

No Free Lunch: Observations on Seed Predation, Cone Collection, and Controlled Germination of Whitebark Pine from the Canadian Rockies

Adrian Leslie, Department of Environment and Sustainability, Royal Roads University, Victoria, BC; and **Brendan Wilson**, School of Renewable Resources, Selkirk College, Castlegar, BC

Abstract—Whitebark pine is a keystone species of high elevation forests in western North America that is experiencing rapid decline due to fire exclusion policies, mountain pine beetle, and the introduced pathogen, white pine blister rust. Restoration activities include collecting cones and growing seedlings from individuals that show mechanisms for resistance to blister rust infections. Collecting viable whitebark pine seeds is challenging due to high rates of cone harvest by wildlife prior to seed maturation. This has led to the practice of placing protective coverings over the cones early in the summer, and then collecting them when they fully mature in September. We investigate if the added time, expense, and complications of using protective coverings over cone bearing branches are required for the collection of viable whitebark pine seeds. Aside from anecdotal sources, there appears to be no quantitative information demonstrating this is necessary. We determined the optimal time for cone collection by comparing the timing of seed development and germination rates compared to the timing of seed harvest by wildlife in a stand in Banff National Park, in the northern region of its range. Results clearly indicate that in to collect viable seeds from whitebark pine, protective coverings must be put over unripe cones so that collections can be made at any time from late August to late September.

Introduction

Whitebark pine (*Pinus albicaulis*) is the sole North American stone pine (*Pinus* subsection *Cembrae*), a group of five pine species found at high elevations in the northern hemisphere, characterized by large, wingless seeds and indehiscent cones (McCaughy and Tomback 2001). In the Rocky Mountains, whitebark pine extends from 42 to 54 degrees north (Ogilvie 1990). It is an extremely long-lived species, with specimens in Canada found to be over 1100 years old (Luckman and Youngblut 1999). Whitebark pine is a keystone species of high elevation sites due to the many ecological roles it plays in these often steep, harsh environments (Tomback and others 2001). Whitebark pine seeds have a high nutritional value (Lanner and Gilbert 1994) and form a major component of the diets of many birds and mammals, including Clark's nutcracker (*Nucifraga columbiana*), red squirrels (*Tamiasciurus hudsonicus*), and grizzly bears (*Ursus arctos*) (Vander Wall and Hutchins 1983, Mattson and others 2001, Lorenz and others 2008). Clark's nutcracker is the only seed dispersal vector for whitebark pine regeneration because they harvest the seeds and cache them throughout the landscape to be retrieved throughout the following year; it is the un-retrieved seeds that can germinate and grow into

new seedlings (Tomback 2001). However, Clark's nutcrackers and squirrels will often compete for seeds during the cone maturation process and often harvest all cones during poor cone crops or in areas with few whitebark pine trees (McKinney and Tomback 2007).

Whitebark pine is a pioneer species at upper subalpine elevations, where it often facilitates the establishment of other tree species following stand-replacing fire, and is a climax species at tree line, where the conditions are too harsh for other species (Callaway 1998). The pine also plays an important role in slowing snowmelt, regulating spring runoff and stabilizing soils at high elevations (Farnes 1990).

The rapid decline of whitebark pine is well documented in the United States (Kendall and Keane 2001) and gaining better awareness in Canada (Wilson 2007; Smith and others 2008). This decline is due to several anthropogenic factors. Whitebark pine can form continuously regenerating climax communities at the upper tree line, but is often reliant on burned areas to regenerate at lower elevations (Arno 2001). The successful fire exclusion policies of the last century have reduced the availability of burned areas for regeneration and promoted successional development of more shade-tolerant species, such as Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Kendall and Keane 2001). In the past, mountain pine beetle attacks on whitebark pine stands sporadically caused severe damage in some areas (Kendall and Keane 2001). Now, the interaction of warming climatic conditions and fire exclusion appears to be allowing pine beetle to expand its range up in elevation and further endanger whitebark pine stands (Raffa and others 2008).

The greatest concern for the survival of whitebark pine as a species is white pine blister rust, which is caused by the fungus, *Cronartium ribicola*. (Kendall and Keane 2001). This non-native disease has killed up to 60 percent and infected up to 97 percent of the trees in some areas in the Canadian Rocky Mountains (Smith and others 2008). Over several years, the infection spreads from needles into the branches and proceeds towards the main stem. The tree's ability to reproduce is eliminated once the infection kills the upper, cone-bearing branches by choking off nutrients, although it may be many years before the tree completely dies (Keane and Morgan 1994).

The impacts of losing whitebark pine on the landscape are manifold. The heavy reliance by grizzly bears and Clark's nutcracker on whitebark seeds will result in reduced habitat value of high elevation forests (Tomback and Kendall 2001).

The loss of this food source may increase negative human – bear interactions by forcing bears to search for other sources of food at lower elevations where human densities are much higher (Mattson and others 1992). The loss of whitebark could change forest structure by altering successional development at lower elevations (Keane and Morgan 1994). At treeline, whitebark pine often initiates krummholz tree islands, so their loss could result in fundamental changes to vegetation structure (Resler and Tomback 2008).

An important conservation effort for whitebark pine populations is the harvest of seeds from cones in trees that show phenotypic resistance to blister rust. Planting blister rust-resistant seedlings grown from those seeds is considered a major component of the future whitebark forest management in the United States, and in Canada (McDonald and others 2004; Smith and others 2008). However it is difficult to collect viable whitebark pine seeds due to the high rates of cone harvest by Clark's nutcracker and red squirrels prior to seed maturation. This has led to the practice of placing protective coverings over the cones early in the summer, and then collecting them when they fully mature in September (Murray 2007). There are two main difficulties with this practice. The first is the cost of having to visit each tree twice in the season to cage and then retrieve the cones. The second is the damage to the tree caused by climbing onto the softer bark found near the cones, although, soft shoes and care may alleviate the latter problem. This leads to an important question of whether there is a time during the seed population's maturation process where cones can be harvested early enough to avoid significant predation, and yet still produce seed that can germinate. If this were true, it would cut the cost of harvesting drastically. Further, is it possible to visually recognise this point in the development of the seeds through observing key features in either the female cones or field dissection of individual seeds to look at the embryos?

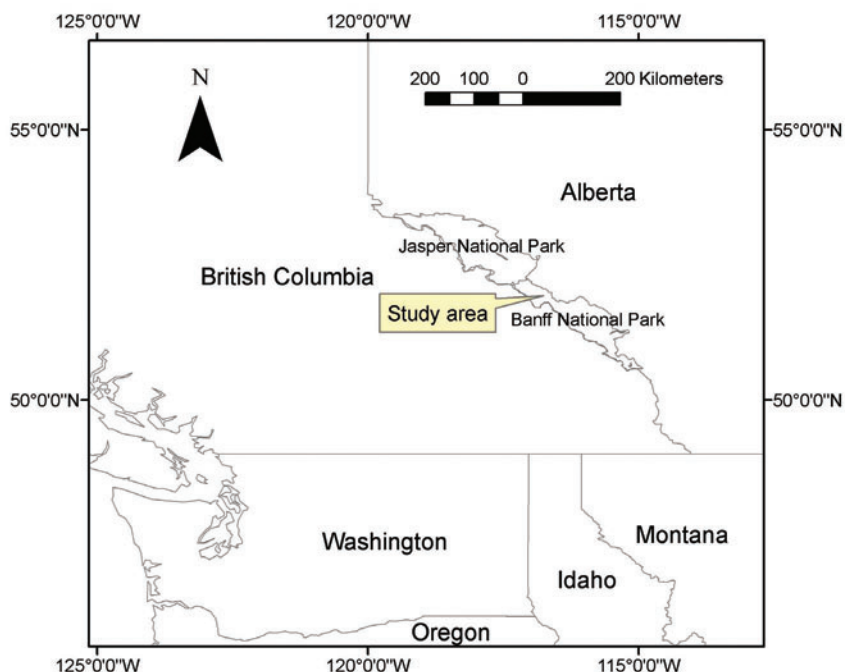
Here we investigate the optimal time for cone collection by comparing the timing of seed development and germination rates versus the timing of seed harvest by wildlife. Our primary purpose is to determine if the added time, expense and complications of using protective coverings over cone bearing branches are required for the collection of viable whitebark pine seeds. Secondly, we wanted to document the morphological changes that occur to the visible cone, and to the seed embryo, through the summer maturation process. We wanted to determine if there was a clear correlation between germination success of seeds and observable characteristics in the exterior cone appearance and with the embryo. This information will allow cone collectors to assess the likely germination rates of seeds based on cone appearance in the field.

Materials and Methods

Study Area

The study was located in the northern part of the whitebark pine range, on the west slope of Mt. Hector, in Banff National Park, Alberta, Canada (51° 35' 08" N 116° 17' 36" E) at 2000m elevation (Figure 1). The average slope of the study site was 62 percent. Walker and others (1982) characterizes the ecosystem type present at this site as having open mixed coniferous vegetation in the upper subalpine eco-region, with calcareous colluvial parent material, and medium textured brunisols or regosols. The site was located in an avalanche path with an understory dominated by *Shepherdia canadensis*, *Arctostaphylos uva-ursi*, *Fragaria virginiana*, *Castilleja miniata*, and several grass species. Repeated breaking and re-sprouting of branches and stems by snow avalanches has created stunted whitebark pine

Figure 1. Study location in Banff National Park, Alberta.



growth forms that allowed easy access to cones from mature trees at ground level.

This area experiences a continental climate. The nearby records from Lake Louise document the recent mean January and July temperatures at -13.8°C and 12.0°C , respectively (Environment Canada 2010).

Cone Observations and Collections

Ten healthy whitebark pine trees with accessible cone bearing branches were located in June 2006. Five of these trees were randomly selected for cone collections and 30 protective cages were placed over cone bearing branches, protecting 72 cones from harvest by wildlife. The remaining five trees had no protective coverings placed over their cones, and were used to monitor timing and rates of wildlife harvest. At the end of June 2006, the numbers of seed bearing cones were counted on each tree, as observed through 8x40 binoculars from marked and recorded locations on the ground. Thereafter, every 11 to 13 days until September 16th, the number of complete, or only partial harvested (<50 percent) cones remaining were recorded from those same locations. Every 11 to 13 days from July 16th until September 16th, a seed lot was collected from 12 protected cones that were randomly selected from the trees with caged branches, for a total of six seed lots from six time periods. The timing of seed and cone development in whitebark pine can vary from site to site and year to year (Halstrom 1993). For this reason, a dissection of three of these cones was completed in the field, where qualitative descriptions of cone and seed development were made. The remaining cones from each collection were dried in a well-ventilated area at room temperature. In late September, seeds could be more easily extracted from the cones, with each cone yielding between 40 and 75 seeds, which were dried at room temperature for 21 days (Young and Young 1992). The six collections resulted in seed lot sizes between 344 and 522 seeds per collection date.

Seed Stratification and Germination

Methods outlined by Burr and others (2001) were followed to break physiological dormancy. All 2,322 seeds were placed in mesh bags and washed for 48 hours under running water, allowing seeds to begin water uptake. All seeds were kept moist and in the dark during a 30-day warm stratification at 21 to 23 degrees Celsius followed with 60-day cold stratification at 2 to 4 degrees Celsius. Every week throughout this period, moldy seeds were removed, and the remaining seeds were cleaned by placing them under a one-hour running water soak.

Each of the six seed lots were evenly and randomly divided into four replicates for germination trials. Twenty five seeds were placed in each 100 x 15mm Petri dish, which were each lined with two United Scientific Supplies Inc. 9 cm circle filter paper. The filter paper was kept moist to allow seeds to uptake water by wicking throughout the germination trial. In a greenhouse, the Petri dishes were randomly

placed under a 12 hr photoperiod at 22°C during the day and 15°C at night. Each week for the next seven weeks, all seeds with emerged radicles exceeding 5mm in length and showed geotropic curvature were deemed to have germinated (Pitel and Wang 1990).

Seed coat dormancy is sometimes dealt with by making a 2 mm nick at the radicle end with a scalpel along the visible line separating the two halves of the seed, which will allow the radicle to emerge from the hardened seed coat (Pitel and Wang 1990). Those seeds that had not yet germinated after the fourth week of the germination trial were nicked in an attempt to increase germination rates.

Data Analysis

The total percent germination was calculated for each replicate from each of the six seedlots. Seeds developing mould during the stratification process and germination trial were included in this calculation as ungerminated seeds. These data were examined for departures from normality as suggested by Sokal and Rohlf (1995), however, no transformations were necessary. The null hypothesis, that there was no difference in germination of seeds between harvest dates, was tested using a one-way ANOVA. A Tukey's HSD post hoc test was used to determine which harvest date means were different. These analyses were only carried out on the collection periods where there was at least some germination recorded (the last four collection periods).

The percent predation of cones was calculated by dividing the number of cones observed on each date by the total number of cones initially observed on each of the five trees in late June. Similar to the germination data, these predation data were assessed for departure from normality. The null hypothesis, that there was no difference in the amount of predation of whitebark pine cones between assessment periods, was tested using a one-way ANOVA. A Tukey's HSD post hoc test was also used to determine which harvest date means were different. With these data, only the middle three recording periods were used in the statistical analysis, as there was no variation in the first two and last three measurement periods (Figure 2). All of these statistical procedures were carried out using R 2.91 (RCDT 2009).

Results

Predation and Germination Trends

Clark's nutcrackers began harvesting the unprotected whitebark pine cones at the start of July, with the birds picking at a few cones but never taking more than 50 percent of the seeds from any one cone. Red squirrels began removing cones and nutcrackers began picking out all the seeds after July 16th. Virtually all cones and seeds had been removed by August 9th (Figure 2). All protective coverings were effective in preventing harvest of cones by wildlife.

At this time, seeds harvested from the trees were just starting to show a low level of germination success. This

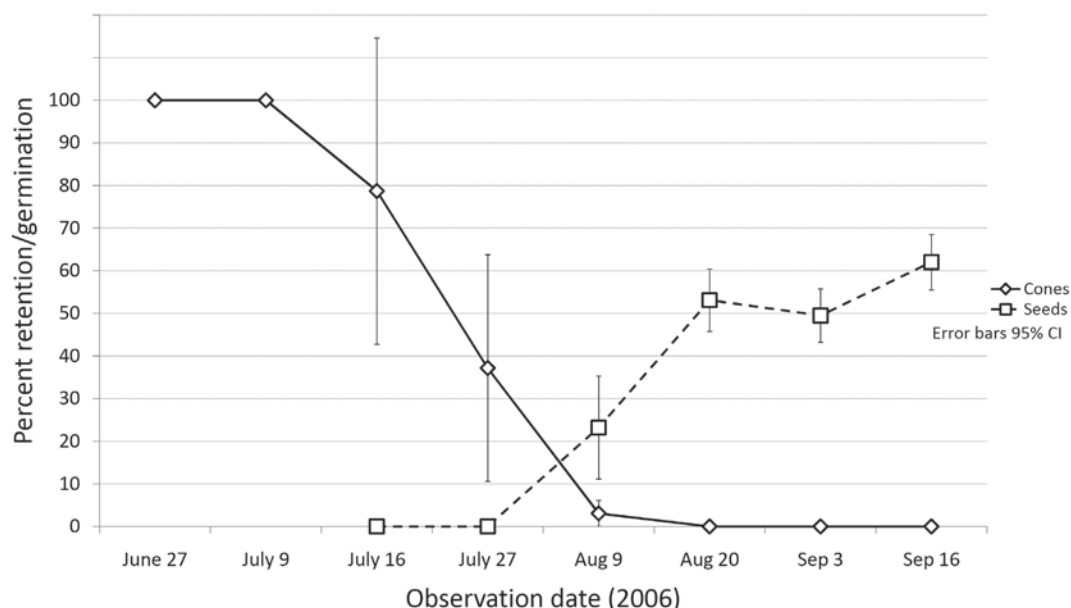


Figure 2. Comparison between the observed percent of cones remaining on study trees to success of seeds germinating from seedlots harvested at the same time of the observations.

success significantly increased over the next two weeks, levelling off to range between 50 percent and just over 60 percent (Figure 2).

Cone Descriptions

Seedlots that had low or no germination were characterized by cones that were very sticky, purple-red in colour, and the cone scales were very difficult to remove by hand. Once the cone scales were removed, some cone scale tissue was still attached to the seed coat (Figure 3). Seeds were soft and easy to cut in half. Seeds that were cut in half revealed embryos that were less than 50 percent of the length of the embryo cavity. The megagametophyte tissue was clear or white and shrunk away from the seed coat.



Figure 3. Appearance of immature cones and seeds harvested on August 9th, 2006. Note the dark red-purple colour of the cone surface and the cone scale tissue still adhering to the seeds.

Conversely, seedlots that had 50 percent germination rates or greater were characterized by cones that were purple—brown, and dry to somewhat sticky to touch. The cone scales were opened slightly or, if closed, came off with little difficulty, exposing two red—brown seeds that were easily removed (Figure 4). No cone scale tissue remained attached to seed coat, and seed coats were very hard. When seeds were sliced in half, embryos extended about 90 percent along the length of the embryo cavity. The mega gametophyte tissue was solid white and did not shrink away from the seed coat, even when left overnight. For a complete qualitative description of each seedlot dissection, see Leslie (2007).

Discussion

The primary goal of this research was to determine if placing protective coverings over whitebark pine cones early in the season is necessary when collecting seeds for restoration purposes. This study showed that during the 2006 field season in this area of Canadian Rockies it was necessary to do so because by the time seeds became mature, almost all cones had been harvested by wildlife. Aside from anecdotal sources, there appears to be no other quantitative information demonstrating this is necessary.

To maximize cone availability, the ideal time to make collection would be just prior to the beginning of wildlife harvest. However, at this time, cones are not yet mature, and no germination is expected. There have been some previous attempts in Alberta to collect seed early and finish its maturation in a controlled nursery environment, but this has not led to successful germination (Barnhardt, personal communication). Waiting until the middle of August when reasonable germination of seeds may be expected means that there may be no cones left to harvest for restoration purposes. There may be a very small window of opportunity for collecting viable seeds without protective coverings in the



Figure 4. Appearance of mature cones and seeds harvested on Sept 16th, 2006. The seeds now are light brown colour and are easily removed from the cone scales.

first week of August, given the data (Figure 2). However even during this time, the numbers of undamaged cones available, and the germination rates of their seeds, would likely be quite small.

The 2006 cone crop in the Canadian Rockies was generally very poor when compared to observations during the previous three summers. During years of good cone crop, slower rates of cone harvest by wildlife is expected (McKinney and Tomback 2007). However, collections for restoration purposes will be taking place in stands where there is a very high rate of blister rust incidence (Mahalovich and Dickerson 2004) where the cone crop will be very small due to the large number of dead, or reproductively dead trees. Where areas of higher blister rust infection have lowered densities of cones produced, these cones are subjected to greater rates of harvest by wildlife, and there are reduced levels of seed dispersal by Clark's nutcracker (McKinney and others 2009). While our study area had low infection rates, the poor cone crop during the study year may have mimicked a cone crop that could be expected when making collections for restoration purposes in areas with high infection rates, such as the stands in the southern border regions (Smith and others 2008).

Recommendations

Our results suggest that when collecting viable whitebark pine seeds, the placing of protective coverings over the cones is necessary. The timing of seed and cone development in whitebark pine can vary between sites and years (Burr and others 2001), so we recommend a visual inspection of the cone and seed development prior to collection. To ensure collection of viable seeds, the optimal time to collect the cones is when the cone is mature to the point that the cone scales are easily removed and dark orange or red seeds are exposed. The seeds should easily come out of the cone and the seed

coat should be hard with no cone scale tissue still attached. We believe that this condition is a strong enough indicator of seed maturity that destructive sampling of a subset of cones is not necessary. In this study, mature seed development was reached by August 20th, but could be slightly earlier or later depending on local conditions.

The germination in the first four weeks before mechanical scarification took place shows that it is not critical to spend the extra time and effort required in this process for mid August seed lots. However, improved germination in the week following the nicking of the seed coat, especially in the two most mature seed lots from September (Leslie 2007), suggests that seed coat dormancy is an issue, especially for the more developed seeds with a harder seed coat.

Germination trials indicate that seeds become fully mature in late August, and remain viable through mid-September (Figure 2). However, because the maturation rate of seeds is variable, and this study was conducted near the northern extent of its range, the timing of cone collection should be based on the stage of cone and seed development rather than the time of year. Seeds are more easily extracted later, as cones dry out and become less sticky. Cone scales open slightly and seeds fall out, making the extraction process easier the longer you wait, but the germination potential will not increase significantly. By mid September, no further development of the seeds is expected and access to the stands may be limited due to the early onset of winter in these high elevation sites.

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