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Post-fire aspen (*Populus tremuloides*) regeneration varies in response to winter precipitation across a regional climate gradient

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ABSTRACT

Altered climate and changing fire regimes are synergistically impacting forest communities globally, resulting in deviations from historical norms and creation of novel successional dynamics. These changes are particularly important when considering the stability of a keystone species such as quaking aspen (*Populus tremuloides* Michx.), which contributes critical ecosystem services across its broad North American range. As a relatively drought intolerant species, projected changes of altered precipitation timing, amount, and type (e.g. snow or rain) may influence aspen response to fire, especially in moisture-limited and winter precipitation-dominated portions of its range. Aspen is generally considered an early-seral species that benefits from fire, but increases in fire activity across much of the western United States could affect the species in unpredictable ways. This study examined post-fire aspen stands across a regional climate gradient spanning from the north-central Great Basin to the northeastern portion of the Greater Yellowstone Ecosystem (USA). We investigated the influence of seasonal precipitation and temperature variables, snowpack, and site conditions (e.g. browsing levels, topography) on density of post-fire aspen regeneration (i.e. all small trees ha^{-1}) and recruitment (i.e. small trees ≥ 2 m tall ha^{-1}) across 15 fires that occurred between 2000 and 2009. The range of post-fire regeneration (2500–71,600 small trees ha^{-1}) and recruitment (0–32,500 small trees ≥ 2 m ha^{-1}) densities varied widely across plots. Linear mixed effects models demonstrated that both response variables increased primarily with early winter (Oct-Dec) precipitation during the 'fire-regen period' (i.e., fire year and five years after fire) relative to the 30-year mean. The 30-year mean of early winter precipitation and fire-regen period snowpack were also positively related to recruitment densities. Both response variables decreased with higher shrub cover, highlighting the importance of considering shrub competition in post-fire environments. Regeneration and recruitment densities were negatively related to proportion browsed aspen leaders and animal pellet densities (no./m^2), respectively, indicating the influence of ungulate browsing even at the relatively low levels observed across sites. A post-hoc exploratory analysis suggests that deviation in early winter precipitation during the fire-regen period (relative to 30-year means) varied among sites along directional gradients, emphasizing the need to consider multiple spatiotemporal scales when investigating climate effects on post-fire successional dynamics. We discuss our findings in terms of dynamic management and conservation strategies in light of changing fire regimes and climate conditions.

1. Introduction

Fire regimes are changing across much of the western United States, including increased fire activity driven by complex interactions among climate, human impacts on fuels, and rates of ignition (Abatzoglou and Williams, 2016; Balch et al., 2013), as well as recovery from historical fire deficits caused by past fire exclusion (Marlon et al., 2012). Fire activity is projected to increase in the future across much of the western United States, as climate change enhances fire-weather conditions and extends the duration of the fire season (Barbero et al., 2015; Westerling, 2016). Under altered fire regimes, substantial shifts may occur in many forest communities within the near future (Burkett et al., 2005; Johnstone and Chapin, 2006; Campbell and Shinneman, 2017). For instance, Westerling et al., (2011) estimated that changing fire-weather conditions projected for the Greater Yellowstone Ecosystem (USA) will likely lead to more frequent fire and potential conversion of conifer forest-dominated landscapes to woodlands or non-forest by the mid-21st century. Indeed, some fire-adapted and early successional forest species such as quaking aspen (*Populus tremuloides* Michx.) may benefit from increasing fire, assuming suitable post-fire climate conditions exist

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or comparable sites can be reached via seed dispersal after disturbance (Yang et al., 2015; Landhäusser et al., 2019).

Aspen is the most widely distributed native tree species in North America (Little, 1971). In the generally semi-arid interior-western United States, aspen is largely limited to mountain environments and often comprises a minor component of the forested landscape, especially in areas dominated by conifers (Bartos, 2008). Aspen provides critical ecosystem services disproportionate to its limited areal extent in the region, including sustaining biodiversity, supporting ecosystem function (e.g. annual water yield), providing forage for wildlife and livestock, and contributing recreational and scenic resources (DeByle, 1985; Chong et al., 2001; LaMalfa and Ryle, 2008). Aspen decline has been documented in portions of western North America, attributed to factors such as fire suppression, drought, ungulate herbivory, conifer encroachment, and disease (Hessl and Graumlich, 2002; Hogg et al., 2005; Worrall et al., 2008). However, aspen are also persisting (Zier and Baker, 2006; Kashian et al., 2007; Kurzel et al., 2007) or expanding in some locations (Kaye et al., 2003; Elliott and Baker, 2004; Kulakowski et al., 2004). These contradictory findings may be due to different disturbance histories, varied environmental settings, and the relative stability of distinct aspen functional types (Rogers et al., 2014). For instance, aspen functional types are associated with different fire regimes, ranging from fire-dependent seral stands to stable stands largely independent of fire (Shinneman et al., 2013; Shinneman and McIlroy, 2019).

Aspen decline in many regions has been strongly linked to drought (Hogg et al., 2005; Anderegg et al., 2013; Worrall et al., 2013), as the species has a poor ability to regulate water loss (Tobiessen and Kana, 1974), and often occurs near the margins of its moisture requirements in the western portion of its range (Rehfeldt et al., 2009; Martin and Maron, 2012; Shinneman and McIlroy, 2019). Studies in the western U.S. have shown that winter precipitation is more important to aspen growth and survival than growing season precipitation (Hanna and Kulakowski, 2012; Love et al., 2019). Specifically, winter precipitation and melting snowpack contribute to soil water and provide moisture into the growing season (Maurer and Bowling, 2014), which is important for aspen productivity (Soderquist et al., 2018) and may also increase resilience to stressors such as drought, disease, and insect herbivory (Worrall et al., 2013; Dudley et al., 2015). Winter snowpack has declined across much of the western United States since the middle of the 20th century (Mote et al., 2018), and climate projections portend a continued transition from predominantly snow- to rain-dominated winter precipitation regimes across much of the region (Klos et al., 2014). Coupled with projections of warmer temperatures (Westerling et al., 2011) and increased drought (Cayan et al., 2010), it is likely that aspen will experience declines in both snowpack and soil water availability in the future (e.g. Marshall et al., 2019).

Previous studies have examined aspen response to wildfire and prescribed burning in the western United States, but most research did not consider climate influence on post-fire aspen regeneration (e.g. Smith et al., 2011; Krasnow et al., 2012; Wan et al., 2014). Research that did consider the influence of climate on aspen regeneration following fire typically focused on single events (e.g. Romme et al., 1995; Smith et al., 2011; Hansen et al., 2016) or specific climate conditions (e.g. drought; Harvey et al., 2016). Although Kaye (2011) compiled data from aspen dendrochronology studies in the central and southern Rocky Mountains to examine the influence of climate in broad-scale establishment patterns after fire and human disturbance, this coarse-scale analysis did not identify temporally or spatially precise relationships. Shinneman and McIlroy (2019) identified correlations between aspen establishment and several climate variables in northern Nevada (USA), but most of the stands included in that study had no evidence of fire. Thus, considering current and projected changes in fire-climate dynamics, there is a need to better understand how post-fire aspen regeneration varies regionally across a range of bioclimatic settings.

To address this knowledge gap, we sampled recently burned aspen stands across a broad climate gradient of winter- to summer-dominated precipitation, representing a substantial cross-section of aspen's bioclimatic niche across the northwestern United States (Fig. 1). We then developed predictive models to explore the capacity of several site-based climate, disturbance, and environmental variables to influence post-fire aspen: a) regeneration density (i.e. all small trees ha^{-1}), and b)

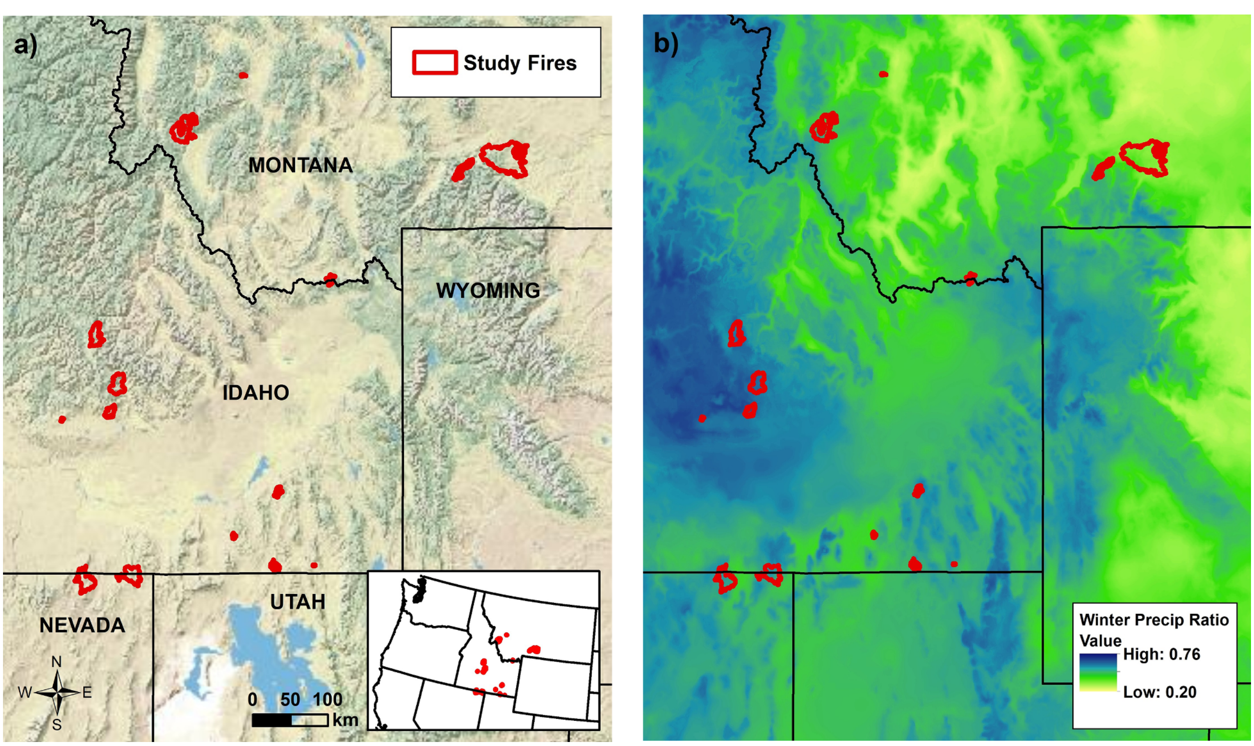

Fig. 1. The study area showing (a) fire locations and (b) a winter (October–March) to annual precipitation ratio. Data are 30-yr normals (1981–2010) from PRISM (http://www.prism.oregonstate.edu/normals/).