Forests for Tomorrow Adaptive Management Initiative

Synthesis of Information on Selected Topics & Clarification of Key Uncertainties

EXCERPT:

Viability of Seed from Dead Lodgepole Pine

Prepared for:

Alanya C. Smith
Forest and Range Evaluation Program/ Forests for Tomorrow
Ministry of Forests and Range, Forest Practices Branch
8th Floor - 727 Fisgard St.
Victoria, BC

Prepared by:

Laurie Kremsater, MSc, RPF, RPBio
Glen Dunsworth, MSc, RPBio
Alan Vyse, MSc, RPF
Carol Murray, MSc, RPBio, ESSA Technologies Ltd.

Contact: Laurie Kremsater
Ph: (604) 856-3329
lkrem@shaw.ca
28360 Starr Rd.
Abbotsford, B.C. V4X 2C5

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The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

How long does seed from dead pine remain viable and have acceptable germination success? How much seed remains in the cone bank of dead pine and how fast does it decline over time? These are question that FFT recipients asked mainly due to concern that areas left to regenerate naturally may not do so due to non-viable seed. Seed viability affects both natural regeneration under stands attacked by mountain pine beetle and determines opportunity to collect seed from those stands. We do not explicitly address the impacts of the mountain pine beetle epidemic on seed availability for nurseries, but rather focus on how seed viability impacts decisions of FFT recipients. We mention cone collection only to suggest broad guidelines should recipients collect their own seed. We do not evaluate impacts to the provincial seed supply of the vast amount of dead pine. Seed viability is one of many factors affecting success of natural regeneration under dead pine stands.

Lodgepole pine is usually characterized by serotinous cones – those that remain closed on the tree when seed maturation is complete. In serotinous cones, the cone scales are sealed together with resin and require a temperature of between 45 and 60ºC for the bond to be broken. Not all trees within a stand will possess serotinous cones, although stands may be predominantly serotinous or non-serotinous. Seed depends mostly on levels of cone serotiny.

Serotinous cones are generally considered to be discrete, closed units isolated from the tree and the environment as long as serotiny is maintained. There have been many observations of viable seed from serotinous cones more than 10 years old. During 2006, BC's Tree Improvement Branch looked at the viability of seed from trees that had been dead for 10 years and found viable seed in all collections investigated.

Concern for loss of viable seed arises when there is a lack of serotiny. Although most MPB-killed lodgepole pine stands may initially have a canopy seed bank, serotiny is being lost on many sites because of the increase in direct and indirect solar radiation reaching the defoliated crowns. Cones closer to the ground will achieve high temperatures sooner and, therefore, open first. Conditions within many of these killed stands are limiting the window of opportunity to secure the canopy seed bank. Whether the disseminated seed will form a stand is uncertain and highly variable by site. Considerations include the rate of seed release, degree of mineral soil exposure, predation of seeds, and the environmental conditions of the site.

Prepared for Alanya Smith, by the FFT AM team: Laurie Kremsater, Glen Dunsworth, Alan Vyse, Carol Murray.
Contact: Laurie Kremsater, Phone: (604) 856-3329, lkrem@shaw.ca, 28360 Starr Rd., Abbotsford, B.C., V4X 2C5

There is also the potential for there to be a seed quality issue if a tree is dying and trying to develop cones at the same time. There may not be adequate reserves to try and prevent dying and transport sugar to the cones, resulting in poor quality or non-viable seed.

Another concern expressed pertains to the storage characteristics of lodgepole pine seed. The Tree Improvement Branch (2008) and Tree Seed Working Group (2007) observed and quantified excellent storage characteristics with this species and estimate an average linear decrease in germination capacity of only 0.05% per year or 1% in 20 years. There should not be any significant concerns regarding the longevity of the large-scale collections taking place today, although seed may be reduced in abundance in the future due to the smaller area of lodgepole pine producing seed post-beetle. (In terms of seed yield (kg of seeds per hl of cones), there has been a trend towards decreased yield in the 2006 and 2007 collection years. Average yield increased from 2001 to 2005, but has subsequently dropped. The most reasonable explanation for this apparent drop in seed yield is the greater proportion of class 3 and class 4 cones appearing in seedlots).

Solutions:

1) For natural regeneration, attempt to promote conditions conducive to seed germination. The probability of natural regeneration can be increased by removing dead pine stems, increasing mineral soil exposure and spreading the cone-bearing branches uniformly across the site. Coates (2008) noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. This is not due to seed viability, but to site and light factors.

2) For seed collection, collect seed from dead trees only if no seed is available from seed orchards or from live natural stands. Follow standard cone collection procedures and be aware of cone classes. Class 4 and 5 are non-serotinous or damaged cones and these should not be collected. Class1 are fully serotinous cones. Classes 2 and 3 are more subjective, as they are based on the proportion of the cone that is weathered. Class 2 cones have partial weathering (up to 66%) and class 3 cones have between 67 and 100% weathering.

The Issue

An outstanding regeneration question is how long seed from dead pine remains viable and has good germination success. This affects FFT recipients' decisions on whether to rely on natural regeneration or plant a stand. It also affects opportunities to collect seed.. Seed viability is one of many factors affecting success of natural regeneration under dead pine stands. Seed viability is maintained for extended periods in serotinous cones of lodgepole pine but seed may not be viable when cones are not serotinous or lose serotiny (see below).

Most of the concern regarding seed viability arises from observations of the lack of natural pine regeneration in stands killed by mountain pine beetle. Coates (2008) for example, noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. *This lack of regeneration, however, is likely not due to seed viability, but to site and light factors. Studies reviewed below suggest that viable seed is present in the cones of beetle killed lodgepole pine trees for at least a decade after trees die.*

Basic Biology of Lodgepole Pine Seed Production

(From TIB 2008): Lodgepole pine cones require two growing seasons to mature after pollination (26–27 months after bud differentiation). Fertilization takes place in the season after pollination

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and is followed by growth and development of the embryo, seed coat and megagametophyte (nutritive tissue). Lodgepole pine can begin to form seed cones at 10–15 years of age. The cones can contain between 100 and 130 cone scales. Not all scales are equally fertile. The basal cone scales are sterile – they do not reflex backwards, as there are no viable seeds to disseminate. With the potential for 2 seeds per scale, the average maximum seed potential is 40–60 seeds per cone.

Lodgepole pine is usually characterized by serotinous cones – those that remain closed on the tree when seed maturation is complete. There is variability in serotiny; not all trees within a stand will possess serotinous cones, although stands may be predominantly serotinous or non-serotinous. The coastal variety (var. *contorta*) of lodgepole pine produces mainly non-serotinous cones. In serotinous cones, the cone scales are sealed together with resin and require a temperature of between 45 and 60ºC for the bond to be broken (see Tinker et al. 1994 for a thorough review). The seeds will remain viable within the cones until fire or high temperatures break the resin bond.

Once the serotinous bonds are broken, the cone scales can open and close with changes in atmospheric conditions. Flexing of the cone scales depends on the moisture content of the scales – the higher the moisture content, the greater degree of cone scale flexing and seed release (Hellum and Barker 1980). This is due to differential shrinkage of the top and bottom of the cone scale (Harlow et al. 1964). Depending on cone scale moisture content and atmospheric conditions, seed release may be instantaneous or may occur over several years. Cone serotiny and the associated traits of asymmetry and thickening of cones scales exposed to weathering (or fire) are considered to be more evolved characteristics of the genus *Pinus* (Tree Improvement Branch 2008). (It has been hypothesized that cone serotiny is controlled by a single gene.)

Without fire or extreme temperatures, the annual production of serotinous cones will contribute to the canopy seed bank. Decreased serotiny has been correlated with increased elevation and with increased latitude. A trend of decreased serotiny has also been observed moving from east to west within the interior of BC (M. Carlson, pers. comm., March 2008 in Tree Improvement Branch 2008). It has been observed by many that cone serotiny is rare in young stands, but far more common in older stands. The age of transition is variable, but has been estimated at between 15 and 30 years (Tree Improvement Branch 2008). Young stands produce less serotinous cones and seed is released annually to take advantage of gaps in stand stocking. As stands mature and stocking stabilizes, trees generally become more serotinous and start to build up the canopy seed bank for future regeneration following fire or other disturbance events. The proportion of serotinous cones in a stand has also been linked to the most recent disturbance type. Stands originating from severe fires showed a high proportion of serotinous cones, and those originating from other disturbances or mixed fire severity regimes show a higher proportion of non-serotinous cones.

With all of these interacting factors, it is difficult to define a consistent pattern of cone serotiny across the landscape. Cone serotiny is a highly evolved characteristic allowing the species to take advantage of a wide variety of sites and conditions.

Results of Past Studies

There is little concern about the seed viability of serotinous cones from dead lodgepole pine trees; the concern arises due to lack of serotiny. Serotinous cones are generally considered to be discrete, closed units isolated from the tree and the environment as long as serotiny is maintained. Viability of seed within old, serotinous cones was noted as early as 1880 when

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Sargent (1880 in Tree Improvement Branch 2008) reported germination of seed from 10-year-old serotinous cones.

There have subsequently been many similar observations (see Tree Improvement Branch 2008 for refs.), and in 2006 the Tree Improvement Branch looked at the viability of seed from trees that had been dead for 10 years and found viable seed in all collections investigated. At the 2003 Forest Genetics Council Northern species committee meeting questions arose about collection of seed from dead lodgepole pine. This was primarily in response to the need for increased seed to regenerate beetle-killed stands. An invitation was extended to operators interested in determining whether stands of dead trees still had viable seed. Nine collections from the Nadina forest district were received at the Tree Seed Centre, cone evaluations performed and seed extracted and hand dewinged. The seed quantities were quite small and so germination tests were carried out on unprocessed seed and performed cutting tests on the ungerminated seed. This did not provide estimates of germination capacity for a seedlot collected from these stands, but provided information regarding whether viable seed is present in these dead stands of lodgepole pine. Results of germination tests were low (between 66 and 85% germinants), below the 95% level obtained by most lodgepole pine seedlots collected today, but in part this reflects unprocessed seed. Regardless of germination standards, results indicate that even ten years after tree mortality viable seed can still be found within the cones. This agrees with many studies on the long-term viability of seed on lodgepole pine trees. The reason for the longevity of viable seed is thought to be because following cone and seed maturity, the vascular connection between the cone and tree are broken and the cone functions independently (no further water or sugar exchange). The serotinous cone provides good insulation and protection for the seed. It is possible that in cooler areas seed may not be released from pine after mountain pine beetle attack because temperatures never reach levels to break serotiny. Even if serotiny is broken eventually then understory vegetation may have increased to levels that may outcompete small pine germinants.

Because serotinous cones house viable seeds, seed viability only becomes a concern when cone serotiny is lost. Although most MPB-killed lodgepole pine stands may initially have a canopy seed bank, serotiny is being lost on many sites because of the increase in direct and indirect solar radiation reaching the defoliated crowns, the higher solar energy breaks serotiny. Cones closer to the ground will achieve high temperatures sooner and, therefore, open first. These conditions are limiting the window of opportunity to secure the canopy seed bank. Whether the disseminated seed will form a stand is uncertain and highly variable by site. Considerations include the rate of seed release, degree of mineral soil exposure, predation of seeds, and the environmental conditions of the site.

There is also the potential for there to be seed quality concerns if a tree is dying and trying to develop cones at the same time. There may not be adequate food reserves to try and prevent dying and transport sugar to the cones, resulting in poor quality or non-viable seed. On the other hand, maybe the stresses result in allocation of available resources to reproduction; there is some anecdotal evidence on collections from red and green attack trees. The Tree Improvement Branch (2004) performed some seed evaluations and found no observable difference between seed collected from red and green attack trees. They did not process this seedlot and so do not know the relative proportions of the two tree types, but the final seedlot did achieve a germination of 96%. (The 2004 paper notes that there are also two more seedlots that were collected in 2004 from green and red attack trees that were currently being processed at a private extractor - results from those should be available by now).

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Another concern is the loss of serotiny combined with slow release of seed over time, therefore decreasing seed yield. Loss of serotiny (breaking of bonds) and cone opening are two distinct events that often, but not always occur at the same time, so that serotiny can be lost, but cones don't open fully or quickly and seed can degrade within the cone.

A final concern expressed pertains to the storage characteristics of lodgepole pine seed, however storage concerns seem unfounded. The Tree Improvement Branch (2008) and Tree Seed Working Group (2007) observed and quantified excellent storage characteristics with this species and estimate an average linear decrease in germination capacity of only 0.05% per year or 1% in 20 years. There should not be any significant concerns regarding the longevity of the large-scale collections taking place today.

Solutions

1) Rely more on natural regeneration where canopies after mountain pine beetle attack are open enough to allow light to the ground and break cone serotiny. Also choose areas where understory competition is not intense. For natural regeneration, attempt to promote conditions conducive to seed germination. Removing the overstory would help natural regeneration if light reaching the canopy floor is low (see point 2 below). The probability of natural regeneration can be increased by spreading the cone-bearing branches uniformly across the site (Tree Improvement Branch 2008). Bancroft (1996 in Tree Improvement Branch 2008) describes post-harvest survey procedures and drag scarification methods for naturally regenerating lodgepole pine stands. Most of these treatments, however, have not been attempted under dead canopies. Studies to assess the rate of pine germination are recommended. Coates (2008) noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. This is likely not due to seed viability, but to site and light factors.

2) Where canopies limit light penetration to the ground (either by having dense dead stems or considerable density of live stems after beetle attack), or where cooler climate make release of seed doubtful, or where getting ahead of understory growth is important, then focus on planting rather than relying on natural regeneration.

3) When collecting lodgepole pine seed, collect from dead trees only if no seed is available from seed orchards or if there is no seed from live natural stands for the area. When collecting seed from dead pine, be aware of cone classes to estimate seed viability (Tree Improvement Branch 2008, see Figure 3 below) as this varies by class. Cones have been categorized into 4 or 5 classes based on the likelihood of having good amounts of viable seeds. Class 4 and 5 are non-serotinous or damaged cones and these should not be collected. Class 1 are fully serotinous cones. Classes 2 and 3 are more subjective, as they are based on the proportion of the cone that is weathered. Class 2 cones have partial weathering (up to 66%) and class 3 cones have between 67 and 100% weathering.

Cone crop ratings are quite general and subjective with regards to total cones on a tree and the proportion of trees having a good crop (Tree Improvement Branch 2008). The individual cone standard was 20 filled seeds per cone, but there are many crops being collected that do not meet this standard. The seed need, harvest cost, and whether orchard crops will become available for an area, will drive the decision for seed collection, but a sample evaluation will provide an indication of what can be expected from the crop and the total volume of cones required.

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Key Uncertainties

There seems to be viable seed for at least a decade after trees die. No further investigations into seed viability seem warranted at this time. However, there still remains considerable uncertainty about the factors governing actual germination success. We investigate some of those factors in other background papers (light reaching the understory, pine grass competition, hare damage, rust and mistletoes, and overstory release).

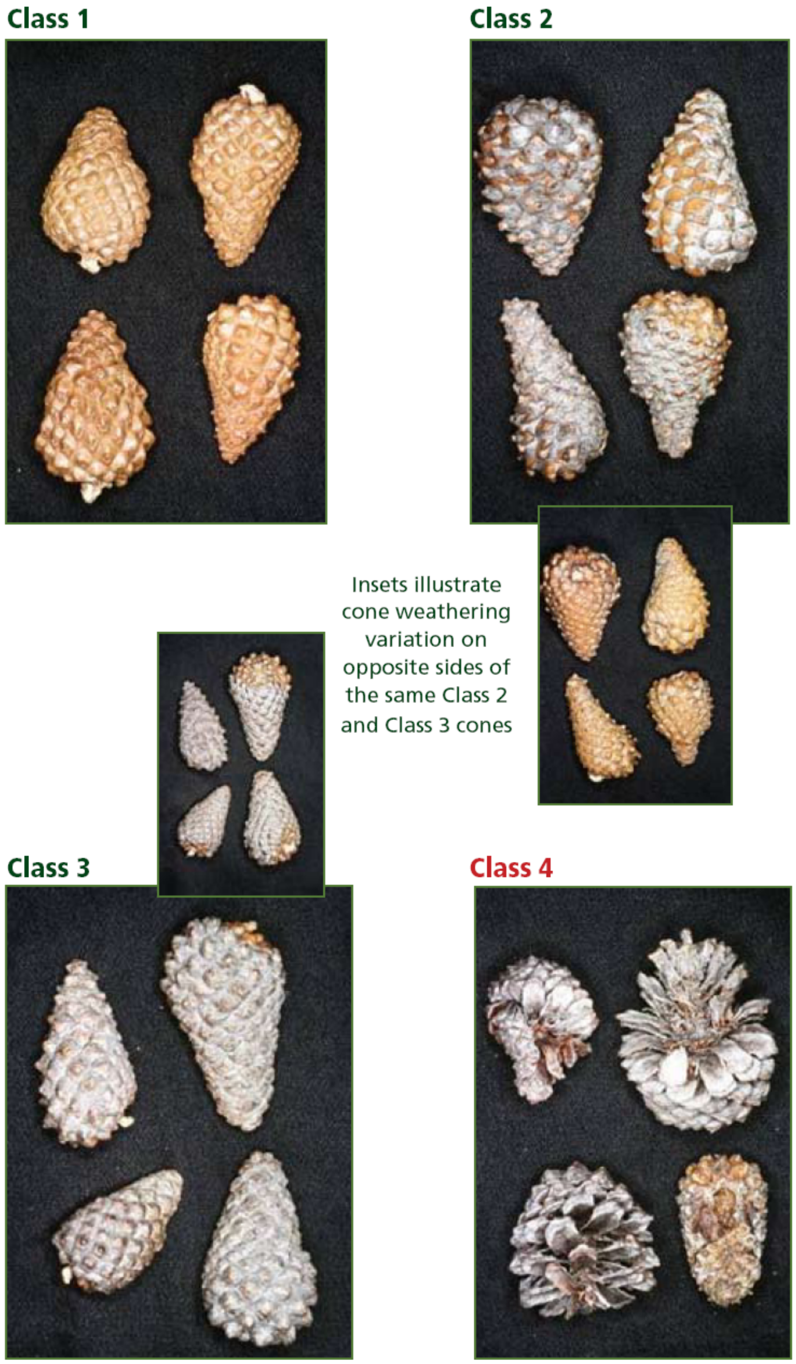

Figure 3. Lodegpole pine cone classes (Tree Improvement Branch 2008).

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