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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

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A B S T R A C T

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.

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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).

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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 (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*.

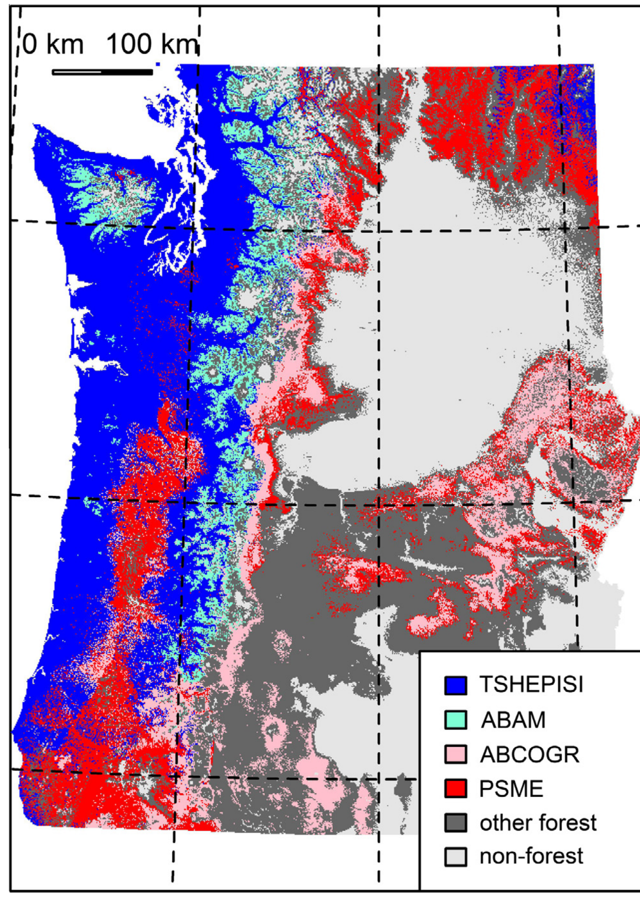

Fig. 1. Map of vegetation zones for study region. ABAM zone (n = 330); ABCOGR zone (n = 869); PSME zone (n = 948); TSHEPISI zone (n = 1363).

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