



Assessing intra- and inter-regional climate effects on Douglas-fir biomass dynamics in Oregon and Washington, USA



David M. Bell ^{*}, Andrew N. Gray

USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, United States

ARTICLE INFO

Article history:

Received 25 April 2016

Received in revised form 14 July 2016

Accepted 18 July 2016

Available online 27 August 2016

Keywords:

Climate

Douglas-fir

Forest inventory

Forest structure

Forest succession

Pacific Northwest

Pseudotsuga menziesii

ABSTRACT

While ecological succession shapes contemporary forest structure and dynamics, other factors like forest structure (dense vs. sparse canopies) and climate may alter structural trajectories. To assess potential sources of variation in structural trajectories, we examined proportional biomass change for a regionally dominant tree species, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), across vegetation zones representing broad gradients in precipitation and temperature with 3510 forest inventory plots in Oregon and Washington, USA. We found that *P. menziesii* biomass change decreased with *P. menziesii* biomass stocks and increased with *P. menziesii* density, remaining positive in older stands only in the wet and warm vegetation zone. Within two of the vegetation zones, biomass change was greatest in warm and wet environments. In dry vegetation zones, positive *P. menziesii* biomass change responses to initial canopy cover and canopy cover change (i.e., increases with cover loss and decreases with cover gain) indicated shifts in forest structure. Variation in *P. menziesii* biomass dynamics within and between vegetation zones imply multi-scale climatic controls on forest structural trajectories for *P. menziesii* and highlight the potential for continued atmospheric carbon sequestration in warm and wet forests of the Pacific Northwest for both young and old forests, given that future climatic conditions support similar forest dynamics.

Published by Elsevier B.V.

1. Introduction

Whether through growth, mortality, or recruitment, forests are constantly changing, defining one of the key challenges in forest ecosystem ecology: understanding forest biomass dynamics throughout forest development. Models of forest succession provide an appealing conceptual framework for understanding forest dynamics and biomass change through time (e.g.; Odum, 1969), but agreement on models and mechanisms has eluded ecologists (Pickett et al., 1987; Taylor et al., 2009). In addition, the effects of density-dependent mechanisms (Connell, 1971; Janzen, 1970), resource availability (Harpole et al., 2011), and disturbance (Connell and Slatyer, 1977) are major determinants of plant succession, and thus vegetation structural development. The strength and effect of such mechanisms will vary by species, in some cases dwarfing the impacts of time upon which successional theory is at least implicitly based (Chen and Taylor, 2012). Geographic variation in tree species responses to successional drivers must be

understood to improve our understanding of biomass change dynamics.

The successional role of some species differs in different vegetation types, possibly due to competition with other species in the community or species vigor and tolerance in different climatic and edaphic conditions (Anderson-Teixeira et al., 2013; Daubenmire, 1966). Geographic distributions of shade tolerance roughly map to moisture gradients, with the abundance of shade-tolerant species being positively correlated with precipitation and negatively correlated with temperature (Lienard et al., 2015) with shade-tolerant species often defining climax vegetation types in many forest ecosystems (e.g.; Franklin and Dyrness, 1973). When disturbances are infrequent, shade-tolerant, late-successional tree species slowly take the place of shade-intolerant, early-successional species over the course of forest succession (Oliver, 1981). However, the consequences of an individual species' shade tolerance on its growth and survival depend on the plant community with which that species must compete (e.g.; Nagel et al., 2013). The change in species abundance or biomass throughout forest development, hereafter structural trajectories, will depend on many factors, including other forest structure characteristics (e.g., open vs. closed canopy) and climatic controls on ecosystem function (Reilly and Spies, 2015).

^{*} Corresponding author at: 3200 SW Jefferson Way, Corvallis, OR 97331, United States.

E-mail addresses: dmbell@fs.fed.us (D.M. Bell), agray01@fs.fed.us (A.N. Gray).

In this study, we assessed biomass responses of a regionally dominant tree species, *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), to differing structural and environmental conditions across four vegetation zones in Oregon and Washington, USA (hereafter, the Pacific Northwest). Specifically, we examined the responses of proportional *P. menziesii* biomass change to structural status, forest canopy status, and climate across an elevational and longitudinal gradient in the Pacific Northwest. Our objective was to assess the consistency (i.e., equivalence between vegetation zones) and conditionality (i.e., interaction effects) of biomass change responses in the dominant species, *P. menziesii*, across the region using repeated measurements of 3510 forest inventory plots. We hypothesized that *P. menziesii* biomass change will decline as forest development progresses across all vegetation zones, but that key transitions in ecosystem behavior, such as the transition from positive to negative biomass change, will differ substantially.

2. Materials and methods

2.1. Study region and forest inventory data

Our study region covered the 9.1 million ha of forested federal land administered by the Pacific Northwest (PNW) Region of the National Forest System (NFS), located in the Pacific Northwest (Fig. 1). For the purposes of this study, we chose four potential (“climax”) vegetation zones as classified by field crews using local guides (Hall, 1998): *Abies amabilis* (Pacific silver fir) zone (ABAM), *Abies concolor* (white fir) and *Abies grandis* (grand fir) zones combined (ABCOGR), *P. menziesii* zone (PSME), and *Tsuga heterophylla* (western hemlock) and *Picea sitchensis* (Sitka spruce) zones combined (TSHEPISI). These four vegetation zones were chosen to represent the elevational gradient controlling temperature (i.e., the cooler high-elevation subalpine forests vs. the warmer low-elevation montane forests) and a latitudinal gradient controlling moisture (i.e., the wetter western flank of the Cascade Mountains vs. the drier eastern flank of the Cascade Mountains). While there is substantial overlap between vegetation zones in climate space, examination of the first two components of a principal components analysis of 14 temperature and precipitation variables (*sensu*; Lintz et al., 2013) support our use of these vegetation zones as proxies for broad temperature and moisture gradients (Fig. A.1). The ABAM zone is generally located at middle elevations (mean = 1140 m in our dataset) west of the Cascade Mountain crest, has mean annual temperature and precipitation equal to 5.8 °C (4.6–6.9 °C for 68% percentile interval) and 2360 mm (1877–2842 mm for 68% percentile interval), and is dominated by *A. amabilis*, *P. menziesii*, and *T. heterophylla*, with smaller components of *Abies procera* (noble fir), *Thuja plicata* (western red-cedar) and *Tsuga mertensiana* (mountain hemlock). The ABCOGR zone is generally located at high elevations (mean = 1480 m) east of the Cascade crest, has mean annual temperature and precipitation equal to 5.5 °C (4.0–6.9 °C for 68% percentile interval) and 977 mm (626–1411 mm for 68% percentile interval), and is dominated by *A. concolor*, *A. grandis*, *Pinus ponderosa* (ponderosa pine), and *P. menziesii*, with smaller components *Larix occidentalis* (western larch) and *Pinus contorta* (lodgepole pine). The PSME zone is generally located at middle elevations (mean = 1200 m) east of the Cascade crest, has mean annual temperature and precipitation equal to 6.2 °C (4.4–8.4 °C for 68% percentile interval) and 895 mm (555–1304 mm for 68% percentile interval), and is dominated by *P. ponderosa* and *P. menziesii*. The TSHEPISI zone is generally located at low elevations (mean = 750 m) west of the Cascade crest, has mean annual temperature and precipitation equal to 7.9 °C

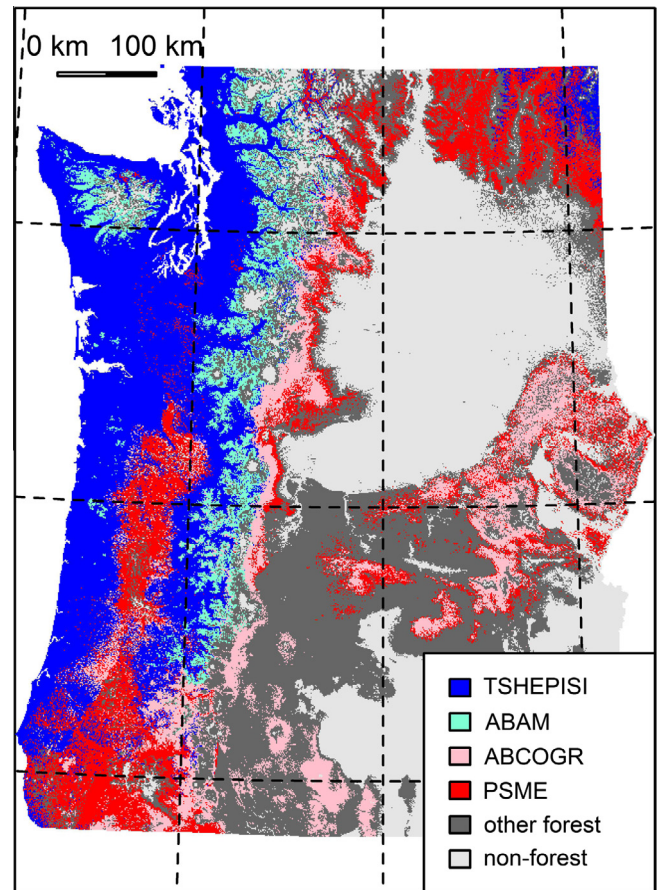


Fig. 1. Map of vegetation zones for study region. ABAM zone ($n = 330$); ABCOGR zone ($n = 869$); PSME zone ($n = 948$); TSHEPISI zone ($n = 1363$).

(6.2–10.0 °C for 68% percentile interval) and 2006 mm (1415–2528 mm for 68% percentile interval), and is dominated by *P. menziesii* and *T. heterophylla*, with smaller components *Alnus rubra* (red alder) and *T. plicata*.

Our study was based on extensive inventory of plots measured for change on NFS lands in the PNW Region using a probability-based sample design (Max et al., 1996). Although change data for private and state lands also exist in the region, intensive management of those lands results in the majority of stands being in the earliest forest development stages (Gray et al., 2014). Plots were established using the Current Vegetation Survey (CVS) design (Max et al., 1996) between 1993 and 1997 (“time 1”) and remeasured between 1997 and 2007 (“time 2”) in four spatially- and temporally-balanced panels. The CVS plot remeasurement period ranged from 1 to 14 years with a mean of 7.1 years. To avoid high sample errors associated with estimating annual rates of change from short remeasurement periods on small numbers of plots, we only used plots from the last three panels, which were remeasured more than 2 years after establishment. The same grid of points was also measured with the nationally-standardized Forest Inventory and Analysis (FIA) design starting in 2001 (Bechtold and Patterson, 2005); we applied the FIA land classification distinguishing forest from non-forest to the CVS data used in this study. We selected those CVS plots that (1) were associated with the four vegetation zones (Fig. 1), (2) had *P. menziesii* as an important component of the stand (i.e., >10% of the biomass and >10 trees ha⁻¹), (3) did not experience fire, harvesting, or other stand replacing disturbance during the measurement interval, and (4) were at least

Table 1

Description of response and predictor variables by region.

Variable type	Variable	ABAM cool, wet	ABCOGR cool, dry	TSHEPISI warm, wet	PSME warm, dry
Response	Proportional biomass change Y_i ($\text{Mg Mg}^{-1} \text{ yr}^{-1}$)	−0.15 to 0.26	−0.24 to 0.22	−0.14 to 0.19	−0.12 to 0.15
Successional development	Log tree biomass B_i ($\ln[\text{Mg ha}^{-1}]$)	0.73–6.26	0.28–6.39	1.18–6.39	0.47–6.00
	Log tree density D_i ($\ln[\text{trees ha}^{-1}]$)	2.31–5.89	2.31–6.13	2.30–6.55	2.31–6.38
Canopy status	Canopy cover C_i (%)	33–98	9–94	19–9	10–95
	Canopy cover change c_i ($\% \text{ yr}^{-1}$)	−2.6 to 3.6	−2.6 to 3.1	−3.0 to 3.5	−2.8 to 2.8
Climate	Temperature index (PCA Axis 1) $P_{1,i}$	−2.6 to 5.9	−4.5 to 5.2	−4.1 to 7.4	−5.9 to 7.6
	Precipitation index (PCA Axis 2) $P_{2,i}$	−1.9 to 4.9	−4.1 to 3.3	−4.2 to 4.3	−5.7 to 3.7

20 years of age. There were 3510 CVS plots within NFS lands that had forested conditions measured 3 or more years apart and meeting our plot selection criteria. Because the CVS plots were located only on NFS lands, our sample is likely biased toward older forests characteristic of public lands in the region, not private industrial lands dominant in some areas, such as coastal Oregon and Washington.

During each measurement event, crews measured live and standing dead trees for different size classes (2.5–7.6 cm, 12.7–33.0 cm, and >33 cm diameter at breast height—DBH) on five subplots of varying size (0.004, 0.020, and 0.076 ha, respectively). Seedlings (<2.5 cm DBH and >15 cm height) were tallied by species on the smallest subplot. Large trees (>76 cm DBH east of the Cascade crest or >122 cm west of the Cascade crest) were measured on the full 1-ha plot. To assess species-specific variation in biomass change among vegetation zones, we estimated total live-tree biomass per hectare for *P. menziesii* and all species combined for each plot during each measurement event based on plot data and established carbon estimation methods (described in Gray and Whittier, 2014). Stand age was estimated by FIA crews from the ages of trees in the dominant size class on the plot, back-calculated to the time of the first CVS measurement. Because no direct measurements of canopy cover were available, live tree canopy cover on each plot was estimated based on the Landsat-based gradient nearest neighbor vegetation maps (Ohmann and Gregory, 2002; Ohmann et al., 2012) and was estimated as the mean of the nine 30-m pixels co-located with the CVS plot extracted during the years of measurement.

In this study, we examined three potential drivers of *P. menziesii* biomass change: structural status, forest canopy status, and climate. We chose to examine proportion *P. menziesii* biomass change because data exploration indicated stronger correlations. Given that *P. menziesii* quickly colonizes disturbed sites, followed by a period of increasing biomass and decreasing tree density across the Pacific Northwest (Franklin and Dyrness, 1973; Franklin et al., 2002; Harmon and Pabst, 2015), especially outside of the dryland forests like ponderosa pine and juniper woodlands (Reilly and Spies, 2015), we selected *P. menziesii* tree biomass and tree densities to represent structural status. Forest canopy status was characterized by initial forest canopy cover and the change in canopy cover during the measurement interval. Increases in canopy cover are assumed to indicate gap-filling or tree encroachment while decreases in canopy cover are assumed to represent tree mortality. To represent geographic variation in average climate conditions, we extracted 14 variables representing the precipitation and temperature regimes of the Pacific Northwest from the Daymet grids of the western United States (Thornton et al., 1997; Table A.1). We performed a principal components analysis (PCA) based on the correlation coefficients among the climate data (*sensu*; Lintz et al., 2013). The first two axes of the PCA explained 85% of the variation and were generally related to temperature and precipitation (Table A.1), which are major correlates with mean annual increment in forests of the Pacific Northwest (Latta et al., 2010).

2.2. Statistical analyses

To examine the response of *P. menziesii* biomass change to forest structural status, forest canopy status, and climate, we modeled the annual proportional change in *P. menziesii* biomass (Y_i) at plot i as a function of log *P. menziesii* tree biomass (B_i), log *P. menziesii* tree density (D_i), canopy cover (C_i), change in canopy cover between measurements (c_i), and the first two axes of a PCA of climate variables representing geographic variation in temperature ($P_{1,i}$) and precipitation ($P_{2,i}$) (Table 1). Note that *P. menziesii* tree biomass and tree density were log-transformed to improve model performance. We incorporated quadratic and bivariate interaction terms to allow for curvilinear and conditional responses to covariates. We assumed that Y_i was distributed normally with mean $x_i\beta$ and variance σ^2 , where x_i was a length K vector of covariates for plot i and β was a length K vector of parameters. In addition, we modeled the inclusion of a given covariate in the regression model using indicator variables I_k where $\beta_k = I_k B_k$ such that $\beta_k = 0$ when $I_k = 0$ and $\beta_k = B_k$ when $I_k = 1$ (Kuo and Mallick, 1998; O'Hara and Sillanpää, 2009). We assumed that I_k was distributed as a Bernoulli with some inclusion probability θ_k . Each region was fit separately using JAGS implemented in an R statistical environment (Plummer, 2014, 2003; R Development Core Team, 2011).

For the purposes of prediction, it has been suggested that the median probability model is best (i.e., the model where all parameters have a marginal probability of inclusion greater than 0.5; Barbieri and Berger, 2016). For the purposes of examining a “best” model, we choose a stricter probability threshold of 0.9. This stricter marginal probability threshold was chosen to increase the parsimony of the model and reduce the chances that relatively high sample sizes (over 1000 plots for some regions) would allow us to identify statistically significant effects where there were no biologically significant effects. Model fit was assessed by examining the root mean square deviations and the correlation between observed and predicted proportional changes in *P. menziesii* biomass.

3. Results

With the exception of log *P. menziesii* tree biomass, the inclusion of other parameters differed among vegetation zones (Fig. 2, Table B.1). The majority of the 24 main effect and vegetation zone combinations (6 main effects $\times$ 4 zones) were included, based on marginal probabilities greater than 0.5 or 0.9 (15 of 24). For all but one zone, probabilities of inclusion were greater than 0.9 for log *P. menziesii* tree density (ABCOGR, ABAM, and TSHEPISI). Probabilities of inclusion were greater than 0.9 in the warm zones for canopy cover (TSHEPISI and PSME), in the dry zones for canopy cover change (ABCOGR and PSME), and in the warm and wet (TSHEPISI) and cool and dry (ABCOGR) zones for both climate variables. Inclusion probabilities for quadratic terms indicated that the effect of log *P. menziesii* tree biomass was curvilinear for all zones. Inclusion probabilities for quadratic terms of canopy cover and climate variables were also greater than 0.9 for TSHEPISI.

intercept	1	1	1	1
log DF biomass (B_i)	1	1	1	1
log DF density (D_i)	1	1	1	0.02
Canopy cover (C_i)	0.02	0.26	1	1
Canopy cover Δ (c_i)	0.39	1	0.03	1
Temperature Index ($P_{1,i}$)	0	1	1	0.13
Precipitation Index ($P_{2,i}$)	0	0.98	1	0
B_i by B_i	1	1	1	0.99
B_i by D_i	1	0.9	1	0
B_i by C_i	0	0.09	1	0.56
B_i by c_i	0.29	0.16	0	1
B_i by $P_{1,i}$	0	1	0.18	0.01
B_i by $P_{2,i}$	0	0.92	0.11	0
C_i by C_i	0	0.13	1	0.09
$P_{1,i}$ by $P_{1,i}$	0	0.8	1	0.01
$P_{1,i}$ by $P_{2,i}$	0	0.66	1	0
$P_{2,i}$ by $P_{2,i}$	0	0.13	0.99	0
Regional Climate	cool wet	cool dry	warm wet	warm dry
Vegetation Zone	ABAM	ABCOGR	TSHEPISI	PSME

Fig. 2. Marginal probability of inclusion for the effects of predictor variables, as well as quadratic and interaction terms. Variables where marginal probabilities of inclusion never exceeded 0.9 for any region were excluded.

Inclusion probabilities indicated that few interaction terms should be included in the models, with only eight total interactions (out of a possible 60 = 15 interaction effects $\times$ 4 zones) had marginal probabilities of inclusion greater than 0.9 (Table B.1). Most of these interactions (seven of eight) involved log *P. menziesii* tree biomass interactions with other variables.

Models incorporating only those parameters for which the marginal probability of inclusion was greater than 0.9 performed well. Root mean squared deviations ranged from 0.021 to 0.030 (Table 2). Squared Pearson correlation coefficients between observed and predicted annual proportional biomass change ranged from 0.16 for ABCOGR to 0.53 for ABAM (Table 2).

Proportional changes in *P. menziesii* biomass decreased with tree biomass in all zones, but the magnitudes of biomass change tended to be greater in warm zones and in wet zones (Fig. 3a). In contrast, increasing proportional biomass change with tree densities observed in three of four zones (ABAM, ABCOGR, and TSHEPISI) did not differ from each other (Fig. 3b). Proportional biomass change increased with canopy cover in the warm and wet zone (PSME) and canopy cover change in the dry zones (ABCOGR and PSME), but not in the wet zones (ABAM and TSHEPISI) (Fig. 3c and d). TSHEPISI even exhibited a decline in biomass change with canopy cover. Proportional biomass change increased with the temperature and precipitation indices in the warm and wet zone (TSHEPISI) and the cool and dry zone (ABAM) (Fig. 3e and f).

Table 2

Root mean squared deviation (mean and 95% credible intervals [95% CI]) and squared Pearson correlation coefficients for models with parameters having a marginal probability of inclusion greater than 0.9.

Veg. zone	Root mean square deviation		Squared Pearson correlation coefficient	
	Mean	95% CI	Mean	95% CI
ABAM	0.027	(0.025–0.029)	0.531	(0.519–0.534)
ABCOGR	0.030	(0.029–0.032)	0.159	(0.138–0.168)
TSHEPISI	0.021	(0.020–0.022)	0.489	(0.483–0.491)
PSME	0.025	(0.024–0.026)	0.227	(0.210–0.232)

Similarly, interaction effects also varied by zone. In the wet and warm zone (TSHEPISI), proportional *P. menziesii* biomass change was highest in forests where low initial biomass co-occurred with high tree density and low canopy cover characteristic of young forest stands (Fig. 4a and b). A weak interaction between the temperature and precipitation indices was also observed for TSHEPISI (Fig. B.1). In the warm and dry zone (PSME), high *P. menziesii* biomass change increased as both initial biomass declined and canopy cover change increased (Fig. 4c). In the cool and dry zone (ABCOGR), the greatest biomass change was observed in locations with high temperature or precipitation indices and low initial biomass (Fig. 4d and e). In the cool and wet zone (ABAM), biomass change was greatest where there were either few large or were many small *P. menziesii* (Fig. 4f).

4. Discussion

Pseudotsuga menziesii biomass change across forests of the Pacific Northwest highlights intra- and inter-regional variation in the successional role of *P. menziesii* as a species and the contrasting consequences for forest biomass dynamics. As expected under traditional forest succession models, young stands (i.e., low biomass and high density of *P. menziesii*) added *P. menziesii* biomass at the greatest rate relative to initial biomass, with biomass change decreasing as initial biomass increased and tree density decreased (Fig. 3a and b). However, comparisons between vegetation zones imply inter-regional variation in the biomass dynamics. Results for dry forests were consistent with this expectation (means were negative, but not significantly so). However, *P. menziesii* biomass in wet forests was not only increasing in early-developmental stands (low biomass and high density of *P. menziesii*), but also in late-developmental stands defined by few, large trees, especially for the warmer zone (TSHEPISI; Figs. 3a and 4a). Despite being dominant early in forest development, *P. menziesii* shows no clear trend toward declining biomass that would be expected if it were being replaced by more shade-tolerant species. These results support our hypothesis that general biomass change patterns would be similar across vegetation zones, but that transitions from positive to neutral or negative biomass change would differ regionally. Thus, *P. menziesii* appears to act as an early-seral species in drier portions and a climax species in wetter portions of the Pacific Northwest. Such high intraspecific variation in species trajectories may contribute to the apparently slow convergence of Pacific Northwest forests toward shade-tolerant communities (Lienard et al., 2015). Furthermore, the interactions between initial biomass and other covariates in all vegetation zones (Fig. 4) indicate differences in how local environment mediate forest structural trajectories.

Across the range of observed *P. menziesii* tree biomass, biomass change was greater in wet vs. dry regions and warm vs. cool regions (Fig. 3a), indicating contrasting impacts of moisture and temperature limitations on tree growth and survival processes at the regional scale. Moisture and temperature limitations on growth have been observed for *P. menziesii* (Williams et al.,

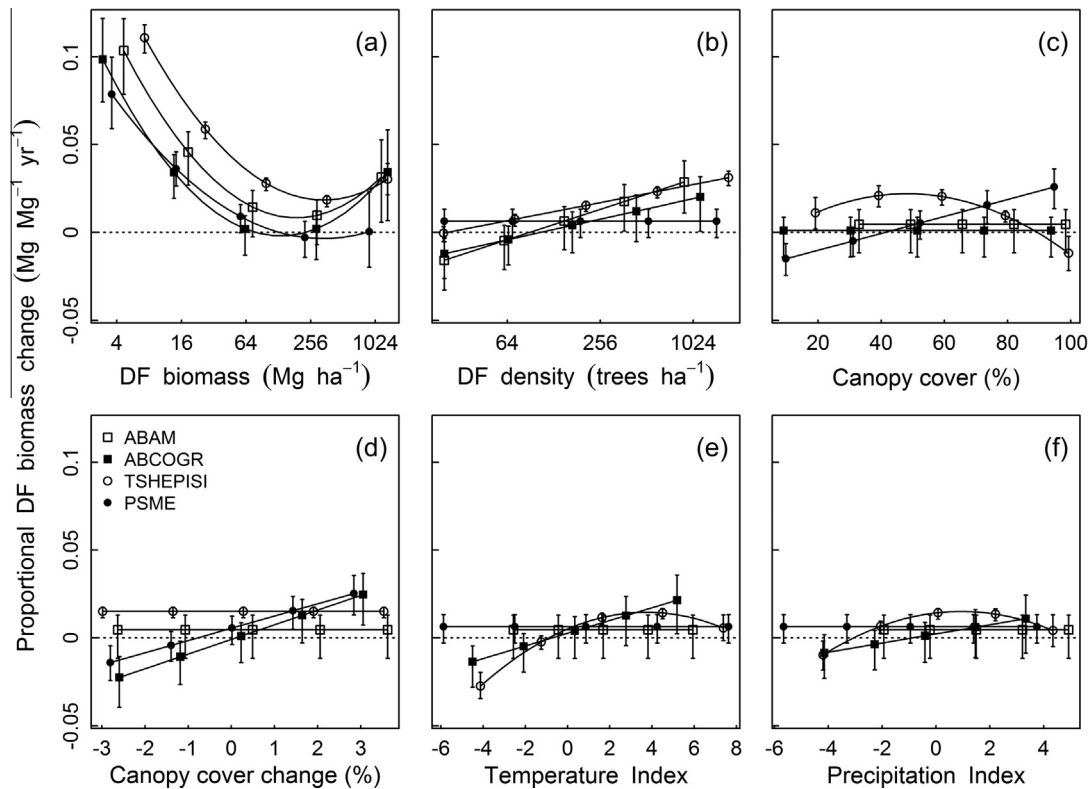


Fig. 3. Predicted proportional Douglas-fir (DF) biomass change as a function of (a) DF biomass, (b) DF tree density, (c) canopy cover, (d) canopy cover change, (e) temperature index, and (f) precipitation index. For each panel, all variables but the variable of interest are held constant at their mean observed values.

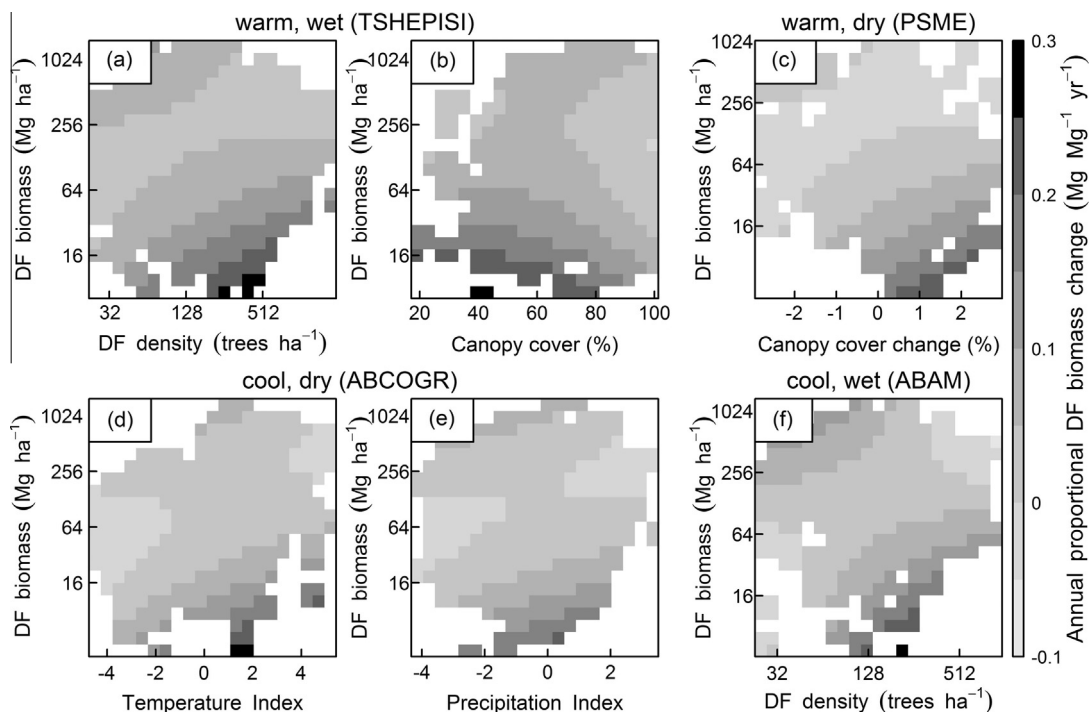


Fig. 4. Proportional DF biomass change responses to covariation in two covariates for (a and b) the warm and wet TSHEPISI, (c) the warm and dry PSME, (d and e) the cool and dry ABCOGR, (f) and the cool and wet ABAM vegetation zones. Only interactions with marginal probabilities of inclusion greater than 0.90 are presented (Fig. 2). For each panel, all variables but the variable of interest are held constant at their mean observed values. White areas indicate no observations for a given portion of the covariate space.

2012), but may not be expressed consistently over the species' range (Chen et al., 2010; Littell et al., 2008). Our results support the idea that low precipitation and low temperature jointly

constrain regional patterns of *P. menziesii* biomass change in Oregon and Washington. In contrast, increasingly common drought-induced mortality in western North America associated with major

biomass loss (Allen et al., 2010; van Mantgem et al., 2009) are often associated with high temperatures (Allen et al., 2015). Given that canopy cover in our study region generally declines as we move into warmer and drier forests, decreasing biomass change with declining canopy cover (Fig. 3c) may represent intra-regional variation in mortality associated with hot droughts. In addition, by censoring plots experiencing major disturbances, some of which were related to climatic stress (e.g., insect and disease events), we may have removed an important component of the drought-induced mortality signal.

Variation in proportional biomass change within vegetation zones highlights intra-regional variation in structural patterns for *P. menziesii*. Both the warm and wet (TSHEPISI) and cool and dry (ABCOGR) vegetation zones exhibited increasing biomass change with temperature and precipitation (Fig. 3e and f). Our results imply both within and between zone climatic influences on the biomass dynamics of a regionally dominant species. Alternatively, genetic variation, such as the known geographic clines for some coniferous species in western North America, could greatly impact variation in species responses to drivers of biomass change (Rehfeldt et al., 2014). Since our data spanned a single measurement interval (up to 14 years), geospatial drivers of biomass dynamics and their consequences are difficult to explore. For example, geographic relationships between biomass dynamics and climate may not represent responses to climate change (Ibáñez et al., 2006). Regardless of the driver of the variation, such results draw into question assessments relying on mean species traits as such variation may have substantial impacts on ecosystem modeling efforts (Moran et al., 2016).

Given that mean annual increment is related to temperature and moisture gradients within the Pacific Northwest (Latta et al., 2010), the presence of within region climate effects was not surprising, but the restriction of the intra-regional climate effects to the TSHEPISI and ABCOGR was unexpected. As the inclusion of intra-regional climate variables did not appear related to the broader climatic gradients represented by the vegetation zones (i.e., stronger effect in wet vs. dry or warm vs. wet vegetation zones), our results may indicate that other non-climatic factors are necessary to set the stage for intra-regional climatic controls. For example, the amplified effects of climate in the ABCOGR zone when initial *P. menziesii* biomass was low (Fig. 4d and e) indicate that climate effects depend on disturbance history. Alternatively, biases in the CVS plot data (no data on highly productive private timber lands) or smaller sample sizes for some regions (330 plots in ABAM compared to 1363 plots in TSHEPISI) may alter our capacity to detect intra-regional climate effects.

The effects of forest canopy status on *P. menziesii* biomass change reflect potential shifts in community and ecosystem structure, especially in the dry vegetation zones. A positive relationship between biomass change and canopy cover as well as canopy cover change in the dry zones (PSME; Fig. 3c and d) could reflect declines in *P. menziesii* in more open habitats generally associated with marginal forest habitat and increasing dominance in closed-canopy forests. Recent increases in the importance of insect attack in dry vegetation zones may contribute to these trends (Meigs et al., 2015). In addition, such patterns may highlight initial phases on species range contraction for which changes in tree recruitment have already been identified as an early indicator (Bell et al., 2014; Monleon and Lintz, 2015; Zhu et al., 2012). However, high biomass change was observed for low *P. menziesii* biomass stands with (1) low initial canopy cover in the warm and wet zone (TSHEPISI; Figs. 3c and 4b) and (2) increasing canopy cover in the warm and dry zone (PSME; Fig. 4c), indicating that *P. menziesii* might be invading at least some canopy openings produced by recent tree mortality or previously dominated by shrubs or herbaceous vegetation.

5. Conclusions

As might be expected given the long life span of *P. menziesii* (Franklin et al., 2002), *P. menziesii* seems to be unwilling to relinquish its status as the landscape dominant in wet portions of the Pacific Northwest. Structural trajectories differed as a function of spatial variation in temperature and precipitation, indicating that the importance of *P. menziesii* throughout forest development diminishes as one moves from warm to cool or wet to dry forests. Temporal resolution and frequency (i.e., two measurements per plot about a decade apart) limits the capacity of this study to address how biomass change might be responding environmental change, such as climate change and CO₂ fertilization. Still, our results imply that shifting climate that alters the geographic distribution of warm vs. cool and wet vs. dry landscapes could dramatically change *P. menziesii* biomass dynamics and alter regional species dominance. The contribution of both regional and local variation in structural trends of *P. menziesii* biomass change appears to imply that the greatest opportunities to store atmospheric C in forest biomass will be in warm and wet productive forest lands also valued for timber production. Conversely, continued accumulation of forest biomass in drier regions may be more limited. However, uncertainties in both climate change exposure and *P. menziesii* sensitivity contribute to an uncertain future for PNW forests dynamics and carbon storage and requires more study.

Acknowledgements

This research was funded by the USDA Forest Service Pacific Northwest Research Station. We thank Matthew Gregory for extracting canopy cover estimates for each plot from the GNN data. We thank Matthew Reilly, Dan Binkley, and two anonymous reviewers for providing comments on the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States government. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the USDA Forest Service.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.07.023>.

References

- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6. <http://dx.doi.org/10.1890/ES15-00203.1>, art129.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684. <http://dx.doi.org/10.1016/j.foreco.2009.09.001>.
- Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., DeLucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. *Glob. Change Biol.* 19, 2001–2021. <http://dx.doi.org/10.1111/gcb.12194>.
- Barbieri, M.M., Berger, J.O., 2016. Optimal predictive model selection. *Ann. Stat.* 32, 870–897.
- Bechtold, W.A., Patterson, P.L., 2005. The Enhanced Forest Inventory and Analysis Program – National Sampling Design and Estimation Procedures, USDA General Technical Report. Gen. Tech. Rep. SRS-GTR-80. Asheville, NC, USDA, Forest Service, Southern Research Station. 85 p.
- Bell, D.M., Bradford, J.B., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* 23, 168–180. <http://dx.doi.org/10.1111/geb.12109>.

- Chen, H.Y.H., Taylor, A.R., 2012. A test of ecological succession hypotheses using 55-year time-series data for 361 boreal forest stands. *Glob. Ecol. Biogeogr.* 21, 441–454. <http://dx.doi.org/10.1111/j.1466-8238.2011.00689.x>.
- Chen, P.Y., Welsh, C., Hamann, A., 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Glob. Change Biol.* 16, 3374–3385. <http://dx.doi.org/10.1111/j.1365-2486.2010.02166.x>.
- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dyn. Popul.*, 298–312. <http://dx.doi.org/10.1890/07-2056.1>.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119. <http://dx.doi.org/10.1086/283241>.
- Daubenmire, R., 1966. Vegetation: identification of typical communities. *Science* 151 (80), 291–298. <http://dx.doi.org/10.1126/science.151.3708.291>.
- Franklin, J.F., Dyrness, C.T., 1973. *Natural Vegetation of Oregon and Washington*. Gen. Tech. Rep. PNW-GTR-8. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR, 417 p.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423. [http://dx.doi.org/10.1016/S0378-1127\(01\)00575-8](http://dx.doi.org/10.1016/S0378-1127(01)00575-8).
- Gray, A.N., Whittier, T.R., 2014. Carbon stocks and changes on Pacific Northwest national forests and the role of disturbance, management, and growth. *For. Ecol. Manage.* 328, 167–178. <http://dx.doi.org/10.1016/j.foreco.2014.05.015>.
- Gray, A.N., Whittier, T.R., Azuma, D.L., 2014. Estimation of aboveground forest carbon flux in Oregon: adding components of change to stock-difference assessments. *For. Sci.* 60, 317–326. <http://dx.doi.org/10.5849/forsci.12-139>.
- Hall, F.C., 1998. *Pacific Northwest Ecoclass Codes for Seral and Potential Natural Communities*. Gen. Tech. Rep. PNW-GTR-418. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Harmon, M.E., Pabst, R.J., 2015. Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades. *J. Veg. Sci.* <http://dx.doi.org/10.1111/jvs.12273>.
- Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation of primary producer communities. *Ecol. Lett.* 14, 852–862. <http://dx.doi.org/10.1111/j.1461-0248.2011.01651.x>.
- Ibáñez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N.E., Wolosin, M.S., 2006. Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology* 87, 1896–1906.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501. <http://dx.doi.org/10.1086/282687>.
- Kuo, L., Mallick, B., 1998. Variable selection for regression models. *Sankhya Indian J. Stat. Ser. B* 60, 65–81. <http://dx.doi.org/10.2307/25053023>.
- Latta, G., Temesgen, H., Adams, D., Barrett, T., 2010. Analysis of potential impacts of climate change on forests of the United States Pacific Northwest. *For. Ecol. Manage.* 259, 720–729. <http://dx.doi.org/10.1016/j.foreco.2009.09.003>.
- Lienard, J., Florescu, I., Strigul, N., 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS ONE* 10. <http://dx.doi.org/10.1371/journal.pone.0117138>.
- Lintz, H.E., Gray, A.N., McCune, B., 2013. Effect of inventory method on niche models: random versus systematic error. *Ecol. Inform.* 18, 20–34. <http://dx.doi.org/10.1016/j.ecoinf.2013.05.001>.
- Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecol. Monogr.* 78, 349–368. <http://dx.doi.org/10.1890/07-0712.1>.
- Max, T.A., Schreuder, H.T., Hazard, J.W., Oswald, D.D., Teply, J., Alegria, J., 1996. *The Pacific Northwest Region Vegetation and Inventory Monitoring System. Res. Paper. PNW-RP-493*. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR, 22 p.
- Meigs, G.W., Kennedy, R.E., Gray, A.N., Gregory, M.J., 2015. Spatiotemporal dynamics of recent mountain pine beetle and western spruce budworm outbreaks across the Pacific Northwest Region, USA. *For. Ecol. Manage.* 339, 71–86. <http://dx.doi.org/10.1016/j.foreco.2014.11.030>.
- Monleon, V.J., Lintz, H.E., 2015. Evidence of tree species' range shifts in a complex landscape. *PLoS ONE* 10, e0118069. <http://dx.doi.org/10.1371/journal.pone.0118069>.
- Moran, E.V., Hartig, F., Bell, D.M., 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Glob. Change Biol.* 22, 137–150. <http://dx.doi.org/10.1111/gcb.13000>.
- Nagel, T., Svoboda, M., Kobal, M., 2013. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecol. Appl.* 24, 663–679. <http://dx.doi.org/10.1890/13-0632.1>.
- O'Hara, R.B., Sillanpää, M.J., 2009. A review of Bayesian variable selection methods: what, how and which. *Bayesian Anal.* <http://dx.doi.org/10.1214/09-BA403>.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270. <http://dx.doi.org/10.1126/science.164.3877.262>.
- Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. *Can. J. For. Res.* 32, 725–741. <http://dx.doi.org/10.1139/x02-011>.
- Ohmann, J.L., Gregory, M.J., Roberts, H.M., Cohen, W.B., Kennedy, R.E., Yang, Z., 2012. Mapping change of older forest with nearest-neighbor imputation and Landsat time-series. *For. Ecol. Manage.* 272, 13–25. <http://dx.doi.org/10.1016/j.foreco.2011.09.021>.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3, 153–168. [http://dx.doi.org/10.1016/0378-1127\(80\)90013-4](http://dx.doi.org/10.1016/0378-1127(80)90013-4).
- Pickett, S.T.A., Armesto, S.L., Armesto, J.J., 1987. Models, mechanisms and pathways of succession. *Bot. Rev.* 53, 335–371. <http://dx.doi.org/10.1007/BF02858321>.
- Plummer, M., 2014. *rjags: Bayesian Graphical Models Using MCMC*. R Packag. Version 3-13.
- Plummer, M., 2003. JAGS: a program for analysis of bayesian graphical models using Gibbs sampling. In: Hornik, K., Leisch, F., Zeileis, A. (Eds.), *Proc. 3rd Int. Work. Distrib. Stat. Comput. (DSC 2003)*, March 20–22, Vienna, Austria. <http://dx.doi.org/10.1.1.13.3406>. ISSN: 1609-395X.
- R Development Core Team, R., 2011. *R: A Language and Environment for Statistical Computing*. R Found. Stat. Comput., R Foundation for Statistical Computing. <http://dx.doi.org/10.1007/978-3-540-74686-7>.
- Rehfeldt, G.E., Leites, L.P., Bradley St Clair, J., Jaquish, B.C., Sáenz-Romero, C., López-Upton, J., Joyce, D.G., 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: clines in growth potential. *For. Ecol. Manage.* 324, 138–146. <http://dx.doi.org/10.1016/j.foreco.2014.02.041>.
- Reilly, M.J., Spies, T.A., 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. *Ecosphere* 6. <http://dx.doi.org/10.1890/ES14-00469.1>, art192.
- Taylor, A.R., Chen, H.Y.H., VanDamme, L., 2009. A review of forest succession models and their suitability for forest management planning. *For. Sci.* 55, 23–36.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251. [http://dx.doi.org/10.1016/S0022-1694\(96\)03128-9](http://dx.doi.org/10.1016/S0022-1694(96)03128-9).
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524. <http://dx.doi.org/10.1126/science.1165000>.
- 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., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3, 292–297. <http://dx.doi.org/10.1038/nclimate1693>.
- Zhu, K., Woodall, C.W., Clark, J.S., 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Change Biol.* 18, 1042–1052. <http://dx.doi.org/10.1111/j.1365-2486.2011.02571.x>.