



## Recent tree mortality and recruitment in mature and old-growth forests in western Washington



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### ABSTRACT

Tree mortality is a fundamental driver of forest ecosystems and occurs both in catastrophic events and as a chronic process. Persistent changes in the rate of chronic or background mortality can dramatically alter the structure and composition of forests stands. Tree recruitment is the complement to tree mortality, combining with mortality to determine changes in tree density and species composition. The purpose of this study is to ascertain trends of mortality and recruitment in mature and old-growth forests in western Washington state, U.S.A. We used a set of permanent plots established in units of the National Park System spanning the environmental gradient of forests in these parks (from near sea-level to 1800 m elevation). Duration of observation was five years for most plots and two or three years for a small number of plots. Principal tree species on the plots were *Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Thuja plicata*, *Abies lasiocarpa*, and *Abies amabilis*. Tree mortality was evaluated annually; recruitment was recorded at the end of the study. For small (dbh 12.7–76.1 cm) and large (dbh >76.1 cm) trees, annual mortality pooled across all elevations, parks, plots, and years was <1% (mean and upper 95% confidence intervals). For saplings (dbh 2.5–12.6 cm), mean mortality was <1% though the upper limit of the confidence interval was slightly greater than 1%. Recruitment outweighed mortality (and growth into the small-tree class) for saplings. Recruitment and losses of stems balanced one another for small trees; both processes were negligible for large trees. Recruitment of saplings increased representation of shade-tolerant species (e.g., *T. heterophylla*, and *A. amabilis*). Biotic factors predominated as the proximate cause of death for all size-classes of trees (i.e., trees died standing), though particular agents of mortality were not identified in most cases. Our results contrasted with a recent report of annual tree mortality >1% for unmanipulated, old-growth forests in the Pacific Northwest.

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### 1. Introduction

Tree mortality is a fundamental driver of forest ecosystems and occurs both as discrete, intense episodes (“forest dieback,” Mueller-Dombois, 1987) and as a chronic process (“background mortality,” Franklin et al., 1987). Persistent changes in the rate of background mortality can dramatically alter the structure and composition of forests stands and the provision of ecosystem

services (van Mantgem et al., 2009). Background mortality occurs throughout the life of any forest stand, though the causes tend to vary with stand age. In younger forests, tree mortality due to competition with other trees is common, whereas in mature or older forests (i.e., at least 80 years old in the Pacific Northwest) the primary drivers of tree mortality are environmental factors external to the stand (Franklin et al., 1987, 2002; Oliver and Larson, 1990). Thus older forests may be more useful in detecting the consequences of climate change (van Mantgem et al., 2009).

To better assess the changing contributions of various biotic and physical factors to tree mortality, it is important to ascribe proximate causes to observed tree deaths to the extent possible (van Mantgem and Stephenson, 2007). Annual observations are critical in this regard (van Mantgem and Stephenson, 2007), inasmuch as signs of relevant insects and pathogens may fade quickly and trees

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that die standing may soon fall or break. In any population made up of sub-populations with different mortality rates (i.e., nearly any closed-canopy forest), longer intervals between observations will bias downwards estimates of the annual rate of tree mortality (Sheil and May, 1996); in addition, longer intervals between observations will result in underestimates of the temporal variability of tree mortality.

Tree recruitment (i.e., addition of new stems to the population) is the complement to tree mortality; together they determine whether the number of trees in a forest is increasing, stable, or declining, and whether or not species composition is changing (Phillips et al., 2004; van Mantgem et al., 2009). Recruitment of shade-tolerant species can occur in mature and old-growth forests in the absence of disturbance (Franklin et al., 2002), leading to stems that persist for decades as slowly-growing seedlings or saplings (Oliver and Larson, 1990). Observations of older forests indicate that recruitment and mortality can be roughly in balance (Franklin and DeBell, 1988), recruitment can exceed mortality (Phillips et al., 2004), or mortality can exceed recruitment (van Mantgem et al., 2009). Thus it is essential to evaluate both processes to fully grasp forest change.

The purpose of our study is to ascertain trends of mortality and recruitment in mature and old-growth forests in western Washington state, U.S.A. Mature and old-growth forests in Washington and elsewhere in the Pacific Northwest provide a host of ecosystem services. They are important habitat for a vast number of terrestrial species (Marcot, 1997), and enhance the quality of aquatic habitats (particularly small streams) (Everest and Reeves, 2007). They host millions of human visitors annually (FEMAT, 1993). They help to regulate the quality and quantity of fresh water (Furniss et al., 2010). Forests of the Pacific Northwest have some of the greatest potential for carbon sequestration in the U.S. and in the world (Keith et al., 2009; Ryan et al., 2010); forests on federal lands in the region have accumulated carbon in recent decades (Krankina et al., 2012).

Forests, and the ecosystem services they provide, are subject to change due to alteration of the global atmosphere and climate. Climate change has been linked to dramatic and extensive recent episodes of tree mortality due to factors such as wildfire and insect outbreaks (Grimm et al., 2013). Recent increases in tree mortality due to climate change, ranging from increases in background mortality to incidents of extensive dieback, have been observed on all the continents that support forest (Allen et al., 2010). Background rates of tree mortality in old-growth forests in the Pacific Northwest have recently been observed to be increasing with a doubling period of 17 years (van Mantgem et al., 2009). On the other hand, increases in tree growth or forest carbon sequestration, presumably due to some combination of increased air temperature, atmospheric CO<sub>2</sub> concentration, and nutrient deposition, have been observed recently in temperate and tropical forests (Lewis et al., 2009; Cole et al., 2010; McMahon et al., 2010). Correlations between climatic variability and tree growth during the 20th century for the Olympic Mountains in western Washington suggest that as the climate warms, tree growth may decrease or increase depending on elevation and changes in precipitation (Nakawatase and Peterson, 2006). At the lowest forested elevations, increasing summer drought is likely to decrease tree growth. At the highest forested elevations, a lengthened growing season due to shorter duration of the snowpack may result in greater tree growth. Middle elevations may be most sensitive to changes in precipitation (Nakawatase and Peterson, 2006), predictions of which are subject to greater uncertainty than predictions of increasing temperature (Furniss et al., 2010). Decreased growth rates are associated with increased risk of tree mortality (Waring, 1987; Antos et al., 2008), so it is reasonable to expect that patterns of tree mortality will correspond to patterns in tree growth.

We established permanent plots in four units of the National Park System (Lewis and Clark National Historical Park (LEWI), Mount Rainier National Park (MORA), North Cascades National Park Service Complex (NOCA), Olympic National Park (OLYM)), tracking tree mortality and recruitment over five years on most plots. The plots were established as part of an initiative by the National Park Service (NPS) to implement long-term ecological monitoring (Fancy et al., 2009; Weber et al., 2009). The plots span the environmental gradient of forests in these parks (from near sea-level to 1800 m elevation) (Acker et al., 2010).

Our study questions were:

- (1) How does the rate of tree mortality in mature and old-growth forests of western Washington compare to expected values?
- (2) How does the rate of tree recruitment compare to the rate of tree mortality in these mature and old-growth forests?
- (3) How is tree mortality in these mature and old-growth forests distributed with respect to proximate cause (i.e., biotic versus physical causes)?

We set an annual mortality rate of 1% as a reasonable standard for comparison, based on previous work in the Pacific Northwest by Franklin et al. (1987), Franklin and DeBell (1988), Edmonds et al. (1993), Acker et al. (2003), and Larson and Franklin (2010).

## 2. Methods

### 2.1. Sampling design

Our objective was to encompass the range of climatic regimes and elevation where forests occur in NPS units in western Washington. We wanted the sample to be interpretable based on vegetation types, yet flexible enough to be useful in the face of expected future changes in community composition and/or elevation range (Gates, 1993) as species respond independently to a changing environment (Peters and Lovejoy, 1992). Therefore, we conducted double-sampling by initially stratifying our sample using elevation, and secondly by current vegetation.

To facilitate replication within different segments of the environmental gradients at the parks, we established 300-m elevation bands as fixed strata within each park. We numbered strata consecutively from low to high elevations. We included one stratum each at low and high elevations, as well as one at intermediate elevations. Two strata were sampled in each of the large parks (MORA (95,395 ha), NOCA (277,045 ha), and OLYM (373,543 ha)), and one in the smaller park (LEWI (2834 ha)). We established plots within stratum 1 (0–300 m at LEWI and OLYM), stratum 3 (600–900 m at MORA, NOCA, and OLYM), and stratum 6 (1500–1800 m at MORA and NOCA).

We used the Generalized Randomized-Tessellation Stratified algorithm (GRTS, Stevens, 1997) to obtain a spatially-dispersed, random sample of our target populations. Permanent plots were added to the sample in the numerical order generated by GRTS. To identify the target number of plots for each combination of stratum and park, we used a set of power analyses based on tree mortality data from existing permanent plots in the Pacific Northwest. We concluded that six plots per combination of stratum and park was an appropriate compromise between statistical power and cost (Acker et al., 2010).

We used sets of vegetation communities as proxies for climate within elevation strata, so as to increase the signal of vegetation change due to external drivers and decrease the potential for noise due to environmental differences within strata. Our general approach was to focus on coniferous forest zones that represent

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