Forest Ecology and Management 299 (2013) 60–69

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Article history:
Available online 19 February 2013

Keywords:
Aspen regeneration
Aspen suckering
Lodgepole pine
Bark beetles
Forest disturbance
Ungulate browsing

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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http://dx.doi.org/10.1016/j.foreco.2013.01.008

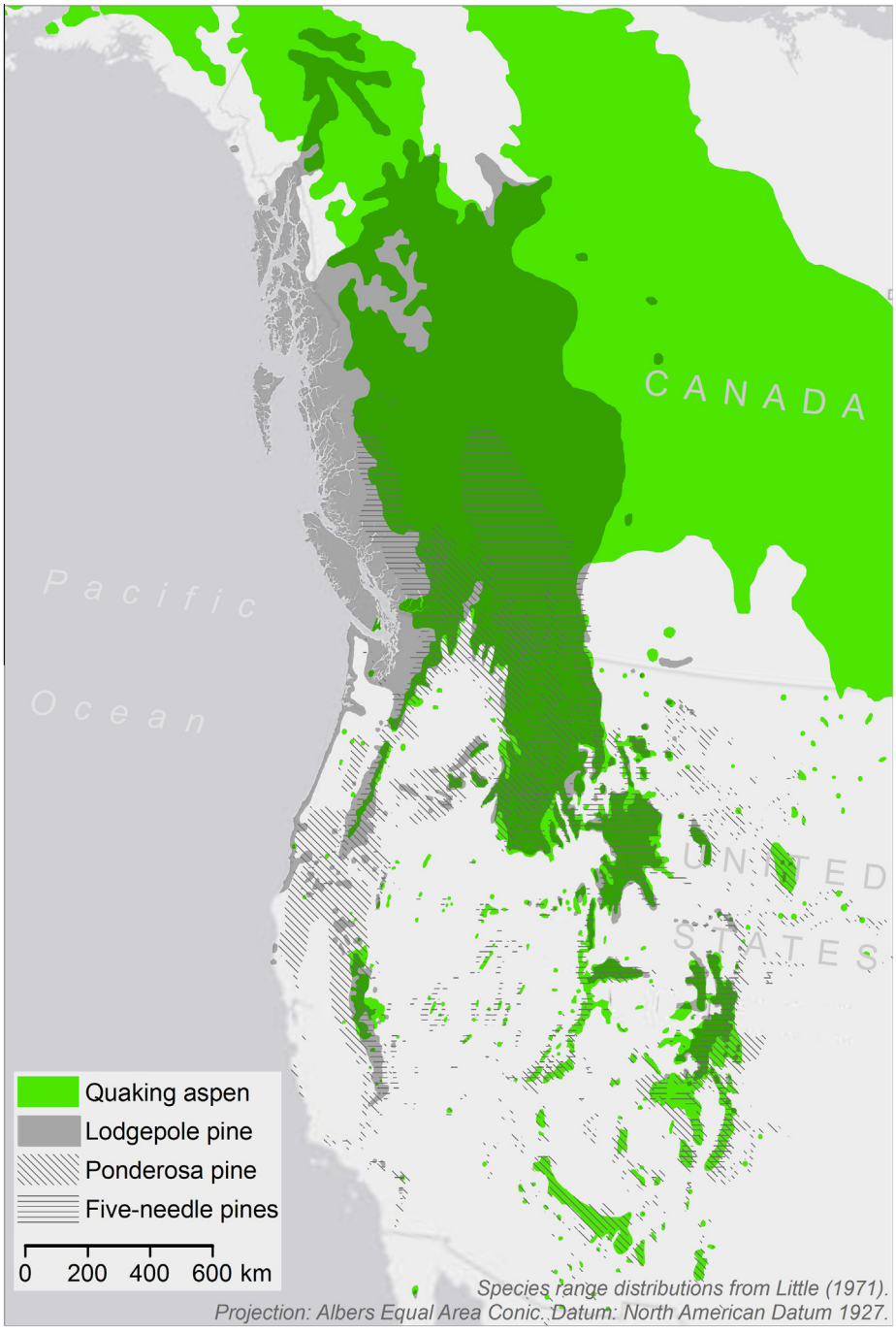

Fig. 1. General ranges of quaking aspen and pine species affected by mountain pine beetle-caused mortality in western North America. Five-needle pines include limber pine (*P. flexilis*), bristlecone pine (*P. aristata*) and whitebark pine (*P. albicaulis*). Meddens et al. (2012) estimate that MPB has 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

is stimulated when root auxin levels are reduced, often by fire, harvest, stem girdling, or non-lethal damage to above-ground aspen (such as defoliation by insects or frost damage) (Farmer, 1962; Schier, 1973; Schier, 1975; Schier et al., 1985; Man and Rice, 2010; Dale Bartos, *personal communication*). Aspen also commonly suckers without apparent damage to aspen stems, perhaps due to seasonal fluctuations in auxin levels and its instability (Schier, 1975; Schier et al., 1985). However, without disturbance, sucker density is often lower than following disturbance (e.g., Suzuki et al., 1999; Shepperd et al., 2001; Binkley, 2008; Smith and Smith, 2005).

Temperature, genetics, soil water conditions, and soil nutrients may affect sucker initiation. Temperature has been thought to be a primary controlling factor of sucker initiation, but it may be less important than has long been assumed (*sensu*Frey et al., 2003). Root section sucker densities increase with constant temperature up to 30 °C (Horton and Maini, 1964; Maini and Horton, 1966; Gifford, 1967), but more recent work has found sucker numbers do not vary with daily maximum temperatures (12–20 °C) when nighttime temperatures are consistently low (8 °C) (Fraser et al., 2002). Genetic variation clearly affects sucker density, as shoot primordia may be four times more dense on roots of one genotype than another (Zasada and Schier, 1973). Very dry or very wet soils inhibit suckering, so moisture conditions can also affect initiation (Horton and Maini, 1964; Schier et al., 1985). Though few studies have examined the direct effects of nutrients on shoot initiation, nitrate appears to enhance sucker density (Frey et al., 2003). In greenhouse experiments, nitrate additions double root segment sucker density, but ammonium, calcium, potassium, phosphate, soil pH (Landhaeusser et al., 2010a) and carbohydrate changes (Fraser et al., 2002) have no effects. It is important to consider that this research has been done on roots sections (eliminating suppression of suckering by auxin) and it is unclear how these factors affect suckering when roots remain attached.

Mountain pine beetle-caused stand structure changes may indirectly stimulate suckering by increasing light, raising soil temperature, or damaging overstory aspen. Reduced canopy cover and related increases in soil temperature may initiate shoot growth if sucker initiation is indeed stimulated by soil temperature changes. At dry sites, though, higher temperatures could reduce soil moisture to a point that suppresses suckering. Increased nitrate availability following MPB outbreak (Griffin et al., 2011) has the potential to initiate sucker growth (Landhaeusser et al., 2010a), especially in high-light environments where nitrogen is likely to be limiting (Calder et al., 2011). If aspen apical dominance remains largely intact following MPB-caused mortality, suckering could be inhibited, as is thought to have occurred in other areas affected by conifer overstory disturbance (Gendreau-Berthaiume et al., 2012). However, MPB-caused forest changes may damage aspen overstory and thereby stimulate suckering (see Section 2.3 for further discussion of possible effects of MPB on overstory aspen).

Aspen regeneration from seed following beetle-caused forest disturbance is possible, though seedling establishment will be limited by substrate and moisture conditions. Aspen seedlings establish almost exclusively on mineral soil substrate (Landhaeusser et al. 2010b), which is scarce in forests immediately following MPB-caused disturbance (Astrup et al., 2008; Vyse et al., 2009; Collins et al., 2011). Aspen seedlings survival in the Rocky Mountains is also thought to be low because summer conditions are often dry (Kay, 1993; Romme et al., 2005). However, ideal microhabitat conditions may be created as MPB-killed snags fall, exposing soil around root balls and creating pits that trap moisture. Overall, aspen seedling establishment following MPB is most likely where elevation or latitude promote suitably mesic conditions (e.g., Landhaeusser et al., 2010b; Romme et al., 2005).

2.2. Sucker survival and recruitment

Sucker growth, once initiated, is strongly influenced by light, temperature, and available resources. Suckers rely on root carbohydrate stores prior to emergence from the soil (Zasada and Schier, 1973) so healthy root systems translate into more growth in critical early stages. Warmer soil temperatures expedite growth, allowing earlier emergence and providing an advantage over slower-growing suckers (Zasada and Schier, 1973; Fraser et al., 2002). Dense roots of grasses or other vegetation may also delay sucker emergence (Landhaeusser et al., 2007). Light availability becomes critical to sucker growth once they reach the surface and are able to photosynthesize (Schier et al., 1985). Aspen growth is greatest in full sun environments, and is significantly limited when any forest overstory remains (Huffman et al., 1999). In shade, aspen preferentially allocates carbon to roots (Landhausser et al., 2001; Landhausser and Lieffers, 2002) and its photosynthetic rate is lowered (Calder et al., 2011). Aspen growing in low light lose mycorrhizal associates correlated with increased photosynthetic rates (Clark and St. Clair, 2011), which may further reduce sucker growth.

MPB-caused overstory mortality will create canopy openings that may allow optimal growth and survival of aspen. Where high forest mortality occurs and few live trees remain, larger canopy gaps will provide high light conditions favoring aspen growth (Groot et al., 2009; Calder et al., 2011). Where MPB-caused mortality is low and/or non-pine conifer densities are high, smaller canopy gaps will promote shade tolerant species, such as subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and white spruce (*Picea glauca*) (e.g., Vyse et al., 2009; Collins et al., 2011; Pelz and Smith, 2012). Vigorous suckers are unlikely in forest dominated by conifers, as aspen mortality is often high due to shading and low soil nutrients (Shepperd et al., 2001; Calder et al., 2011; Clark and St. Clair, 2011, 2012), and live aspen root sections become less dense as mortality progresses (Schier, 1975; DesRochers and Lieffers, 2001). Low light in conifer-dominated areas may also increase browse susceptibility of regenerating aspen due to reduced production of defensive compounds (Calder et al., 2011).

2.3. Effects of MPB-caused mortality on aspen overstory present before beetle attack

Overstory aspen should experience a growth release following MPB-caused mortality if increases in light, water and nutrient availability are sufficient. However, in forests with high surviving conifer basal area, aspen may be unable to increase growth due to competition and related mortality (Shepperd et al., 2001; Calder and St. Clair, 2012). Aspen is susceptible to mechanical wounding, drought stress, and freeze–thaw events (Walters et al., 1982; Frey et al., 2004) that could occur following MPB-caused forest structure changes. Sudden canopy openings may damage aspen by reducing humidity, leading to atmospheric water stress (Bladon et al., 2008) and increasing evaporative demand (Yao et al., 2001; Solarik et al., 2012). Increases in direct light from canopy opening could lead to sunscald by making bark more likely to thaw during sunny winter days and re-freeze at night (Walters et al., 1982; Frey et al., 2004).

We can look at aspen response to conifer removal in partial harvesting studies to inform how aspen may respond to canopy openings caused by MPB. Four years after partial cutting of overstory in boreal mixed hardwood and conifer forest, aspen growth had doubled compared to pre-harvest rates (Gendreau-Berthiaume et al., 2012). However, aspen mortality increased 2–5-fold over background levels following harvest of >50% of conifer basal area (Bladon et al., 2008; Solarik et al., 2012). Elevated mortality has

Fig. 2. Forest of MPB-killed lodgepole pine and aspen. These co-dominant aspen trees grew in a densely-forested environment, resulting in low crown and high height to diameter ratios. These characteristics are likely to elevate risk of mortality following MPB-caused forest structure changes (Bladon et al., 2008; Solarik et al., 2012). Lodgepole snag fall could also damage aspen stems.

been attributed to wounding during harvest and subsequent infection of aspen stems (Walters et al., 1982; Nichols et al., 1993). More recently, Solarik et al. (2012) analyzed variables of harvest treatments, tree characteristics and proximity to machinery corridors and found that the proportion of overstory removed was the strongest predictor of aspen mortality. In forest where 80% and 90% of basal area was removed, residual aspen mortality reached 30% within 5 years, and was 50% by 10 years after harvest. Aspen trees that are co-dominant, have short crown ratios, or have large height to diameter ratios are most susceptible to mortality following partial harvest (Bladon et al., 2008; Solarik et al., 2012), and trees with these characteristics may be negatively affected following MPB-caused mortality (Fig. 2). Aspen mortality was not elevated following harvests that retained half or more of the overstory (Solarik et al., 2012). Together, these studies suggest that aspen growth will likely increase following MPB but may be offset by elevated mortality where MPB kills a majority of the overstory. However, if MPB-caused forest structure changes do increase aspen mortality, there will likely be a secondary "wave" of suckering allowing aspen to persist in these areas (see Section 2.2 for further discussion of regeneration).

3. Mountain pine beetle effects on stand structure and composition

We are not aware of any published research that has explicitly focused on the effects of MPB-caused mortality on aspen. However, several studies of MPB or spruce beetle (*Dendroctonus rufipennis*) effects on forest structure and composition have reported information about aspen (Klutsch et al., 2009; DeRose and Long, 2010; Collins et al., 2011; Diskin et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012). Much of this work has been in nearly pure lodgepole pine forests, so results do not adequately represent the effects of MPB on forest of different compositions that occur across the MPB-affected landscape. Also, pre-disturbance data to compare with post-MPB conditions is lacking. This research provides insight into the effects of MPB-caused tree mortality on aspen but must be interpreted cautiously because of these limitations.

The obvious initial effect of MPB-caused tree mortality is a large loss of live overstory, and, potentially, a shift in species composition toward non-MPB host species present, usually subalpine fir, Engelmann, white or hybrid spruce, and/or aspen (Table 1) (Klutsch et al., 2009; Vyse et al., 2009; Collins et al., 2011; Diskin et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012). Lodgepole pine density and basal area has been reduced by 50–90% in many areas affected by the current outbreak. The impact of this mortality on overall stand condition will depend on forest species composition and structure before the outbreak (Diskin et al., 2011; Collins et al., 2011; Pelz and Smith, 2012). In nearly pure lodgepole pine forest, total live basal area has been reduced by up to 94% (Collins et al., 2011). A high MPB-caused mortality rate will necessarily increase aspen relative abundance/basal area where there is a substantial component of aspen and small component of other conifers (Diskin et al., 2011; Pelz and Smith, 2012). In forests where there is high spruce and fir basal area, aspen is, and is likely to remain, a small component following beetle outbreak (Table 1) (Klutsch et al., 2009; Diskin et al., 2011; Collins et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012). It is difficult to know how many of the millions of hectares affected by MPB have experienced a relative increase in aspen because of variation in forest composition and MPB mortality (Meddens et al., 2012).

Average aspen regeneration (stems < 2.5 cm dbh) densities are highly variable in MPB-affected forests where aspen is present, ranging from ~100 to 2000 stems ha^{-1} (Table 1). Though sucker densities are high in some areas (Diskin et al., 2011; Collins et al., 2011; Pelz and Smith, 2012), a clear relationship between aspen sucker density and overstory pine mortality has not yet been demonstrated (Nelson, 2009; Pelz and Smith, *unpublished data*). Klutsch et al. (2009) did not find greater sucker density in areas with than without MPB-caused mortality. Aspen sucker numbers reported in MPB-affected forests are similar to those in stands without beetle disturbance (e.g., Kashian et al., 2007; Kulakowski and Veblen, 2007; Kurzel et al., 2007; Rogers et al., 2010; Smith and Smith, 2005). Qualitatively, aspen regeneration density in MPB-affected forests seems most related to aspen presence/basal area, and negatively related to shade tolerant conifer basal area. In Colorado, highest aspen densities occur where overstory aspen are present but there are few shade tolerant conifers (Diskin et al., 2011; Collins et al., 2011; Pelz and Smith, 2012). This is not surprising because of the positive relationship between aspen suckering and overstory basal area (Graham et al., 1963; Frey et al., 2003) and the negative effect of increasing conifer density on aspen suckering and vigor (Shepperd et al., 2001; Calder and St. Clair, 2012).

Regeneration density could also be related to dead or damaged aspen overstory because apical dominance can suppress suckering (Farmer, 1962; Schier et al., 1985; Frey et al., 2003). We found only two studies of MPB effects that report dead overstory aspen stems, and in both dead aspen stems equal or surpass live aspen stems (Table 1) (Kayes and Tinker, 2012; Pelz and Smith, 2012). In aspen-dominated forests, regeneration density can be very inconsistent despite universal aspen presence (Kashian et al., 2007; Rogers et al., 2010). Regeneration in these forests is thought to occur in patches initiated following overstory aspen dieback (Kashian et al., 2007). Similar patch mortality and regeneration dynamics will likely be at play in mixed aspen and conifer forests following MPB-caused mortality.

Aspen recruitment to the overstory will be limited by competition with conifers, even where substantial suckering occurs. In the majority of MPB-affected forest surveys, subalpine fir is the most abundantly regenerating species and its density often exceeds several thousand stems per hectare (Klutsch et al., 2009; Vyse et al. 2009; Diskin et al., 2011; Collins et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012). In forests where >15% of the overstory is subalpine fir and Engelmann spruce, aspen makes up ⩽10% of the regeneration density (Table 1). Aspen is one-third of total regeneration in forests with few overstory shade-tolerant conifers,

Table 1
Reported average (standard deviation) aspen regeneration and overstory following the 2000s mountain pine beetle outbreak. All values are per hectare; basal area measured in m^2 ha^{-1}. Aspen suckers are stems <1.4 m tall and aspen saplings are stems >1.4 m tall and <2.5 cm dbh, except aspen saplings include stems up to 3.8 cm dbh for Pelz and Smith (2012). Aspen regeneration is highly variable, in part likely due to variation in aspen presence within sites. Note the high dead aspen stems number in studies where dead aspen overstory is reported. Data collection for all studies occurred from 4 to 9 years following the onset of epidemic-level MPB-caused mortality. Table includes all peer-reviewed literature regarding MPB in North America that report aspen density numbers. "–" indicate data not reported by publication.

Study	Location	Forest species	Stems	Basal area	Overstory characteristics								Understory characteristics		
					MPB mortality		Lodgepole pine		Aspen				Aspen densities		
					% Stems killed	% Basal area killed	% Stems before/after MPB	% Basal area before/after MPB	% Stems before/after MPB	% Basal area before/after MPB	Live stems	Dead stems	Suckers	Saplings	% of total regeneration
Klutsch et al. (2009)	Central Colorado, USA	Lodgepole, spruce, fir, aspen	1534	36	28	54	67/56	77/54	3/4	1/3	42 (12)	–	–	70 (15)	3
Diskin et al. (2010)	North-central Colorado, USA	Lodgepole, spruce, fir, aspen	950	–	67	–	70/50	–	<1/<1	–	2 (2)	–	117 (80)	8 (5)	2
		Lodgepole, aspen	563	–	58	–	87/73	–	9/16	–	456 (110)	–	2406 (776)	216 (114)	67
Collins et al. (2011)	Central Colorado, USA	Lodgepole, spruce, fir, aspen	1099	31.3	59	94	97/93	98/92	1/2	1/5	11(0.4)	–	449 (150)	784 (249)	43
Pelz and Smith (2012)	West-central Colorado, USA	Lodgepole, aspen	702	33.6	36	48	71/54	77/55	18/29	14/26	128 (39)	107 (98)	906 (189)	916 (165)	36
		Lodgepole, spruce, fir, aspen	701	29.9	12	17	43/35	49/38	3/4	2/2	24 (11)	46 (105)	190 (106)	123 (55)	3
Kayes and Tinker (2012)	South-central Wyoming, USA	Lodgepole, spruce, fir, aspen	1162	–	38	–	82/71	–	2/3	–	51 (109)	105 (229)	382 (879)	81 (224)	11

but is still often outnumbered by conifers (Table 1). The only exception is in the dry lodgepole pine forest type reported by Diskin et al. (2011), where aspen is 67% of the regeneration density.

Research on the longer term (>10 years) effects of beetle outbreaks shows there is potential for aspen to increase in areas where forest stand structure, species composition, and browsing conditions are favorable (DeRose and Long, 2010; Seager, 2010; Pelz and Smith, 2012). Aspen will likely respond more positively to MPB in forests with few shade-tolerant conifers (Collins et al., 2011; Pelz and Smith, 2012) than forests with more shade-tolerant conifers (Pelz and Smith, 2012). In forest with 91–100% lodgepole overstory before MPB-caused mortality, Collins et al. (2011) predict that aspen portion of the overstory will increase substantially. Using forest growth simulations, they project aspen will increase from nearly zero to about 25% of overstory basal area (about 7 m^2 ha^{-1}) by 40 years after outbreak, after which aspen will decline in dominance. This increase is due to recruitment of about 1100 aspen stems ha^{-1} post-outbreak. In forest of similar composition elsewhere in Colorado, there was a trend, though not statistically significant, of aspen basal area growth following a 1980s MPB outbreak (Pelz and Smith, 2012). Basal area increased from 2.1 ± 0.6 in the 1980s to 4.6 ± 1.7 m^2 ha^{-1} by the 2010s. However, in contrast to projections by Collins et al. (2011), there was not consistent aspen recruitment following the 1980s outbreak in these lodgepole-aspen forests. Aspen overstory density did not change in the 30 years following the 1980s outbreak (from 106 ± 37 stems ha^{-1} to 128 ± 39 stems ha^{-1}), and stems 3.8–12.7 cm dbh decreased (from 191 ± 126 to 44 ± 16 ha^{-1}). Aspen density only increased (from 11 ± 11 to 916 ± 165 ha^{-1}) in the smallest size class (<3.8 cm dbh), and most of these stems likely initiated during the current MPB outbreak. In forests with subalpine fir and Engelmann spruce in the overstory, neither aspen basal area nor density increased despite high lodgepole pine mortality and sucker numbers after the 1980s MPB outbreak (Pelz and Smith, 2012).

The contrast between projections of substantial aspen recruitment following MPB-caused mortality (Collins et al., 2011) and the minimal recruitment observed by 30 years after MPB outbreak in western Colorado (Pelz and Smith 2012) may be due to the effects of browsing. Aspen stems are often damaged by wild ungulates, such as elk (*Cervus canadensis*) and deer (*Odocoileus* spp.), and by domestic livestock. Aspen recruitment is unlikely when animals browse on 40% or more of aspen stems (Ripple and Beschta, 2007; Zeigenfuss et al., 2008), and high browsing damage levels can prevent aspen recruitment even if sucker numbers and growth are high (Baker et al., 1997; Suzuki et al., 1999; Kaye et al., 2005; Romme et al., 2005; Neff et al., 2007). In MPB-affected areas of Rocky Mountain National Park, approximately 75% of suckers were browsed in 2007 (Nelson, 2009). When forests were re-surveyed 3 years later, suckers were much less prevalent and in many cases had disappeared (Renwick, 2012). In Utah, recruitment following spruce beetle outbreak was limited by intense browsing. Aspen in most areas were heavily browsed and were dramatically younger and shorter than aspen growing where protected by inaccessible, rough, igneous terrain. Aspen that initiated following 1970s/1980s spruce beetle-caused forest mortality successfully recruited only on this lava substrate, despite suckering of aspen elsewhere (DeRose and Long, 2010).

Fallen MPB-killed snags could protect suckers from browsing. Forests in many areas affected by MPB will have 50–100 + Mg ha^{-1} of tree boles on the forest floor within 20–30 years (Page and Jenkins, 2007a; Page and Jenkins, 2007b; Klutsch et al., 2009; Simard et al., 2011; Pelz and Smith, 2012), providing a formidable barrier to domestic, and perhaps wild, ungulate browsing. Following a 1970s/1980s MPB outbreak in eastern Oregon, density of aspen stems >2.5 m tall was highest in areas surrounded by fallen boles

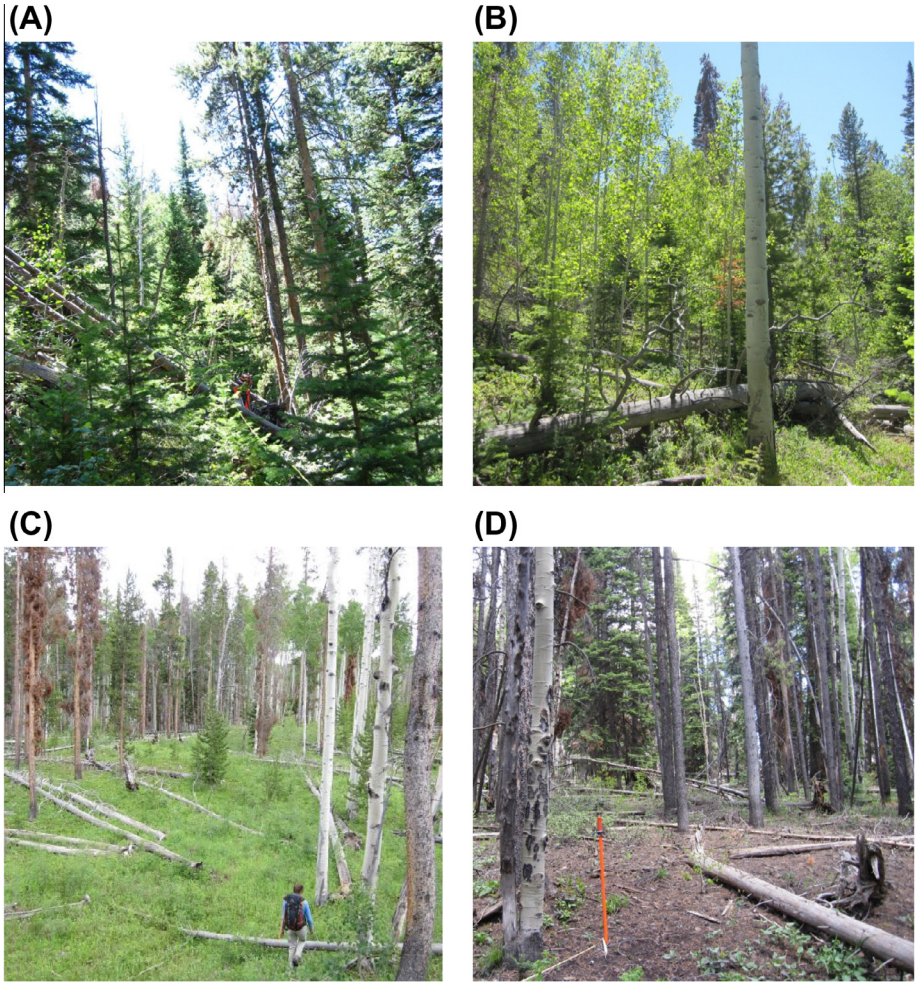

Fig. 3. Variation in aspen regeneration and forest conditions in western Colorado. These areas had substantial mortality from a 1980s outbreak and are also being affected by the current outbreak. (A) Aspen sprouts are present in this forest with a large Engelmann spruce and subalpine fir component. Relatively dense surviving overstory following 1980s MPB likely favored shade-tolerant regeneration. Aspen is unlikely to recruit to the overstory surrounded by dense shade-tolerant competition. (B) Successful aspen recruitment. Low residual overstory following the outbreak provides ample opportunity for aspen growth. The single older aspen may indicate that aspen overstory damage/mortality occurred, promoting sucker growth. Fallen MPB-killed snags may provide protection for these stems from browsing. Note the subalpine fir regeneration beneath the aspen; with time, these shade-tolerant trees will likely take over this area. (C) There is very little recruitment of aspen despite an open canopy created by the fall of snags killed in the 1980s. Dense forb and grasses cover could have reduced successful suckering, or perhaps intense browsing pressure eliminated most sprouts in this area. (D) There was no aspen recruitment following 1980s mortality in this area with relatively low light, high density of shade-tolerant conifers and declining aspen overstory. All photos from Pelz and Smith (2012) study area.

(Seager, 2010). We observed that patchy aspen recruitment following 1980s MPB-caused mortality in western Colorado occurred in some areas, perhaps where suckers were protected from browsing by fallen snags and/or topography (Fig. 3).

Currently published research does not clearly show that aspen forest cover will increase due to MPB. We therefore suggest a series of questions that warrant further research (Table 2). Systematic studies that quantify suckering response to nutrient increases, light availability or soil warming would help us understand if, and to what extent, MPB-caused forest changes trigger aspen suckering. It is clear that that even high initial post-outbreak sucker densities may not result in successful aspen growth to overstory (e.g., Baker et al., 1997; Romme et al., 2005; Forester et al., 2007; DeRose and Long, 2010; Pelz and Smith, 2012; Kulakowski et al., 2012). Future studies should continue to investigate the role of forest density and composition in determining aspen recruitment. We know aspen suckers in partial shade environments (common in mixed aspen-conifer forest) have slowed growth and increased mortality (Longpre et al., 1994; Smith and Smith, 2005). Is there a light level at which we can expect substantial aspen recruitment to occur? It is also not clear if conifer species plays an important role in aspen success if light environments are held constant. Is aspen more likely to recruit to the overstory with lodgepole pine than subalpine fir if forests are of a similar basal area/density? Finally, more information about browsing damage to aspen suckers in MPB-affected forests is essential.

4. MPB effects on aspen at the large-scale and over the long-term

In previous sections, we have reviewed ways MPB-caused tree mortality may affect aspen regeneration, growth, and health at local scales. However, MPB is affecting lodgepole pine forest throughout much of its range, and has caused mortality on thousands of hectares dominated by other pine species (Fig. 1) (Meddens et al., 2012). To predict response to MPB, it is therefore necessary to examine how factors that affect aspen at local scales will vary at large spatial scales. We also consider how large-scale, long-term processes such as climate change and future fires will affect aspen response to MPB-caused forest disturbance in western North America.

Table 2
Research which specifically targets these questions will help us better predict if aspen will increase its dominance in the millions of hectares of pine forests affected by mountain pine beetle in western North America.

(1) Factors that control aspen suckering and successful recruitment:
a. How do soil conditions (temperature, moisture content and nutrient availability) affect suckering when apical dominance remains intact?
b. To what extent does apical dominance of intact aspen stems inhibit growth of suckers from the same clone following MPB-caused forest disturbance?
c. To what extent does light availability control aspen growth and recruitment? Is there a threshold light availability level that allows for successful aspen recruitment and survival in the overstory? Does species composition of surrounding forest impact sucker growth and recruitment success if light availability is held constant?
(2) MPB-caused effects on suckering and forest conditions that could affect suckering/recruitment:
a. How do aspen sucker densities in MPB-affected forests compare to sucker densities without MPB disturbance?
b. How does MPB-caused forest structure change affect abiotic factors that may initiate aspen suckering, including light, soil temperature, moisture and nutrient availability, and how do these factors vary with canopy opening patterns? How do forest MPB mortality rate, species composition, age structure and density affect post-MPB canopy opening patterns?
(3) MPB-caused effects on existing overstory aspen:
a. Does abrupt canopy opening following MPB-caused mortality increase rates of aspen overstory growth or mortality?
b. Will falling MPB-killed snags cause overstory aspen damage and mortality?
c. If post-MPB overstory aspen mortality occurs, does it promote a second "wave" of suckering? How successful is this secondary suckering at recruiting to the overstory?
(4) Characteristics of MPB-affected areas that will affect aspen response at largest scales:
a. What is the presence and condition of aspen in MPB-affected forests of western North America?
b. In forest where aspen is present, how much of the forest overstory has been killed by MPB? What is the density and species composition of remaining overstory?
c. What are rates of browsing damage to aspen stems across MPB-affected areas? In what areas can we expect browsing to limit aspen recruitment?
d. How will changing temperature and precipitation regimes affect aspen and its response to MPB-caused forest disturbance?

4.1. Variation of post-outbreak forest conditions and browsing pressure in MPB-affected landscapes

Suckering density, growth and future survival of aspen are affected by forest conditions, which vary substantially among MPB-affected areas. Quantification of forest species compositions, MPB-caused mortality levels, overstory and regeneration density in forests where aspen occurs would be useful in predicting aspen response. The interaction of outbreak-caused mortality rates and different species compositions will produce a number of different forest conditions. Determining the effect of the various forest conditions on factors likely to affect aspen health, such as light levels, soil temperature, soil moisture, nutrient availability, and aspen overstory mortality, will result in a better understanding of the potential effects MPB-caused mortality will have on aspen at large spatial scales.

Understanding how browsing damage varies across the MPB-affected landscape would improve predictions of aspen response to MPB-caused mortality. Wild and domestic animal densities can vary widely, and management practices can have a huge effect on ungulate numbers. Wild ungulate densities are often extremely high in protected areas (Baker et al., 1997; Suzuki et al., 1999; Romme et al., 2005). Grazing allotments are common on public lands, which add domestic to wild ungulate browsing pressure (Kay and Bartos, 2000; Jones et al., 2011). High forage quality and quantity in an area may reduce browsing damage rates to aspen (Edenius and Ericsson, 2007; van Beest et al., 2010), but the positive effect of landscape context disappears with very high browsing pressure (e.g., Kaye et al., 2005). Browsing rates are likely to be lower on steep slopes (Suzuki et al., 1999; Forester et al., 2007; Binkley, 2008). These and other published relationships between browsing and topography, animal numbers/range management practices, and landscape-scale forage availability could be used to create maps estimating the probability or severity of ungulate damage to aspen. Together, information about browsing intensity and post-outbreak forest composition/structure across the range of MPB-affected forests would allow general predictions about where, and to what extent, aspen cover might increase. This could also help managers prioritize efforts to promote aspen, such as browsing protection or silvicultural treatments, in areas where recruitment might otherwise be unlikely.

4.2. Potential effects of changing climate on aspen following MPB

Changes in temperature and precipitation will mediate aspen response to MPB. However, teasing apart the effects of MPB-caused forest changes and climate is complicated due to their interaction. MPB outbreaks (Raffa et al., 2008) and aspen mortality events (Worrall et al., 2010; Hanna and Kulakowski, 2012) are both associated with warm temperatures and drought. Consequently, disentangling their effects on aspen health is difficult without experiments, rigorous models or other carefully-designed research. As discussed earlier, canopy openings following MPB-caused mortality are likely to change humidity and temperature, which can negatively affect aspen (Yao et al., 2001; Bladon et al., 2008; Solarik et al., 2012). These effects may be similar to those from climate warming, and the negative effects of climate and canopy structure change on aspen health are likely to be additive. Research quantifying the relative contribution of forest canopy opening and climate change to aspen stress and mortality would therefore have important management applications.

Climate will alter aspen regeneration because temperature and moisture are important drivers of aspen sucker growth. We must consider that climatic fluctuations and MPB-caused changes in forest structure will interact in their effects on aspen regeneration. Kaye (2011) attributed an aspen recruitment pulse initiated during the 1970s and early 1980s in the central and southern Rockies to wetter conditions related to oscillations in oceanic temperature cycles. Yet, this pulse also coincides with a MPB outbreak that affected large areas in Colorado, Wyoming, Montana, Oregon, Alberta, and British Columbia, so forest structure changes rather than climate may have initiated regeneration. Finally, as climate warms MPB could facilitate aspen expansion to higher elevations and latitudes (e.g., Hawkes et al., 2004; Zier and Baker, 2006; Landhaeusser et al., 2010b), despite the fact that seedling survival may be low in much of the Rocky Mountains due to lack of mineral soil exposure following MPB (Astrup et al., 2008; Vyse et al., 2009; Collins et al., 2011) and typically dry summer weather patterns (Kay, 1993; Romme et al., 2005). For example, aspen established by seed in new locations following 1980s mortality in forest of British Columbia (Hawkes et al., 2004), indicating that MPB-mediated range expansion is possible and already occurring.

4.3. Compound effects of fire and MPB-caused mortality on aspen

Fires that occur following MPB-caused mortality may affect aspen differently than if fires occurred without MPB. The interaction of these disturbances seems likely to favor aspen over conifer regeneration (Kulakowski and Veblen, 2007; Buma and Wessman, 2012; Kulakowski et al., 2012). Aspen regenerates vigorously following fires, often taking over sites with high pre-fire conifer basal area (e.g., Schier et al., 1985; Buma and Wessman, 2012; Smith et al., 2011). Lodgepole pine also can dominate sites after fire. Lodgepole cones are often serotinous, and following fire they can release large numbers of seed that germinate and grow well on mineral soil. By killing overstory trees, MPB-caused mortality reduces lodgepole pine seed source and will potentially decrease post-fire lodgepole pine seedling density. Reduced conifer seedling density post-fire is likely to favor aspen (Kulakowski et al., 2012).

MPB-caused mortality may also affect aspen by changing fuel complex and potential fire effects on post-fire regeneration. There is ongoing debate about the effects of MPB on fuels and fire and a full discussion of this topic is beyond the scope of this review (e.g., Bigler et al., 2005; Jenkins et al., 2008; Klutsch et al. 2009; Kulakowski and Veblen, 2007; Page and Jenkins, 2007a; Page and Jenkins, 2007b; Kulakowski and Jarvis, 2011; Simard et al., 2011; Hicke et al., 2012; Jenkins et al., 2012; Pelz and Smith, 2012; Schoennagel et al., 2012). Generally, small fuels (needles and twigs) accumulate on the forest floor in the first decade following outbreak (Page and Jenkins, 2007b; Simard et al., 2011). As time passes, a buildup of regeneration foliage and coarse woody debris (due to snag fall) near the forest floor is likely to increase soil heating and organic matter consumption if a fire occurs, potentially reducing conifer seedling establishment due to loss of soil biota, structure and organic matter (Neary et al., 1999). Fires that burned in areas with heavy coarse woody fuel loads following blowdown in northwestern Colorado may have similar effects on aspen regeneration to fires that follow MPB-caused mortality. After fire, aspen suckering was equally vigorous in areas that had and had not experienced blowdown, but conifer densities were significantly lower in areas affected by blowdown than unaffected areas (Buma and Wessman, 2012; Kulakowski et al., 2012). The different conifer densities led to different species dominating 8 years after fire: aspen was dominant in areas affected by blowdown, while areas unaffected by blowdown were dominated by conifers (Kulakowski et al., 2012). Because the heavy surface fuels following MPB will be similar to those following blowdown, fires that occur in MPB-affected forests are also likely to favor aspen over conifer regeneration.

5. Conclusion

Aspen recruitment and growth following MPB-caused mortality is likely to be limited by factors including competition with conifers, sucker damage due to browsing, and climate. If promoting aspen is a management priority, protecting suckers from browsing in forest with otherwise favorable conditions could increase recruitment success. In areas dominated by shade-tolerant conifers, promoting fire (Smith et al., 2011) or mechanical harvests where fire is unacceptable (Collins et al., 2011), may be necessary to encourage aspen recruitment following MPB. Managers should also consider that wildfires are likely to increase in frequency/size due to climate change (Westerling et al., 2006), which could favor aspen over conifers in MPB-affected areas (Kulakowski et al., 2012). Overall, though it is reasonable to believe that decreased competition for resources following MPB mortality will have a positive effect on aspen, currently published research cannot confirm or refute this. We suggest that future studies which focus specifically on aspen response to MPB-caused mortality, and how this response may vary across the affected landscape, will further our understanding of how this widespread disturbance will affect aspen in western North America.

Acknowledgements

Discussions about aspen ecology with Wayne Shepperd were very helpful to the ideas presented in this review. Thank you to Seth Ex for helpful comments. We also thank the organizers and attendees of the Western Aspen Alliance's Resilience in Quaking Aspen symposium for insightful conversation regarding aspen response to mountain pine beetle. Suggestions from the guest editor and two reviewers greatly improved the quality of this manuscript.

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