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Long-term aspen cover change in the western US

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ABSTRACT

Quaking aspen (*Populus tremuloides* Michx.) is one of the most important tree species in the western United States due to its role in biodiversity, tourism, and other ecological and aesthetic values. This paper provides an overview of the drivers of long-term aspen cover change in the western US and how these drivers operate on diverse spatial and temporal scales. There has been substantial concern that aspen has been declining in the western US, but trends of aspen persistence vary both geographically and temporally. One important goal for future research is to better understand long-term and broad-scale changes in aspen cover across its range. Inferences about aspen dynamics are contingent on the spatial and temporal scales of inquiry, thus differences in scope and design among studies partly explain variation among conclusions. For example, major aspen decline has been noted when the spatial scale of inquiry is relatively small and the temporal scale of inquiry is relatively short. Thus, it is important to consider the scale of research when addressing aspen dynamics.

Successional replacement of aspen by conifer species is most pronounced in systems shaped by long fire intervals and can thus be seen as part of a normal, long-term fluctuation in forest composition. Aspen decline was initially reported primarily at the margins of aspen's distribution, but may be becoming more ubiquitous due to the direct effects of climate (e.g. drought). In contrast, the indirect effects of recent climate (e.g. forest fires, bark beetle outbreaks, and compounded disturbances) appear to favor aspen and may facilitate expansion of this forest type. Thus, future aspen trends are likely to depend on the net result of the direct and indirect effects of altered climate.

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1. Introduction

Forest ecosystems are changing worldwide due to interacting effects of climate change, altered disturbance regimes, invasive species, and land use. Identifying short-term changes is informative for discerning acute impacts of these factors, but a comprehensive understanding of forest ecosystem dynamics also requires examining processes driving ecological patterns at a range of spatial and temporal scales. Quaking aspen (*Populus tremuloides* Michx.) is the most widely-distributed tree species in North America and the most widespread deciduous tree species in the United States Rocky Mountains (Little, 1971; Perala, 1990). In the Rocky Mountains and other regions, aspen forests exist in a wide variety of ecological settings (Little, 1971; Mueggler, 1988), which necessitates a nuanced perspective in examining their ecological patterns and dynamics. There has been substantial concern that aspen cover and condition have been declining over the past century in western US landscapes (e.g., Kay, 1997; Knight, 2001), but the trends of aspen decline versus persistence appear to vary both geographically and temporally (e.g., Kulakowski et al., 2004, 2006; Kashian et al., 2007; Kurzel et al., 2007; Sankey, 2008). Inferences about trends in aspen decline are also likely to be contingent on the spatial and temporal scales of inquiry (e.g. stand vs. landscape scale and decadal vs. centennial scale) (Suzuki et al., 1999).

This paper provides an overview of the drivers of long-term aspen cover change in the western US and where possible, discusses the cumulative consequences of those drivers on overall aspen cover. The dearth of aspen studies conducted at suitable temporal and spatial scales precludes a comprehensive meta-analysis of long-term and broad-scale aspen cover trends at the time of this writing, and such studies remain a top research priority. Nevertheless, important advances have been made over the last decade that offer a glimpse into the drivers and trends of both aspen cover change and its responses to the direct (e.g. drought) and indirect (e.g. altered disturbance regimes) consequences of climate change.

More than a decade ago Knight (2001) stressed the need to understand aspen dynamics in a long-term framework, and correctly speculated that widespread disturbances in the West in the late 1800s and early 1900s may have increased the amount of aspen in the Rocky Mountains. Several studies over the last decade have affirmed Knight's speculation that aspen decline may be

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understood as one phase in a series of normal fluctuations and have provided insight into these dynamics. Likewise, more than a decade ago climate change was identified as a potential threat to aspen forests (Knight, 2001), and since then a number of studies have investigated the details of how climate is driving aspen mortality across its range.

As the extent of forest cover is ultimately a function of both tree regeneration and mortality, we review key variables that drive these two processes as well as their net result. Where possible, we also discuss the overall changes in aspen cover at different scales. Finally, we suggest potential areas of future research in aspen dynamics.

2. Study region

In this review we focus on quaking aspen in the western US, where it is found in all thirteen western contiguous states and Alaska and where it occurs at elevations up to 3500 m (Burns et al., 1990). In New Mexico, Colorado, Utah, and Arizona, aspen can form extensive pure stands, whereas in other regions aspen patches can be smaller, though still ecologically important. The ecological role of aspen across this region varies substantially with biophysical setting, climate, disturbance regimes, and the presence of other tree species. Although we aim to highlight some of this variability, our review is limited by existing literature, which is not equally distributed across the extent of aspen, but rather is concentrated in several key states.

3. Characteristics of studies

Studies of aspen dynamics vary substantially in the temporal and spatial scale at which they have been conducted. Given the difficulty of extrapolating across scales, it is critical to recognize this variation when comparing studies. Studies that focus on small areas or short time periods (e.g. Bartos and Campbell, 1998) are valuable, but may not be easily or accurately scaled up to provide insights into broad-scale and/or long-term patterns. Thus, studies may lead to very different conclusions about aspen dynamics even within the same study region depending on the spatial and temporal scale of observation. These differences, as well as geographic variation in aspen ecology, can explain much of the varying and at times contradictory conclusions among studies.

Compared to other forest types in the western United States, the study of long-term aspen dynamics is encumbered by several methodological limitations. Aspen ramets are relatively short-lived and prone to heart-rot, which has made long-term (i.e. >100 year) dendroecological studies difficult. Second, stand-replacing disturbances such as fires, which often re-initiate aspen stands, erase evidence of pre-disturbance stand conditions and processes (Shinneman et al. this volume). Furthermore, although most studies of aspen focus primarily on above-ground stems, the clonal habit of aspen (Barnes, 1966) makes aging ramets relatively uninformative for aging the clone itself. Additionally, studies of forest dynamics are sometimes limited to reconstructions at the scale of a stand (<c. 1000 ha), which although valuable for insights into relatively fine-scale processes, make broad-scale inferences challenging. Consequently, landscape-to-regional studies of aspen are often restricted to snapshots of aspen structure. The few long-term or broad-scale assessments of aspen change have generally been based on analyses of repeat photographs or historical maps, both of which facilitate discerning dynamics over larger extents more so than dendrocological studies, but which are hindered by the lack of available images representing most of the western landscape. Methodological limitations of studying broad-scale aspen dynamics are further complicated by the inherent diversity of scales at which the processes that drive aspen regeneration and mortality operate (Fig. 1), which necessitates that research and management be conducted at scales appropriate to each driver. For example, browsing effects on aspen regeneration are largely limited to areas of significant ungulate populations while the impacts of high-severity fires on aspen regeneration is most prevalent in subalpine forests.

4. Regeneration

Aspen regeneration dynamics are integral to aspen cover change and have been the subject of much inquiry in the context of disturbances, climate variability, and browsing by ungulates. Adding complexity to the issue of aspen regeneration is its occasional regeneration by seed that complements the more common vegetative reproduction. Sexual regeneration of aspen is much more important to the overall genetic diversity of aspen (Mock et al. this volume) than to overall aspen dominance at broad scales, but is far less studied than asexual reproduction and thus is not as well understood.

Variation in aspen ecology, even over relatively small distances, may be partially explained by the clonal nature of aspen, in which a clone contains genetically identical ramets but may differ morphologically, physiologically, and ecologically even from adjacent clones (Barnes, 1966; Kemperman and Barnes, 1976; Mock et al. this volume). This variation may lead to different regeneration dynamics and other ecological properties. For example, Kemperman and Barnes (1976) were able to discern aspen clones in Utah in part based on their distinct timing of spring leaf flush.

Modes of aspen regeneration can vary even within a relatively restricted area. Kurzel et al. (2007) found that in the majority (seven of eight) of seral stands (both aspen dominated and mixed aspen-conifer) in northwestern Colorado, regeneration of the stand was associated with coarse-scale, severe disturbance by fire. However, in the same study area, most aspen-dominated stands showed signs of aspen self replacement despite presence of conifers. Furthermore, in persistent aspen stands showing no conifer

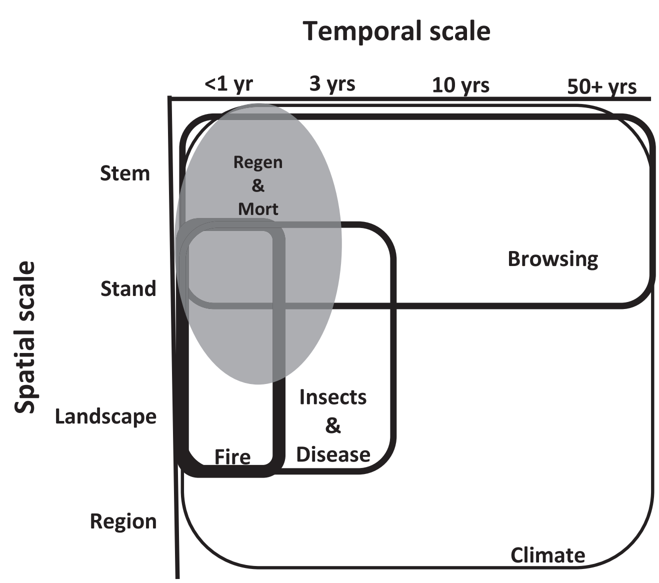

Fig. 1. Diversity of spatial and temporal scales for processes (white boxes) that drive that aspen regeneration and mortality (grey oval) in the western US. Each polygon represents the extent of a given process and thickness of the black border represents the intensity of impact on aspen, such that thicker lines represent more acute impacts. Processes range in influence from short scale and acute (e.g. fire), to broad scale and moderate (e.g. climate). When possible, research should occur at spatial and temporal scales that reflect the scale of influence of that process.

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