Examine the utility of advance regeneration for reforestation and timber production in unsalvaged stands killed by the mountain pine beetle: Controlling factors and management implications

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Abstract

In unsalvaged stands killed by the mountain pine beetle, the release and growth of shade-tolerant advance regeneration may provide an important reforestation pathway. Stands developing from advance regeneration may restock quickly and provide short- to mid-term harvest opportunities, but the variability in release and growth responses among these stands will create numerous management challenges. This paper reviews and synthesizes relevant scientific literature to suggest some important differences between reforestation from advance regeneration following mountain pine beetle (MPB) attack and conventional reforestation (i.e., planting or natural reforestation following “normal” disturbance events) in regards to stand dynamics and growth. Particular attention is given to the primary traits of advance regeneration that may determine its successional and growth trends following MPB attack, including species composition, abundance and spatial distribution, developmental characteristics, and overall health. Effective management of advance regeneration following MPB attack will require a better understanding of the stand-level conditions and processes that control its growth. As well, management tools such as stocking standards that are suited to managing even-aged forests may need to be re-examined to address the unique conditions of unsalvaged MPB stands.

KEYWORDS: advance regeneration, mountain pine beetle, reforestation, stand composition, stand dynamics, timber supply.

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Introduction

Salvage harvesting and planting in stands attacked by mountain pine beetle (Dendroctonus ponderosae Hopkins; MPB) in British Columbia are widely employed to maximize economic recovery from the current infestation and to quickly reforest the affected areas (Eng 2004; Coates and Hall 2005). Due to economic, operational, ecological, and social constraints, a large portion of the infestation will not be salvaged in the short term, if at all (Eng 2004; Hawkes et al. 2004; Pedersen 2004a and 2004b; Stockdale et al. 2004; Coates and Hall 2005; Mitchell 2005). The reforestation and productivity of these unsalvaged stands looms as a critical concern (Mitchell 2005) with predictions of an impending mid-term timber supply shortage.

Silviculture treatments (including site preparation, planting, and thinning) may be necessary to ensure timely restocking of unsalvaged MPB-attacked stands. Operational and economic barriers to these treatments may limit their widespread use (Mitchell 2005), and many stands will be left to regenerate naturally. The release of existing advance regeneration in these stands may provide an important pathway in addressing future timber-supply shortages (Veblen et al. 1991; Archibald and Arnup 1993; Oliver and Larson 1996; Puttonen and Vyse 1998; Greene et al. 1999; Coates 2006). However, a reliance on advance regeneration following MPB attack may have important and unknown implications on portions of the timber harvesting land base. Stands developing from advance regeneration following MPB attack may be quite different than managed forests or forests originating after other types of disturbances, and these differences should be incorporated into management objectives and timber-supply predictions. This paper reviews and synthesizes relevant literature to suggest how stands developing from advance regeneration after MPB attack may be unique in species composition, abundance and spatial distribution of regeneration, developmental traits of regeneration, and health and long-term viability of regeneration. Particular attention is given to potential implications of MPB disturbance on stand development, yields, and forest management practices in unsalvaged stands.

Given the lack of specific information on stand development following MPB epidemics of the current scale, observations from similar stand-releasing disturbances (e.g., windthrow, partial cutting, intermediate-utilization logging, other bark-beetle outbreaks) that mimic stand-level MPB impacts may provide insight into post-attack stand dynamics and advance regeneration development. Such analogous studies are incorporated into this discussion.

Natural Reforestation Pathways Following Mountain Pine Beetle Attack

Natural forest regeneration following disturbance typically occurs along two pathways (which can co-occur):

1. the reorganization of existing vegetation (e.g., advance regeneration), and (or)
2. the recruitment of new vegetation (McCarthy 2001).

Epidemic bark-beetle infestations have been traditionally viewed as “stand-releasing” disturbances that favour the former pathway, with existing understorey trees and vegetation being released from suppressing canopy cover to form the new forest (Veblen et al. 1991; Oliver and Larson 1996; Greene et al. 1999; Hawkes et al. 2004; Schulze et al. 2005). Stand-releasing disturbances generally do not favour the establishment of new seedlings. Where understorey vegetation exists (either tree advance regeneration or non-tree vegetation), its development following stand-releasing events can limit the recruitment of new tree seedlings through competitive exclusion (Wickman et al. 1986; Cole et al. 1999; Webb and Scanga 2001; Wohlgemuth et al. 2002; Shepperd et al. 2004; van Hees 2005), sometimes restricting the recruitment of new tree regeneration for many decades (Cole et al. 1999; Wohlgemuth et al. 2002). As well, some stand-releasing disturbances do not create suitable conditions (e.g., seedbed, understorey light) for seedling germination and establishment (Oliver and Larson 1996; Mitchell 2005). In MPB-attacked stands with limited advance regeneration, natural reforestation through new seedling establishment may be highly
variable (Mitchell 2005); such stands should be identified for possible silviculture interventions to ensure timely restocking (Coates and Hall 2005; Mitchell 2005).

Advance Regeneration in Stand Development After Disturbance

Lodgepole pine has among the widest ecological amplitudes of any conifer in British Columbia (Klinka et al. 2000), and it can occur as a dominant seral species under a wide range of climatic and edaphic environments in the province. The greatest residual abundance of advance regeneration following MPB attack likely occurs in stands in which pine is a seral species. Where advance regeneration exists, its growth following MPB attack should increase in most stands in response to the enhanced availability of primary resources (i.e., light, moisture, and nutrients) associated with canopy death and breakup. In the absence of subsequent disturbances (e.g., fire or harvesting), this understory tree cohort should form a major component of the next forest stand (Veblen et al. 1991; Coates et al. 1994; Oliver and Larson 1996). The successional patterns and processes of stands forming from advance regeneration remain largely unknown, however, as most studies have focussed on their early developmental characteristics (Messier et al. 1999). As such, a gap in understanding remains about succession and growth in stands of advance-regeneration origin, from establishment up to full maturity or rotation, particularly as it relates to anomalous disturbances (e.g., large-scale MPB attack) that can create unpredictable conditions.

Existing literature suggests that development and yields of stands originating from advance regeneration following MPB attack will be variable. Stands with healthy, vigorous, and well-spaced advance regeneration may develop quickly after MPB attack (given sufficient release) and become merchantable within 40–80 years after release in partial-cut stands in the Engelmann Spruce–Subalpine Fir and Interior Cedar–Hemlock biogeoclimatic zones (Meidinger and Pojar 1991).

Uncertainty regarding the growth of released advance regeneration in unsalvaged MPB-attacked stands will challenge the capacity of forest practitioners to set management objectives and predict future yields and harvests (Messier et al. 1999), at least relative to even-aged stands of silvicultural origin or natural reforestation after fire. Some of the primary factors controlling the response of advance regeneration to release following MPB attack (discussed below) include species composition, abundance and spatial distribution, developmental traits of the trees (i.e., height–age relationships), and general health and long-term viability.

Species Composition of Advance Regeneration in Stand Development Following Mountain Pine Beetle Attack

Where advance regeneration is being employed to address timber-supply gaps, tree species composition of regenerating MPB-attacked stands must be considered in the context of market demands (Shepperd et al. 2004) and industry-processing capacities. Whereas stands of fire origin tend to be colonized by fast-growing pioneer species, stands of advance-regeneration origin tend to form from more shade-tolerant species (Oliver and Larson 1996). Within the range of the current MPB infestation, common advance-regeneration species include Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco), interior spruce (Picea glauca Voss × P. engelmannii Parry), and subalpine fir (Coates et al. 1994; Schulze et al. 2005).
Mitchell 2005). Even under canopies dominated by other species, these species may be found in high densities because of their tolerance of low-light conditions (Veblen et al. 1991; Kneeshaw and Burton 1997; Kobe and Coates 1997; Shepperd et al. 2004) and their ability to germinate on undisturbed forest floors (Burton et al. 2000). Shade-intolerant species, such as lodgepole pine (Pinus contorta Doug.), trembling aspen (Populus tremuloides Michx.), or paper birch (Betula papyrifera Marsh.), may be found within the advance-regeneration cohort in uneven-aged stands on edaphically limiting sites (Stuart et al. 1989; Williams et al. 1999; Kneeshaw et al. 2002; Hawkes et al. 2004; Daintith et al. 2005), or associated with large canopy gaps (McCarthy 2001).

Following overstorey death, the growth responses of understory trees will vary between co-occurring species. Strong release responses (i.e., large growth increases) have been observed in more shade-tolerant species, such as spruce and subalpine fir, following windstorm or insect disturbance (Groot 1984; Doucet 1988; McCaughey and Ferguson 1988), even after prolonged suppression (Alexander 1984; Kneeshaw et al. 1998; Antos et al. 2000). Shade-tolerant trees can adjust their crown physiology and structure in response to different light regimes, which makes them well adapted to shaded understories and highly responsive to incremental increases in light following disturbance (Messier et al. 1999; McCarthy 2001). Understorey subalpine fir and spruce were found to release well following a spruce bark-beetle epidemic with sustained growth for over 40 years, possibly up to 100 years in some cases (Veblen et al. 1991). True firs generally release faster following light changes than co-occurring species such as spruce (Doucet and Boily 1995); in some studies, however, species such as spruce have been shown to exhibit more sustained release (McCaughey and Schmidt 1982; Boily and Doucet 1993).

Conversely, shade-intolerant species (where present in the advance-regeneration cohort) will likely exhibit relatively poorer release responses compared to shade-tolerant species following MPB attack due to their more fixed crown physiology and structure (Messier et al. 1999; Williams et al. 1999) and more lingering effects of prolonged suppression (Gavrikov and Sekretenko 1996; Wright et al. 2000; Kneeshaw et al. 2002). If management targets seek to utilize shade-intolerant advance regeneration to form future tree crops on some sites, it will be critical for forest managers to assess the potential of these trees to release and achieve adequate growth.

Release differences between shade-tolerant and shade-intolerant trees may be amplified by residual stand structure after MPB attack. Coates and Hall (2005) estimated that understorey light in MPB-attacked stands might remain quite stable for up to 5 years following canopy death due to residual crown structure. They further suggest that pine snags will continue to shade these understories for up to 10 years. Large numbers of snags may remain standing on attacked sites for 15 years or longer (Veblen et al. 1991; Lewis and Hartley 2005; Schulze et al. 2005). Shade-tolerant species should better utilize the gradual increases in light levels likely to follow MPB attack compared to shade-intolerant trees (Messier et al. 1999; McCarthy 2001; Krasowski and Wang 2003). The residual shading of snags and live-canopy trees should limit the expansion of aggressive, non-tree vegetation (Lieffers and Stadt 1994; Ricard and Messier 1996; Krasowski and Wang 2003; Kurulok and McDonald 2004), which could otherwise suppress advance regeneration after MPB disturbance (Bassman et al. 1992; Stone and Wolfe 1996).

Generally, MPB disturbance will favour the release of shade-tolerant species over shade-intolerant species, which may result in the rapid conversion of stands from lodgepole pine to more shade-tolerant conifers. In stands with mixed-species advance regeneration, competitive interactions between species may direct stand dynamics and growth following MPB attack. For example, Shepperd et al. (2004) found that subalpine fir formed dense thickets in pine forest understories in Colorado, restricting the growth of co-occurring spruce and pine advance regeneration. In such a scenario, the species composition of the advance-regeneration cohort may need to be manipulated to promote faster growth and release of target species, if spruce and pine are preferred species compared to subalpine fir.

Abundance and Spatial Distribution of Advance Regeneration in Stand Development Following Mountain Pine Beetle Attack

Low densities and (or) clumpy distributions of advance regeneration associated with stand and site conditions may be common in MPB-attacked stands (Figures 1 and 2; Bella 1983; Stuart et al. 1989; Weetman and Vyse 1990; Arnup 1996; Kneeshaw and Bergeron 1996; Puttonen and Vyse 1998; McCarthy 2001; Parish and Antos 2005). This raises concerns about the extent of silviculture interventions (e.g., thinning and planting) which may be required to ensure adequate and well-spaced stocking under current reforestation requirements (Archibald and Arnup 1993; Shepperd et al. 2004). Although pure pine stands comprise a minority of the land base currently under MPB attack (Burton 2006), these stands will
endure the most severe impacts of the beetle infestation. Advance regeneration can be infrequent under pure pine stands unless significant canopy gaps exist (Stuart et al. 1989; Mitchell 2005). In the absence of adequate advance regeneration, special reforestation interventions may be required. The abundance of advance regeneration should generally increase with greater diversity in overstorey tree species (Arnup 1996; Greene et al. 1999).

Inventories of advance regeneration in the area affected by MPB are generally lacking (Burton 2006); however, some studies suggest that relatively high densities of advance regeneration are fairly common. Coates (2006) found that 30–45% of sample plots contained densities of advance regeneration (seedlings and saplings) above 700 stems per hectare in pine-leading, MPB-killed stands in the Sub-Boreal Spruce zone. Burton (2006) described a study that found 41% of forest stands or strata with greater than 80% lodgepole pine by volume had conifer-regeneration densities of over 600 stems per hectare. A partial-cutting study in the Interior Douglas-fir zone by Kaipainen et al. (1998) found that total advance-regeneration densities under mixed canopies of lodgepole pine and Douglas-fir were above 400 stems per hectare.

Total stem densities of advance regeneration may not necessarily indicate “sufficient stocking.” Non-uniform spatial patterns (i.e., clumping), which often characterize advance regeneration in natural forests, are a result of both stand dynamics (e.g., gap-forming processes) and stand structure (e.g., nurse logs, exposed mineral soil on tip-up mounds) (Weetman and Vyse 1990; Arnup 1996; Puttonen and Vyse 1998). Clumpy distributions can result in low overall stand occupancy even when stem densities are high, leading to reduced release potential because of competitive stress (Oliver and Larson 1996), and diminished timber yields (Smith 1988). Clumping can also affect traits important for future stand regeneration, such as seed production (Daniel et al. 1979). Management goals that target timber production may need to consider interventions to address clumping issues in some cases. For instance, dense thickets of subalpine fir may require thinning to promote crown expansion and rapid release of target trees (Oliver and Larson 1996).
Tree Age–Height Relationships in Advance Regeneration in Stand Development Following Mountain Pine Beetle Attack

Because of the complex interactions in age–height relationships, the size of advance-regeneration trees may not indicate their release potentials in MPB-attacked stands. Studies examining the release of advance regeneration have observed conflicting patterns in trees at different developmental stages. Superior release responses in advance regeneration were observed in smaller trees (Givnish 1988; Oliver and Larson 1996; Claveau et al. 2002), larger trees (McCaughey and Schmidt 1982; Peterson and Pickett 1995; Webb and Scanga 2001), younger trees (Oliver and Stephens 1977; Ferguson and Adams 1980; Helms and Standiford 1985), or without any age dependence (Johnstone 1978; Boily and Doucet 1993; Puttonen and Vyse 1998). This suggests complex condition-specific responses. The age and size distribution within the advance-regeneration cohort may vary widely in any given stand, resulting in non-uniform release responses following MPB attack. Consequently, some stands developing from advance regeneration following MPB attack may be characterized by structures and distributions that become increasingly complex and uneven-sized over time. Accurate growth and yield predictions in such stands will likely be difficult, especially compared to even-aged managed forests where regeneration cohorts display relatively uniform size and growth over the rotation.

It may be possible to identify biologically based indicators to assess the release potentials of advance regeneration at different developmental stages. Ruel et al. (2000) suggested that age–height growth relationships may be controlled by tree live crown, which has been shown as a good indicator for release potential (Helms and Standiford 1985; Tesch et al. 1993; Ruel et al. 1995). Other potential tree release indicators may include pre-release height growth, height-to-diameter ratios, the degree of internodal and nodal branching, and the degree of apical control (McCaughey and Ferguson 1988; Murphy et al. 1999; Ruel et al. 2000). Additional consideration of potential release indicators for advance regeneration can be found in Ruel et al. (2000).

Health and Long-term Viability of Advance Regeneration in Stand Development Following Mountain Pine Beetle Attack

The initial health and vigour of advance regeneration will directly influence its release potential in MPB-attacked stands. In some conditions, advance-regeneration trees in MPB-attacked stands will have poor vigour and form, rendering them unacceptable for timber objectives. Rakochy (2005, as cited by Mitchell 2005) found that only about 50% of advance regeneration (all species) could be categorized as healthy within sample plots in MPB-killed stands. Kaipainen et al. (1998) obtained similar results in an advance-regeneration study in the Interior Douglas-fir zone. In addition, some species that will compose a major portion of the advance-regeneration cohort in many MPB-attacked stands (e.g., subalpine fir) may be particularly susceptible to health problems during stand development (Herring 1977; Weetman and Vyse 1990; Ruel et al. 2000).

Furthermore, the long-term health and vigour of released advance regeneration, which will determine its commercial value, may be diminished by stand-level processes resulting from MPB attack. Physical damage to advance regeneration may occur as large quantities of branches and tree stems begin falling into the understorey during stand deterioration following MPB attack. Such damage can result in diminished tree form and health for advance regeneration, although studies have observed conflicting responses of advance regeneration to logging damage (which may provide a good analog for physical damage related to MPB-stand breakup). Damage can also result in disease and subsequent stem decay, a factor that may be especially prevalent in advance-regeneration subalpine fir (Weetman and Vyse 1990; Ruel et al. 2000), though studies have found conflicting results. Studies show both diminished health and vigour (Herring 1977; Weetman and Vyse 1990; Tesch et al. 1993) and resilient recovery (Gordon 1973; McCaughey and Schmidt 1982; Tesch et al. 1993; Ruel et al. 1995) in advance-regeneration responses to logging damage for many of the key species that constitute understorey cohorts in MPB-attacked stands. Overall, little is known about advance-regeneration response to physical wounds (Ruel et al. 2000), and this represents an important gap in our understanding of the reforestation of MPB-killed stands.

Additionally, the long-term health and vigour of advance regeneration may be indirectly influenced by MPB attack through changes in hydrological cycling on some sites (Rex and Dubé 2006). The death of overstorey trees reduces evapotranspiration and precipitation interception (Hélie et al. 2005; Rex and Dubé 2006), which can increase soil moisture. On moist sites, anaerobic soil conditions may develop (Oliver and Larson 1996), potentially leading to reduced vigour and (or) increased mortality in advance regeneration (Kozlowski et al. 1991).
**Management Implications**

The utilization of advance regeneration for reforestation and timber production in MPB-attacked stands may entail some important management implications worth considering.

**Stocking Criteria**

Current reforestation stocking standards may be hard to achieve within the advance-regeneration cohort in MPB-attacked stands because of undesirable species compositions and irregular spacing. Some accommodations in stocking standards may be required to promote the utilization of advance regeneration for reforestation in appropriate MPB-attacked stands.

**Species Composition**

Some advance-regeneration species (e.g., subalpine fir) are not considered preferred or acceptable in certain subzones (Weetman and Vyse 1990) where they may dominate the understories. Currently, forest managers must consider the consequences of either accepting these species or undertaking expensive silviculture interventions (e.g., planting, thinning) to manipulate species composition in unsalvaged, MPB-attacked stands.

**Tree Spacing**

The implications of advance-regeneration spatial patterns in MPB-attacked stands on timber-yield predictions need to be better understood. Although total densities of advance regeneration in some MPB-attacked stands may indicate adequate stocking, poor spatial distributions may cause release responses to be low. Currently, forest managers must consider the consequences of correcting stocking within the advance-regeneration cohort (e.g., planting and/or thinning) to meet well-spaced stocking requirements, which may not be economically and/or operationally feasible in many unsalvaged, MPB-attacked stands.

**Growth and Yield**

Potential yields in stands of advance-regeneration origin may be modest compared to even-aged managed forests. To maximize productivity in these stands, forest managers might consider a range of options. Stands with sufficient healthy advance regeneration may become merchantable relatively quickly (Archibald and Arnup 1993; Puttonen and Vyse 1998; Coates 2006). However, because of the complexities of advance-regeneration response to disturbance, many stands may require silviculture interventions, such as planting or thinning to increase yields and/or reduce rotation length. Stand fertilization may also be useful in increasing understorey tree growth and reducing rotation length following MPB attack. This treatment is effective at releasing dense fire-origin stands of height-suppressed lodgepole pine (e.g., Newsome and Perry 2003). Fertilization may be particularly well suited to cohorts of suppressed lodgepole pine advance regeneration that may exhibit delayed or diminished growth response after release. The feasibility of this treatment for advance regeneration should be investigated.

Mixed-species stands with live canopy trees after attack may provide unique opportunities for partial cutting and uneven-aged silviculture. Heath and Al-faro (1990) found that volume losses from MPB-killed pine could be partially offset by an increase in radial growth by dominant Douglas-fir. Cole and Amman (1980) found similar results for spruce and Douglas-fir stand recovery after MPB outbreaks in Wyoming and Idaho. Delaying harvesting (Hawkes et al. 2004) or selectively harvesting only attacked pine in these stands may result in stand-level growth increases that will partially offset volume losses attributable to MPB.

Given the possible management options available to forest practitioners, growth and yield predictions in complex stands with advance regeneration will present a significant knowledge gap. The inherent complexity of advance regeneration (in species abundance or composition, development, health, and degree of release) and the scale of the current MPB infestation may significantly diminish the utility of models (Kimmins et al. 2005) for predicting stand growth and yield. Rather, forest managers may be forced to make stand-level decisions (Kimmins et al. 2005) to identify conditions with sufficient, well-distributed, and healthy advance regeneration that can be expected to release and develop into a merchantable harvest within a reasonable time frame. The current MPB outbreak provides a unique opportunity to establish permanent sample plots in unsalvaged stands, which should enhance our understanding of regeneration and stand dynamics in complex conditions following large, stand-releasing disturbances.

**Operational Limitations**

Where stands of advance-regeneration origin are assessed as understocked or requiring some management to maximize productivity, the implications of stand conditions and limitations must be considered. Planting may be needed on sites with low or patchy stocking of advance regeneration, which may be prohibitively expensive due,
in part, to unique safety issues created by MPB attack. Residual snags will likely require removal from the stand to ensure worker safety and to create suitable planting microsites. The non-timber value of these snags must be balanced against the range of management objectives. Vegetation competition may become a critical limiting factor after site preparation or once the snags have fallen. Given its expense and difficulty, planting may be a silviculture treatment best reserved for productive sites with low advance regeneration.

Dense thickets of advance regeneration may require thinning to control species composition or inter-tree competition. Again, the presence of residual snags will limit the ability to work safely in these stands, and removal of these snags will have to be considered carefully from an economic and ecological perspective for all potential stand treatments, including harvesting (either partial cutting or complete salvage). Finally, residual snags and fallen stems from MPB-attacked trees in unsalvaged stands may create operational access and safety limitations at rotational harvest of the advance regeneration, particularly on mature, productive sites where the best advance regeneration may occur.

Conclusions

British Columbia’s impending mid-term timber supply shortage in the wake of the MPB infestation will increase pressure to maximize production on the timber harvesting land base. Forest managers must carefully consider how to manage unsalvaged MPB-killed stands, which may contribute significantly to future timber supplies and other non-timber values. The production potential of advance regeneration following MPB attack and its potential contribution to mid-term timber supplies will be highly variable due to complex interactions among primary factors that are poorly understood (e.g., species composition, abundance and spacing, developmental characteristics, general health and vigour, and the degree of release following MPB attack). Unsalvaged MPB-killed stands and their characteristics will force managers to consider unique and specific options that best reflect the condition of a stand and balance social, ecological, and economic values.

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Unsalvaged MPB-killed stands and their characteristics will force managers to consider unique and specific options that best reflect the condition of a stand and balance social, ecological, and economic values.

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Examining the utility of advance regeneration for reforestation and timber production in unsalvaged mountain-pine-beetle-killed stands: Controlling factors and management implications

How well can you recall some of the main messages in the preceding discussion paper? Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. In general, the release of what understorey tree species should be be favoured by stand conditions after mountain pine beetle attack?
   a) Fast-growing pioneer species such as lodgepole pine.
   b) Mid- to late-seral species, such as spruce, Douglas-fir, and subalpine fir.
   c) Deciduous species, such as trembling aspen and paper birch.
   d) No particular preference will likely be observed.

2. What factors may permit the presence of lodgepole pine advance regeneration in forest understories?
   a) Large canopy gaps.
   b) Edaphic site limitations (moisture or nutrient deficits).
   c) Uneven-aged stands.
   d) All of the above.

3. Some studies have suggested that a significant portion of MPB-attacked stands have high densities of advanced regeneration. Some of these stands, however, may not become well-stocked, productive forests because:
   a) Clumpy spacing may result in poor stand occupancy and low production.
   b) Composition may be dominated by unacceptable species.
   c) Health and vigour of advance regeneration may be diminished by poor spacing.
   d) Health and vigour of advance regeneration may be diminished by physical damage during stand breakup.
   e) All of the above.

**Answers**

1. b
2. d
3. e