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# How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps

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ABSTRACT

There has been speculation that quaking aspen (*Populus tremuloides*) dominance of forests will increase due to mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) (MPB). High aspen sucker densities have been observed in the years following MPB-caused pine mortality, but it remains unclear if this disturbance will result in a pulse of aspen recruitment to forest overstories. Many factors will affect aspen recruitment and overstory health. Surviving conifer overstory and advance regeneration will limit available light and other resources, potentially decreasing aspen suckering, growth, and survival. Following the creation of MPB-caused canopy openings, mortality rates of overstory aspen may increase due to exposure or damage by falling snags. Severe browsing damage may prevent suckers from successfully recruiting to the canopy where there are high domestic and/or wild ungulate densities, even where forest conditions promote aspen recruitment. Climate and weather variability will also mediate aspen response to MPB. Research that focuses specifically on effects of MPB-caused forest structure changes on aspen suckering, recruitment, and overstory health, and the potential for browsing and climate to interact with these effects, is needed to inform our understanding of how MPB-caused mortality will affect aspen in western North America.



## 1. Introduction

There has been speculation that quaking aspen (*Populus tremuloides*) will become more dominant in forests following tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) (MPB) (Kaufmann et al., 2008; Diskin et al., 2011). An increase in aspen would be socially desirable, as aspen is valued for its aesthetics, supports high biodiversity, and can act as an effective forest fire fuel break (Van Wagner, 1977; Bigler et al., 2005). Concern about aspen decline in the scientific and land management communities (Frey et al., 2003; Worrall et al., 2010) has furthered interest in the potential for aspen cover increase following MPB.

Mountain pine beetle has affected millions of ha of pine (*Pinus* spp.) trees throughout western North America in the past decade (Raffa et al., 2008; Meddens et al., 2012). According to recent estimates, MPB has killed approximately 8.5 million ha of forest, mostly dominated by lodgepole pine (*Pinus contorta*) (Meddens et al., 2012). In the US, the beetle is affecting lodgepole pine throughout much of its range and has caused mortality of over 3 million ha of forest. About 235,000 ha of forest have been killed in areas dominated by ponderosa pine (*Pinusponderosa*) and five-needle pines such as limber pine (*Pinusflexilis*), bristlecone pine (*Pinusaristata*), and whitebark pine (*Pinusalbicaulis*) (Meddens et al., 2012). Quaking aspen co-occurs with these pine species (Fig. 1) so an increase in available light, water, and nutrients following MPB-caused mortality may facilitate successful aspen recruitment (i.e., survival to the forest overstory). However, it is not certain outbreaks will result in widespread aspen increase, as recruitment will be affected by competition with conifers and ungulate browsing. Futhermore, aspen health is likely to be affected by changing climatic conditions (Worrall et al., 2010; Hanna and Kulakowski, 2012).

This paper will first review how MPB-caused disturbance will potentially affect aspen regeneration and recruitment dynamics. We then synthesize studies that report aspen response to beetle-caused conifer mortality and identify important gaps in this science. Finally, we will briefly discuss how variation in forest conditions across the landscape, climate change, and multiple disturbances may affect aspen response to MPB at broad spatial and long-term time scales.

## 2. Potential effects of MPB-caused mortality on aspen regeneration and growth

Aspen recruitment has several stages, all of which could be affected by MPB-caused tree mortality. Aspen, a clonal tree species, regenerates vegetatively, often following fire or other disturbance

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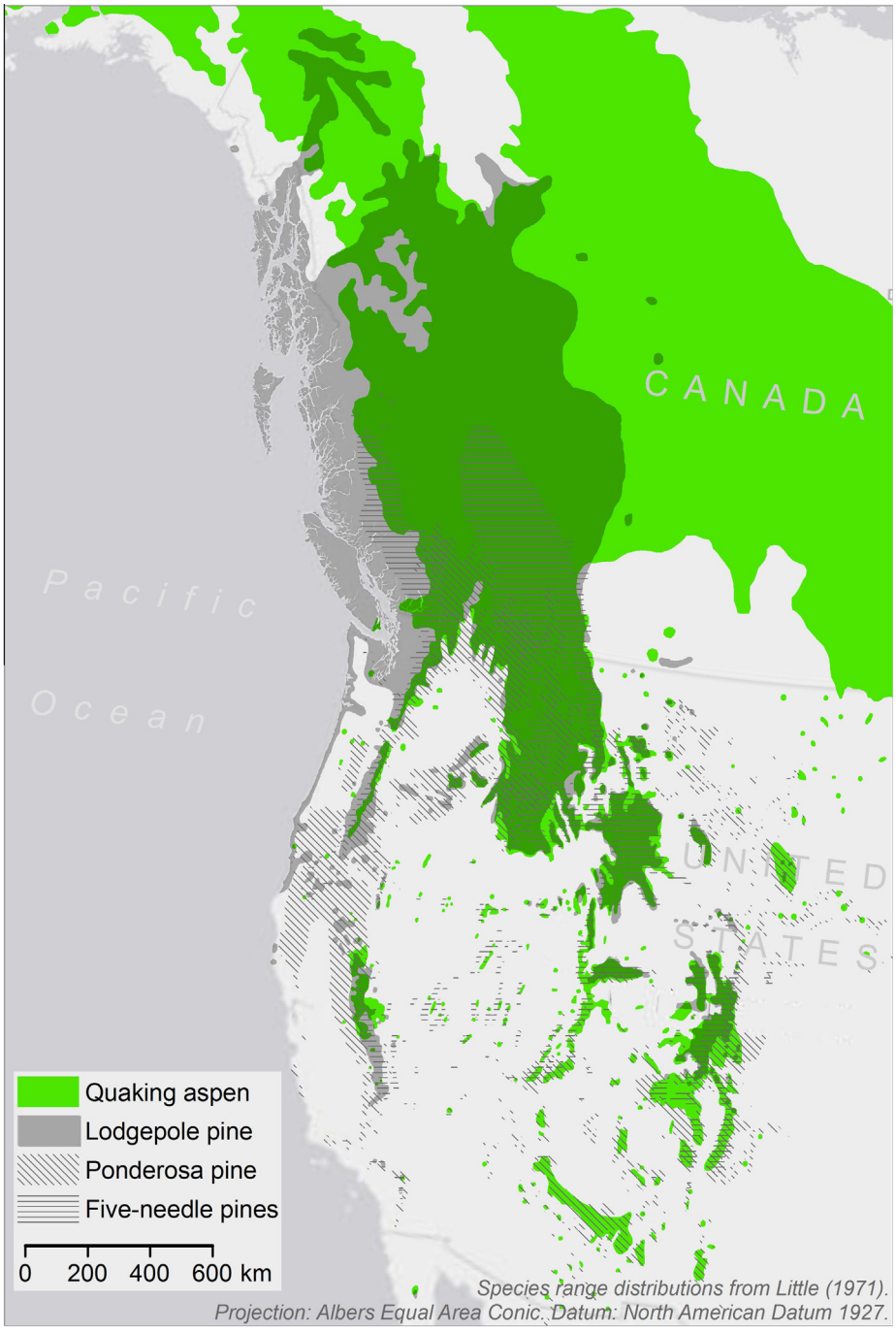


**Fig. 1.** General ranges of quaking aspen and pine species affected by mountain pine beetle-caused mortality in western North America. Five-needle pines include limber pine (*P. flexilis*), bristlecone pine (*P. aristata*) and whitebark pine (*P. albicaulis*). Meddens et al. (2012) estimate that MPB has caused mortality on 8.5 million ha, predominantly in lodgepole pine. Aspen occurs throughout much of the range of lodgepole pine and other affected pine species. Species range maps from Little (1971).

that kills or damages aspen stems (*sensu* Frey et al., 2003). Recent genetic analyses show aspen sexual reproduction also occurs in western North America (Mock et al., 2008, 2013; Zeigenfuss et al., 2008; DeWoody et al., 2009) though seedling establishment is less common than vegetative regeneration (Kay, 1993; Romme et al., 2005; Zeigenfuss et al., 2008; Long and Mock, 2012). In this section, we review the physiology of aspen suckering and growth, and the potential effects of MPB-caused mortality on factors controlling aspen regeneration. We focus on vegetative reproduction as it is responsible for the majority of aspen stem establishment (Zeigenfuss et al., 2008; Long and Mock, 2012; Mock et al., 2013) (for a thorough review of factors affecting vegetative aspen regeneration see Frey et al., 2003).

### 2.1. Sucker initiation and seedling establishment

Plant hormones associated with apical dominance have long been thought to play an important role in controlling aspen sucker initiation (Schier et al., 1985; Frey et al., 2003). The primary hormone associated with apical dominance, auxin, is produced in above-ground buds and leaves and inhibits sucker initiation when translocated to roots (*sensu* Schier et al., 1985). Initiation of suckers