wy}}$ gradients. For instance, annual $\mathrm{CMI}_{\overline{wy}}$ 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 $\mathrm{CMI}_{\overline{wy}}$ encountered along this gradient in the Cascades almost spanned the full range in $\mathrm{CMI}_{\overline{wy}}$ 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 $\mathrm{CMI}_{\overline{wy}}$ (Fig. 1, 2, Table 2). We focused on forests in areas where $\mathrm{CMI}_{\overline{wy}}$ 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 NPP_{field}, BIO_{field}, and CRT_{field} all exhibited a strong, positive association with $\mathrm{CMI}_{\overline{wy}}$ (r_s=0.93-0.96, p<0.001). 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~~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. 1b, c, d, 2c, d; Table 2). Median NPP_{sat}, BIO_{sat}, and CRT_{sat} all showed a strong, positive relationship with $\mathrm{CMI}_{\overline{wy}}$ (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 $\mathrm{CMI}_{\overline{wy}}$ 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 $CMI_{\overline{wy}}$ was more curvilinear than the ~~responses observed in the~~ field measurements~~, with the satellite data sets plateauing~~ and plateaued in areas where ~~annual~~ $CMI_{\overline{wy}}$ ~~was above~~exceeded ~100 cm yr^{-1}. Furthermore, while magnitude of NPP_{sat} and NPP_{field} response to $CMI_{\overline{wy}}$ were similar, the magnitude of BIO_{sat} and CRT_{sat} responses to increased $CMI_{\overline{wy}}$ were much more muted than the magnitude of response in BIO_{field} and CRT_{field}. ~~There~~Nevertheless, field- and satellite-derived estimates of median NPP, BIO, and CRT were strongly correlated (r_s=0.90-0.95; $p<0.001$).

Formatted: Subscript

Furthermore, there were again strong relationships among median NPP_{sat}, BIO_{sat}, and CRT_{sat} along the western US ~~ecoclimatic~~bioclimatic gradient (r_s=0.93-0.97, $p<0.001$).

Formatted: Indent: First line: 0"

4 Discussion and conclusions

4.1 Climate moisture index

~~Climatic water~~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 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 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 $CMI_{\overline{wy}}$; however, quantifying soil water storage capacity even at individual sites is challenging given uncertainty in soil structure and plant rooting capacity ~~(Running, 1994).~~(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).~~(Fischer et al., 2016;Johnstone and Dawson, 2010). This potentially explains why there were areas with low $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ along the central and northern coast of California that supported forests with higher NPP and BIO than other forests with similar $\mathrm{CMI}_{\overline{\mathrm{wy}}}$. 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 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. 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 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 $\mathrm{CMI}_{\overline{wy}}$ 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~~Building on these prior efforts, 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~~estimates of NPP covering ~18 Mha~~.~~ of forestland.

The NPP-$\mathrm{CMI}_{\overline{wy}}$ 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 ($\mathrm{CMI}_{\overline{wy}}$ ≈ 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~~. MODIS did show NPP leveling off in the wettest parts of WAORCA ($\mathrm{CMI}_{\overline{wy}}$ ≈ 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 $\mathrm{CMI}_{\overline{wy}}$ 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

Formatted: Indent: First line: 0.5"

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 and Goulden, 2014). Forests~~—occupying the wettest areas and having the highest~~ had higher APAR~~—~~ than other plant communities and, furthermore, exhibited the smallest increase in APAR per unit increase in precipitation of any ~~vegetation~~plant community~~ whether assessed along a spatial or a temporal gradient~~, suggesting that ~~forests were~~forest productivity was less sensitive to changes in precipitation than productivity of other ~~vegetation~~plant communities (Jin and Goulden, 2014). ~~The lack of~~ In contrast with the field measurements, the asymptotic response ~~in our field measurements together with the asymptotic response of both~~ 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 ~~NPP~~plant productivity to changes in water availability in wet~~, densely forested area.~~ areas with high biomass.

Formatted: Font: +Body (Calibri), 11 pt

Formatted: Font: +Body (Calibri), 11 pt

Mechanistically, the strong $\text{NPP-CMI}_{\overline{\text{wy}}}$ 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 ~~(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).~~(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 $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ 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 $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ across both WAORCA and the broader western US, reflecting underlying shifts in NPP and, likely, ~~tree~~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 time scales ~~(Olson, 1963).~~(Olson, 1963). Hence, the increase in NPP with increasing $\mathrm{CMI}_{\overline{\mathrm{wy}}}$ 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~~Our analysis did not investigate how tissue senescence or mortality ~~from natural disturbances. Several~~ varied along the regional bioclimatic gradient, though a recent ~~studies~~study found that ~~tree~~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 ~~(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 potentially lower ~~rates of~~BIO mortality rates 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~~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 LTER sites spread across the conterminous US ~~(Webb et al., 1983) and at~~(Webb et al., 1983) and at 8-12 sites in Oregon ~~(Berner and Law, 2015;Gholz, 1982) similarly showed a general increase in tree biomass with increasing water availability.~~(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 $\text{CMI}_{\overline{\text{wy}}}$, 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 $\text{CMI}_{\overline{\text{wy}}}$ was less pronounced ~~(~~(~410% increase) when assessed across the western US. Furthermore, median BIO_{sat} plateaued around 175 Mg C ha^{-1} in areas where $\text{CMI}_{\overline{\text{wy}}}$ was ~100-200 cm yr^{-1}. The response of BIO to increasing $\text{CMI}_{\overline{\text{wy}}}$ was likely more muted when assessed using the satellite-derived maps than the field measurements for several reasons. ~~Areas~~The maps are largely derived from optical, multi-spectral 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. ~~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., 2012).

4.4 Carbon residence time in tree biomass

~~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 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±23 years (± 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.~~

~~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 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~~ We computed CRT as BIO/NPP and found that median CRT_{field} increased persistently with $CMI_{\overline{wy}}$ 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 acknowledge that BIO can gradually increase during subsequent centuries (Hudiburg et al., 2009), which would lead us to underestimated CRT. Conversely, drought and insect-induced defoliation in the early 2000s could have suppressed NPP (Berner and 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 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_{field} averaged 79±23 years (± 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 and Niering, 1975) and across nine mature stands in a range of forest communities in Oregon (Gholz, 1982). Although this pattern has been previously documented at 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 (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 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-$\mathrm{CMI}_{\overline{wy}}$ 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 ($\mathrm{CMI}_{\overline{wy}} < -100$ cm yr^{-1}) and very wet ($\mathrm{CMI}_{\overline{wy}} > 100$ 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 a climate zone. Our study demonstrates that CRT in live tree biomass was strongly influenced by water availability, yet 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).

4.5 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 (Walsh et al., 2014;Dai, 2013;Cook et al., 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;Creeden et al., 2014;Williams et al., 2012;Anderegg et al., 2015;McDowell et al., 2015). The strong NPP-CMI~~$_{wy}$~~, BIO-CMI~~$_{wy}$~~, and CRT-CMI~~$_{wy}$~~ 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.~~

. 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 (Wilcox et al., 2016;Jin and Goulden, 2014). Near-term effects of climate variability depend on the physiological characteristics of species in the extant plant community, yet bioclimatic relationships derived from spatial data reflect gradual adjustment of community composition and population size to climate over long periods of time (Wilcox et al., 2016;Jin and Goulden, 2014). 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 CO_2 fertilization (Soulé and Knapp, 2015); (2) increased likelihood of tree mortality due to hotter drought (Adams et al., 2009); or (3) novel changes in disturbance regimes (Hicke et al., 2006;Dale et al., 2001). 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 (Law, 2014;Hudiburg et al., 2013). Although spatial models may not be suitable for near-term projection of ecosystems 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 forestlands.

4.6 ~~Conclusions~~Summary and conclusions

~~Forests in~~Water availability varies widely across the western US~~.~~, giving rise to forests that range from dry~~,~~, low-biomass 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.~~ that are among 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 ~~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~~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 ~~likely due to the increased~~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, ~~along with a decreased proportion of live~~and, possibly, lower biomass ~~lost to annual~~ mortality~~. Forest~~ rates from natural disturbance (e.g., bark beetles, fires). Tree productivity and biomass derived from field- and satellite-measurements exhibited ~~broadly~~ similar ~~sensitivities to changes in climatic~~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 ~~carbon residence time with increasing~~ 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~~ suggests that efforts to increase terrestrial carbon storage as a tool~~; however, the observed bioclimatic relationships are not suitable for near-term projections of future ecosystem response to ~~combat climate~~regional drying. Predicting near-term ecosystem response to drying and other environmental change (e.g., increased CO_2) 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~~require mechanistic ecosystem models, ~~in~~ which ~~carbon residence time is a principle source of uncertainty in future projections of the global carbon cycle.~~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 ~~are widely sensitive to changes in climatic water availability in the western US, suggesting that~~ranging from dry woodlands to coastal temperate rainforests. Future efforts are needed to anticipate and mitigate the impacts of projected warming and drying ~~over~~on forest ecosystems in the western US and elsewhere around 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.~~world.

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.

Acknowledgements

This work was supported by NASA Headquarters under the NASA Earth and Space Science Fellowship Program (Grant NNX14AN65H), the USDA National Institute of Food and Agriculture (Grant 2013-67003-20652), and the ARCS Foundation Scholar program. T.W.H. was supported by the National Science Foundation Idaho EPSCoR Program (Grant IIA-1301792). We thank the researchers who provided the geospatial data sets used in this analysis. We cite no conflicts of interest.

References

Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., Troch, P. A., and Huxman, T. E.: Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought, Proceedings of the National Academy of Sciences of the United States of America, 106, 7063-7066, 10.1073/pnas.0901438106, 2009.

Allen, C. D., Breshears, D. D., and McDowell, N. G.: On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene, Ecosphere, 6, 1-55, 2015.

Allen, R. G., Pereira, L. S., Raes, D., and Smith, M.: Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56, FAO, Rome, 300, 1998.

Anderegg, W. R., Flint, A., Huang, C.-y., Flint, L., Berry, J. A., Davis, F. W., Sperry, J. S., and Field, C. B.: Tree mortality predicted from drought-induced vascular damage, Nature Geoscience, 8, 367-371, 10.1038/ngeo2400, 2015.

Andreu-Hayles, L., Planells, O., Gutierrez, E., Muntan, E., Helle, G., Anchukaitis, K. J., and Schleser, G. H.: Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of tree growth at five Iberian pine forests, Global Change Biology, 17, 2095-2112, 2011.

Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in: Progress in photosynthesis research, Springer, 221-224, 1987.

Bechtold, W., and Patterson, P.: The enhanced forest inventory and analysis program-- national sampling design and estimation procedures, USDA Forest Service General Technical Report SRS-80, Asheville, NC, 98, 2005.

Berner, L. T., Beck, P. S. A., Loranty, M. M., Alexander, H. D., Mack, M. C., and Goetz, S. J.: Cajander larch (Larix cajanderi) biomass distribution, fire regime and post-fire recovery in northeastern Siberia, Biogeosciences, 9, 3943-3959, 10.5194/bg-9-3943-2012, 2012.

Berner, L. T., Beck, P. S. A., Bunn, A. G., and Goetz, S. J.: Plant response to climate change along the forest-tundra ecotone in northeastern Siberia, Global Change Biology, 19, 3449-3462, 10.1111/gcb.12304, 2013.

Berner, L. T., and Law, B. E.: Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon, Biogeosciences, 12, 6617-6635, 2015.

Berner, L. T., and Law, B. E.: Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999–2014, Scientific Data, 3, 160002, 10.1038/sdata.2016.2, 2016.

Berner, L. T., Law, B. E., Meddens, A. J. H., and Hicke, J. A.: Regional assessment of forest biomass, productivity, and mortality from disturbance across the western US (2003-2012), in review.

Biederman, J., Scott, R., Goulden, M., Vargas, R., Litvak, M., Kolb, T., Yepez, E., Oechel, W., Blanken, P., and Bell, T.: Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America, Global change biology, 2016.

Blackard, J., Finco, M., Helmer, E., Holden, G., Hoppus, M., Jacobs, D., Lister, A., Moisen, G., Nelson, M., and Riemann, R.: Mapping US forest biomass using nationwide forest inventory data and moderate resolution information, Remote Sensing of Environment, 112, 1658-1677, 2008.

Burke, E. J., Brown, S. J., and Christidis, N.: Modeling the recent evolution of global drought and projections for the twenty-first century with the Hadley Centre climate model, Journal of Hydrometeorology, 7, 2006.

Cairns, M. A., Brown, S., Helmer, E. H., and Baumgardner, G. A.: Root biomass allocation in the world's upland forests, Oecologia, 111, 1-11, 1997.

Carroll, A. L., Sillett, S. C., and Kramer, R. D.: Millennium-Scale Crossdating and Inter-Annual Climate Sensitivities of Standing California Redwoods, PLoS ONE, 9, e102545, 10.1371/journal.pone.0102545, 2014.

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J. S., Westoby, M., Wright, I. J., and Zanne, A. E.: Global convergence in the vulnerability of forests to drought, Nature, 491, 752-755, doi:10.1038/nature11688, 2012.

Churkina, G., and Running, S. W.: Contrasting climatic controls on the estimated productivity of global terrestrial biomes, Ecosystems, 1, 206-215, 1998.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W. J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A. J., and Wehner, M.: Long-term Climate Change: Projections, Commitments and Irreversibility, in: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P. M., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1029–1136, 2013.

Cook, B. I., Ault, T. R., and Smerdon, J. E.: Unprecedented 21st century drought risk in the American Southwest and Central Plains, Science Advances, 1, e1400082, 2015.

Cook, E. R., Woodhouse, C. A., Eakin, C. M., Meko, D. M., and Stahle, D. W.: Long-term aridity changes in the western United States, Science, 306, 1015-1018, 2004.

Creeden, E. P., Hicke, J. A., and Buotte, P. C.: Climate, weather, and recent mountain pine beetle outbreaks in the western United States, Forest Ecology and Management, 312, 239-251, http://dx.doi.org/10.1016/j.foreco.2013.09.051, 2014.

Dai, A.: Drought under global warming: a review, Wiley Interdisciplinary Reviews: Climate Change, 2, 45-65, 2011.

Dai, A.: Increasing drought under global warming in observations and models, Nature Climate Change, 3, 52-58, doi: 10.1038/nclimate1633, 2013.

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., and Michael Wotton, B.: Climate Change and Forest Disturbances, BioScience, 51, 723-734, 10.1641/0006-3568(2001)051[0723:ccafd]2.0.co;2, 2001.

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., and Pasteris, P. P.: Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States, International Journal of Climatology, 28, 2031-2064, 2008.

Dawson, T. E.: Fog in the California redwood forest: ecosystem inputs and use by plants, Oecologia, 117, 476-485, 1998.

Dennison, P. E., Brewer, S. C., Arnold, J. D., and Moritz, M. A.: Large wildfire trends in the western United States, 1984–2011, Geophysical Research Letters, 41, 2014GL059576, 10.1002/2014GL059576, 2014.

Diffenbaugh, N. S., Swain, D. L., and Touma, D.: Anthropogenic warming has increased drought risk in California, Proceedings of the National Academy of Sciences, 112, 3931-3936, 2015.

Droogers, P., and Allen, R. G.: Estimating reference evapotranspiration under inaccurate data conditions, Irrigation and drainage systems, 16, 33-45, 2002.

Fischer, D. T., Still, C. J., Ebert, C. M., Baguskas, S. A., and Park Williams, A.: Fog drip maintains dry season ecological function in a California coastal pine forest, Ecosphere, 7, 2016.

Franklin, J. F., and Dyrness, C. T.: Natural vegetation of Oregon and Washington, in, Oregon State University Press, Corvallis, 452, 1988.

Friedl, M. A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., and Huang, X.: MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets, Remote Sensing of Environment, 114, 168-182, 2010.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D. B., Dankers, R., and Falloon, P. D.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO2, Proceedings of the National Academy of Sciences, 111, 3280-3285, 2014.

Gholz, H. L.: Environmental Limits on Aboveground Net Primary Production, Leaf Area, and Biomass in Vegetation Zones of the Pacific Northwest, Ecology, 63, 469-481, 10.2307/1938964, 1982.

Girardin, C. A. J., Malhi, Y., Aragao, L., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley, K., Rapp, J., SILVA-ESPEJO, J., and Silman, M.: Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes, Global Change Biology, 16, 3176-3192, 2010.

Goetz, S., and Dubayah, R.: Advances in remote sensing technology and implications for measuring and monitoring forest carbon stocks and change, Carbon Management, 2, 231-244, 10.4155/cmt.11.18, 2011.

Goetz, S. J., Sun, M., Zolkos, S., Hansen, A., and Dubayah, R.: The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness, Environmental Research Letters, 9, 034013, 2014.

Hargreaves, G. H., and Samani, Z. A.: Reference crop evapotranspiration from temperature, Applied Engineering in Agriculture, 1, 96-99, 1985.

Hicke, J. A., Logan, J. A., Powell, J., and Ojima, D. S.: Changing temperatures influence suitability for modeled mountain pine beetle (Dendroctonus ponderosae) outbreaks in the western United States, Journal of Geophysical Research: Biogeosciences (2005–2012), 111, 2006.

Hicke, J. A., Meddens, A. J., Allen, C. D., and Kolden, C. A.: Carbon stocks of trees killed by bark beetles and wildfire in the western United States, Environmental Research Letters, 8, 035032, 2013.

Hijmans, R. J., and van Etten, J.: raster: Geographic analysis and modeling with raster data, 2.1-25 ed., R Foundation for Statistical Computing, Vienna, 2013.

Hobbins, M., Wood, A., Streubel, D., and Werner, K.: What drives the variability of evaporative demand across the conterminous United States?, Journal of Hydrometeorology, 13, 1195-1214, 2012.

Hogg, E., Brandt, J. P., and Kochtubajda, B.: Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects, Canadian Journal of Forest Research, 32, 823-832, 2002.

Hogg, E., Brandt, J., and Michaelian, M.: Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests, Canadian Journal of Forest Research, 38, 1373-1384, 2008.

Hogg, E. H.: Climate and the southern limit of the western Canadian boreal forest, Canadian Journal of Forest Research, 24, 1835-1845, 1994.

Hogg, E. H., and Hurdle, P.: The aspen parkland in western Canada: A dry-climate analogue for the future boreal forest?, Water, Air, and Soil Pollution, 82, 391-400, 1995.

Holdridge, L. R.: Determination of World Plant Formations From Simple Climatic Data, Science, 105, 367-368, 10.1126/science.105.2727.367, 1947.

Hudiburg, T., Law, B., Turner, D. P., Campbell, J., Donato, D., and Duane, M.: Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage, Ecological Applications, 19, 163-180, 2009.

Hudiburg, T. W., Law, B. E., Wirth, C., and Luyssaert, S.: Regional carbon dioxide implications of forest bioenergy production, Nature Climate Change, 1, 419-423, 10.1038/nclimate1264, 2011.

Hudiburg, T. W., Law, B. E., and Thornton, P. E.: Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests, Biogeosciences, 10, 453-470, 10.5194/bg-10-453-2013, 2013.

Jin, Y., and Goulden, M. L.: Ecological consequences of variation in precipitation: separating short-versus long-term effects using satellite data, Global Ecology and Biogeography, 23, 358-370, 2014.

Johnstone, J. A., and Dawson, T. E.: Climatic context and ecological implications of summer fog decline in the coast redwood region, Proceedings of the National Academy of Sciences, 107, 4533-4538, 2010.

Keith, H., Mackey, B. G., and Lindenmayer, D. B.: Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests, Proceedings of the National Academy of Sciences, 106, 11635-11640, 2009.

Kellndorfer, J., Walker, W., LaPoint, E., Bishop, J., Cormier, T., Fiske, G., Hoppus, M., Kirsch, K., and Westfall, J.: NACP Aboveground Biomass and Carbon Baseline Data (NBCD 2000), U.S.A., 2000 Data set, ORNL DAAC, Oak Ridge, Tennessee, U.S.A. , 2012.

Krankina, O. N., DellaSala, D. A., Leonard, J., and Yatskov, M.: High-Biomass Forests of the Pacific Northwest: Who Manages Them and How Much is Protected?, Environmental Management, 54, 112-121, 2014.

Law, B. E., Thornton, P. E., Irvine, J., Anthoni, P. M., and Van Tuyl, S.: Carbon storage and fluxes in ponderosa pine forests at different developmental stages, Global Change Biology, 7, 755-777, 2001.

Law, B. E., Falge, E., Gu, L. V., Baldocchi, D. D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A. J., Falk, M., and Fuentes, J. D.: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, Agricultural and Forest Meteorology, 113, 97-120, 2002.

Law, B. E., Sun, O. J., Campbell, J., Van Tuyl, S., and Thornton, P. E.: Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, Global Change Biology, 9, 510-524, 2003.

Law, B. E.: Regional analysis of drought and heat impacts on forests: current and future science directions, Global Change Biology, 20, 3595-3599, 10.1111/gcb.12651, 2014.
Lévesque, M., Siegwolf, R., Saurer, M., Eilmann, B., and Rigling, A.: Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions, New Phytologist, 203, 94-109, 2014.
Major, J.: A climatic index to vascular plant activity, Ecology, 44, 485-498, 1963.
McCabe, G. J., Palecki, M. A., and Betancourt, J. L.: Pacific and Atlantic Ocean influences on multidecadal drought frequency in the United States, Proceedings of the National Academy of Sciences, 101, 4136-4141, 2004.
McDowell, N. G., Williams, A., Xu, C., Pockman, W., Dickman, L., Sevanto, S., Pangle, R., Limousin, J., Plaut, J., and Mackay, D.: Multi-scale predictions of massive conifer mortality due to chronic temperature rise, Nature Climate Change, 6, 295-300, 10.1038/nclimate2873, 2015.
Means, J. E., Hansen, H. A., Koerper, G. J., Alaback, P. B., and Klopsch, M. W.: Software for computing plant biomass--BIOPAK users guide, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 184, 1994.
Mitchell, K. E., Lohmann, D., Houser, P. R., Wood, E. F., Schaake, J. C., Robock, A., Cosgrove, B. A., Sheffield, J., Duan, Q., and Luo, L.: The multi-institution North American Land Data Assimilation System (NLDAS): Utilizing multiple GCIP products and partners in a continental distributed hydrological modeling system, Journal of Geophysical Research: Atmospheres, 109, 2004.
Mote, P. A., Snover, K., Capalbo, S., Eigenbrode, S. D., Glick, P., Littell, J., Raymondi, R., and Reeder, S.: Northwest, in: Climate Change Impacts in the United States: The Third National Climate Assessment, edited by: Melillo, J. M., Richmond, T. C. C., and Yohe, G. W., U.S. Global Change Research Program, Washington, DC, 487-513, 2014.
Myneni, R., Hoffman, S., Knyazikhin, Y., Privette, J., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., and Smith, G.: Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data, Remote sensing of environment, 83, 214-231, 2002.
Nakawatase, J. M., and Peterson, D. L.: Spatial variability in forest growth-climate relationships in the Olympic Mountains, Washington, Canadian journal of forest research, 36, 77-91, 2006.
Neeti, N., and Kennedy, R.: Comparison of national level biomass maps for conterminous US: understanding pattern and causes of differences, Carbon Balance and Management, 11, 19, 10.1186/s13021-016-0060-y, 2016.
Olson, J. S.: Energy storage and the balance of producers and decomposers in ecological systems, Ecology, 44, 322-331, 1963.
Pan, Y., Chen, J. M., Birdsey, R., McCullough, K., He, L., and Deng, F.: Age structure and disturbance legacy of North American forests, 2011.
Peñuelas, J., Canadell, J. G., and Ogaya, R.: Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, Global Ecology and Biogeography, 20, 597-608, 2011.
Peterman, W., Waring, R. H., Seager, T., and Pollock, W. L.: Soil properties affect pinyon pine–juniper response to drought, Ecohydrology, 6, 455-463, 2013.
R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, 2015.
Ruefenacht, B., Finco, M., Nelson, M., Czaplewski, R., Helmer, E., Blackard, J., Holden, G., Lister, A., Salajanu, D., and Weyermann, D.: Conterminous US and Alaska forest type mapping using forest inventory and analysis data, Photogramm. Eng. Remote Sens, 74, 1379-1388, 2008.
Ruehr, N., Law, B., Quandt, D., and Williams, M.: Effects of heat and drought on carbon and water dynamics in a regenerating semi-arid pine forest: a combined experimental and modeling approach, Biogeosciences, 11, 4139-4156, 2014.

Running, S. W.: Testing Forest-BGC Ecosystem Process Simulations Across a Climatic Gradient in Oregon, Ecological Applications, 4, 238-247, 1994.

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., and Hashimoto, H.: A continuous satellite-derived measure of global terrestrial primary production, BioScience, 54, 547-560, 2004.

Runyon, J., Waring, R., Goward, S., and Welles, J.: Environmental limits on net primary production and light-use efficiency across the Oregon transect, Ecological Applications, 4, 226-237, 1994.

Sanford, W. E., and Selnick, D. L.: Estimation of Evapotranspiration Across the Conterminous United States Using a Regression With Climate and Land-Cover Data1, JAWRA Journal of the American Water Resources Association, 49, 217-230, 2013.

Schroeder, P. E., McCandlish, B., Waring, R. H., and Perry, D. A.: The relationship of maximum canopy leaf area to forest growth in eastern Washington, Northwest Science, 56, 121-130, 1982.

Schuur, E. A.: Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation, Ecology, 84, 1165-1170, 2003.

Schwalm, C. R., Williams, C. A., Schaefer, K., Baldocchi, D., Black, T. A., Goldstein, A. H., Law, B. E., Oechel, W. C., and Scott, R. L.: Reduction in carbon uptake during turn of the century drought in western North America, Nature Geoscience, 5, 551-556, 2012.

Seager, R., and Vecchi, G. A.: Greenhouse warming and the 21st century hydroclimate of southwestern North America, Proceedings of the National Academy of Sciences, 107, 21277-21282, 2010.

Singh, D., Swain, D. L., Mankin, J. S., Horton, D. E., Thomas, L. N., Rajaratnam, B., and Diffenbaugh, N. S.: Recent amplification of the North American winter temperature dipole, Journal of Geophysical Research: Atmospheres, 2016.

Smith, J. E., Heath, L. S., Skog, K. E., and Birdsey, R. A.: Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States, USDA Forest Service General Technical Report NE-343, Newtown Square, PA, 222, 2006.

Soulé, P. T., and Knapp, P. A.: Analyses of intrinsic water-use efficiency indicate performance differences of ponderosa pine and Douglas-fir in response to CO2 enrichment, Journal of Biogeography, 42, 144-155, 2015.

Spies, T. A., Ripple, W. J., and Bradshaw, G.: Dynamics and pattern of a managed coniferous forest landscape in Oregon, Ecological Applications, 4, 555-568, 1994.

Thomas, C. K., Law, B. E., Irvine, J., Martin, J. G., Pettijohn, J. C., and Davis, K. J.: Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semiarid mature ponderosa pine forest in central Oregon, Journal of Geophysical Research: Biogeosciences (2005–2012), 114, 2009.

Van Tuyl, S., Law, B., Turner, D., and Gitelman, A.: Variability in net primary production and carbon storage in biomass across Oregon forests—an assessment integrating data from forest inventories, intensive sites, and remote sensing, Forest Ecology and Management, 209, 273-291, 2005.

Walsh, J., Wuebbles, D., Hayhoe, K., Kossin, J., Kunkel, K., Stephens, G., Thorne, P., Vose, R., Wehner, M., Willis, J., Anderson, D., Doney, S., Feely, R., Hennon, P., Kharin, V., Knutson, T., Landerer, F., Lenton, T., Kennedy, J., and Somerville, R.: Our Changing Climate, in: Climate Change Impacts in the United States: The Third National Climate Assessment, edited by: Melillo, J. M., Richmond, T. C., and Yohe, G. W., U.S. Global Change Research Program, 19-67, 2014.

Waring, R.: Estimating forest growth and efficiency in relation to canopy leaf area, Adv. Ecol. Res, 13, 327-354, 1983.

Waring, R. H., and Franklin, J. F.: Evergreen coniferous forests of the Pacific Northwest, Science, 204, 1380-1386, 1979.

Waring, R. H., and Running, S. W.: Forest Ecosystems: Analysis at Multiple Scales, 3rd ed., Elsevier Academic Press, Burlington, MA, 420 pp., 2007.

Webb, W. L., Lauenroth, W. K., Szarek, S. R., and Kinerson, R. S.: Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States, Ecology, 134-151, 1983.

Whittaker, R. H.: Estimation of net primary production of forest and shrub communities, Ecology, 42, 177-180, 1961.

Whittaker, R. H., and Niering, W. A.: Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient, Ecology, 56, 771-790, 1975.

Wickham, H., and Francois, R.: dplyr: A Grammar of Data Manipulation, R package version 0.4.2, http://CRAN.R-project.org/package=dplyr, 2015.

Wilcox, K. R., Blair, J. M., Smith, M. D., and Knapp, A. K.: Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions?, Ecology, 97, 561-568, 2016.

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., and Grissino-Mayer, H. D.: Temperature as a potent driver of regional forest drought stress and tree mortality, Nature Climate Change, 3, 292-297, 2012.

Williams, A. P., Seager, R., Macalady, A. K., Berkelhammer, M., Crimmins, M. A., Swetnam, T. W., Trugman, A. T., Buenning, N., Noone, D., and McDowell, N. G.: Correlations between components of the water balance and burned area reveal new insights for predicting forest fire area in the southwest United States, International Journal of Wildland Fire, 24, 14-26, 10.1071/WF14023, 2014.

Williams, M., Rastetter, E., Fernandes, D., Goulden, M., Wofsy, S., Shaver, G., Melillo, J., Munger, J., Fan, S. M., and Nadelhoffer, K.: Modelling the soil-plant-atmosphere continuum in a Quercus–Acer stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties, Plant, Cell & Environment, 19, 911-927, 1996.

Williams, M.: Deforesting the Earth: From Prehistory to Global Crisis, University of Chicago Press, Chicago, USA, 543 pp., 2006.

Wilson, B. T., Woodall, C., and Griffith, D.: Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage, Carbon balance and management, 8, 1, 2013.

Yan, K., Park, T., Yan, G., Liu, Z., Yang, B., Chen, C., Nemani, R. R., Knyazikhin, Y., and Myneni, R. B.: Evaluation of MODIS LAI/FPAR Product Collection 6. Part 2: Validation and Intercomparison, Remote Sensing, 8, 460, 2016.

Yang, Y., Fang, J., Ma, W., and Wang, W.: Relationship between variability in aboveground net primary production and precipitation in global grasslands, Geophysical Research Letters, 35, 2008.

Zhao, M., Running, S., Heinsch, F. A., and Nemani, R.: MODIS-derived terrestrial primary production, in: Land Remote Sensing and Global Environmental Change: NASA's Earth Observing System and the Science of ASTER and MODIS, edited by: Ramachandra, B., Justice, C. O., and Abrams, M. J., Springer, New York, 635-660, 2010.

Zotarelli, L., Dukes, M. D., Romero, C. C., Migliaccio, K. W., and Morgan, K. T.: Step by step calculation of the Penman-Monteith Evapotranspiration (FAO-56 Method), Institute of Food and Agricultural Sciences. University of Florida, 2010.

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.

Formatted: Font: Not Bold

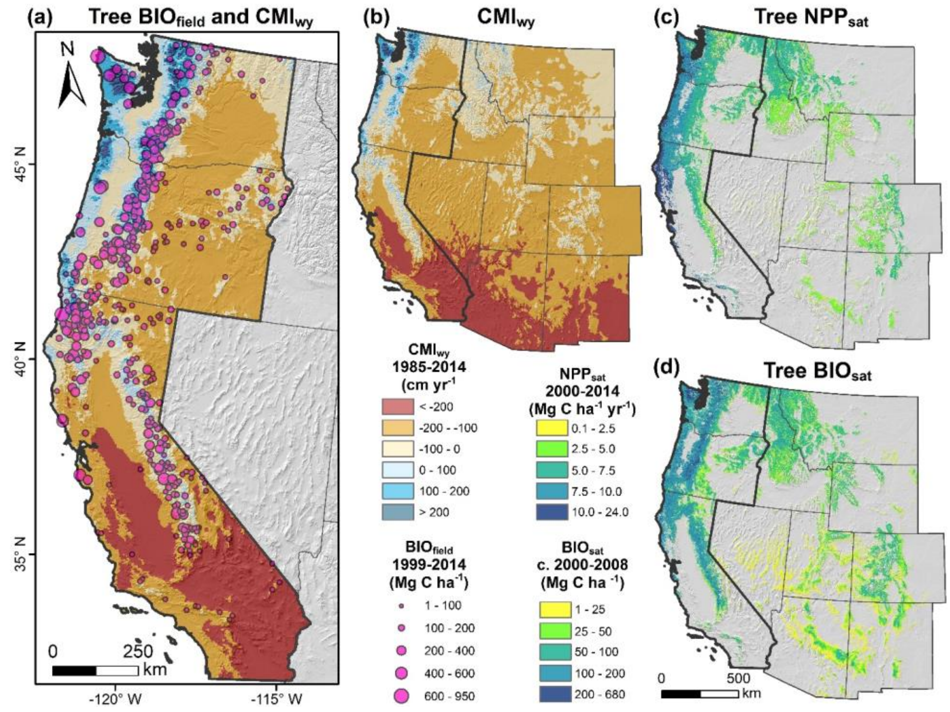
Domain	Variable	Units	Time span	Mean (SD)	Range
WAORCA	NPP_{field}	Mg C ha^{-1} yr^{-1}	2001-2006	4.3 (2.5)	0.6 – 20.9
	BIO_{field}	Mg C ha^{-1}	2001-2006	158 (135)	2 – 947

	$\text{CRT}_{\text{field}}$	year	2001-2006	33 (19)	2 – 137
Western US	NPP_{sat}	Mg C ha^{-1} yr^{-1}	2000-2014	5.3 (2.0)	0.1 – 227
	BIO_{sat}	Mg C ha^{-1}	2000-2008	83 (54)	2 – 669
	CRT_{sat}	year	2000-2008	15 (9)	2 – 1390

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 ($\text{CMI}_{\overline{\text{wy}}}$; 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 $\text{CMI}_{\overline{\text{wy}}}$ 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~~Spearman's correlation (r_s) between $\text{CMI}_{\overline{\text{wy}}}$ and the median forest characteristic computed at 10 cm yr^{-1} $\text{CMI}_{\overline{\text{wy}}}$ intervals. All correlations were statistically significant at $\alpha < 0.001$.

Formatted: Font: Not Bold

Domain	Variable	Units	Median of…		Change…		$\mathrm{CMI}_{\overline{wy}}$ cor.
			Driest 5%	Wettest 95%	Abs.	%	r_s
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


(a) Tree BIO$_{field}$ and CMI$_{wy}$
N
45° N
40° N
35° N
0 250 km
-120° W
-115° W
(b) CMI$_{wy}$
(c) Tree NPP$_{sat}$
(d) Tree BIO$_{sat}$
CMI$_{wy}$ 1985-2014 (cm yr^{-1})
< -200
-200 - -100
-100 - 0
0 - 100
100 - 200
> 200
NPP$_{sat}$ 2000-2014 (Mg C ha^{-1} yr^{-1})
0.1 - 2.5
2.5 - 5.0
5.0 - 7.5
7.5 - 10.0
10.0 - 24.0
BIO$_{field}$ 1999-2014 (Mg C ha^{-1})
1 - 100
100 - 200
200 - 400
400 - 600
600 - 950
BIO$_{sat}$ c. 2000-2008 (Mg C ha^{-1})
1 - 25
25 - 50
50 - 100
100 - 200
200 - 680
0 500 km

Figures

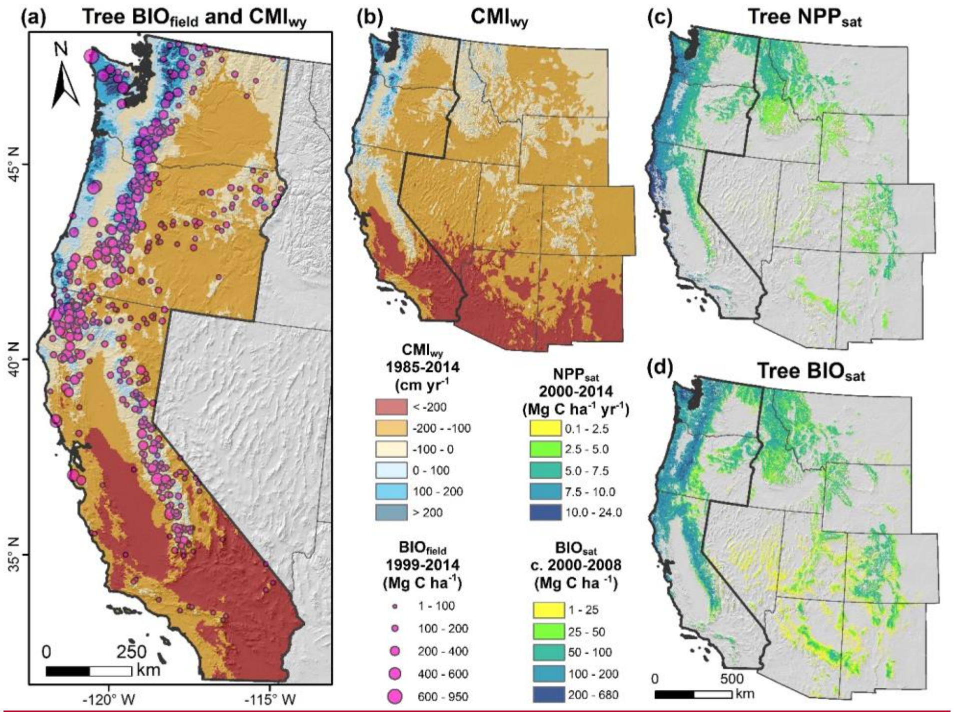
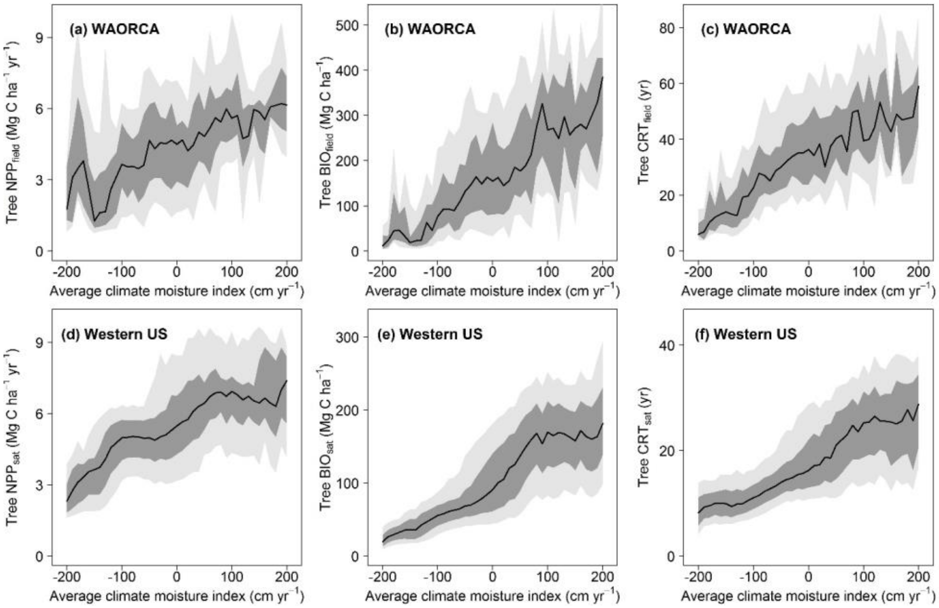


Figure 1. Mean climatic moisture index ($CMI_{\overline{wy}}$; cm yr^{-1}), tree net primary productivity (NPP; Mg C ha^{-1} yr^{-1}), and live tree biomass (BIO; Mg C ha^{-1}) in the western US. (a) BIO derived from field measurements (BIO_{field}) at mature sites (>100 years) in WAORCA. For visual clarity only 20% of the 1,953 sites are depicted. (b) $CMI_{\overline{wy}}$ 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}).

Formatted: Font: Not Bold

Formatted: Normal, Line spacing: Double


(a) WAORCA
Tree NPP$_{field}$ (Mg C ha^{-1} yr^{-1})
0
3
6
9
(b) WAORCA
Tree BIO$_{field}$ (Mg C ha^{-1})
0
100
200
300
400
500
(c) WAORCA
Tree CRT$_{field}$ (yr)
0
20
40
60
80
(d) Western US
Tree NPP$_{sat}$ (Mg C ha^{-1} yr^{-1})
0
3
6
9
(e) Western US
Tree BIO$_{sat}$ (Mg C ha^{-1})
0
100
200
300
(f) Western US
Tree CRT$_{sat}$ (yr)
0
20
40
-200
-100
0
100
200
Average climate moisture index (cm yr^{-1})

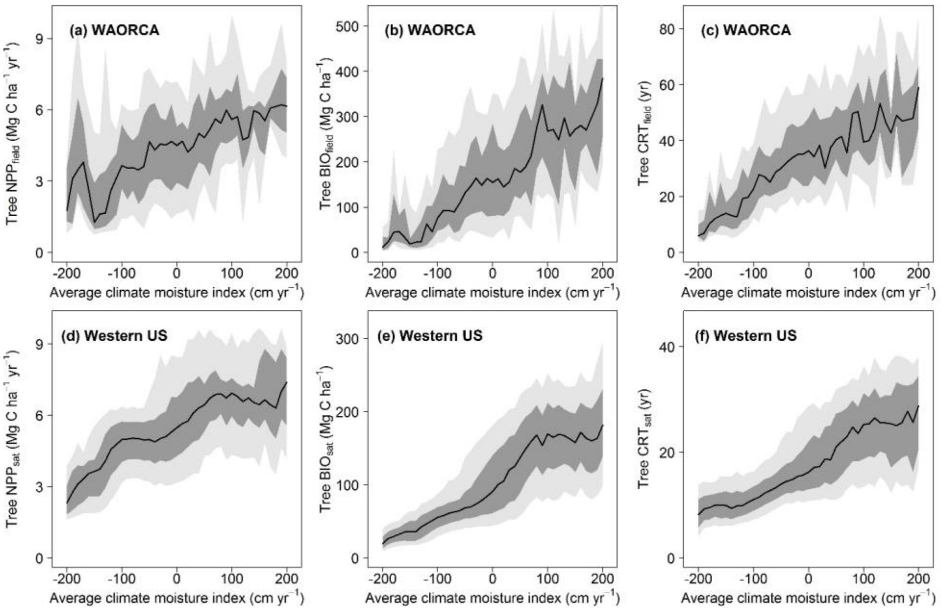


Figure 2. Tree net primary productivity (NPP; Mg C ha^{-1} yr^{-1}), live biomass (BIO; Mg C ha^{-1}), and carbon residence time (CRT; years) increased with increasing ~~climatic~~ water availability across both WAORCA (a-c) and the broader western US (d-f). Forest characteristics were derived from field 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$_{sat}$ was characterized using MODIS data averaged ~~annual~~annually from 2000 to 2014. BIO$_{sat}$ 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 ($\mathrm{CMI}_{\overline{wy}}$). The region was partitioned into 10 cm yr^{-1} (non-overlapping) $\mathrm{CMI}_{\overline{wy}}$ bins, pixels/plots were allocated to

Formatted: Font: Not Bold

bins, and then forest characteristics were summarized within each bin. In each panel, the bold line 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).

Formatted: Normal, Line spacing: Double