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Assessing post-harvest interim seed storage conditions: a case study of four boreal plant species

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Abstract

The longevity of seeds in storage is modulated by the initial quality as well as the storage conditions. Seeds of four boreal species were stored for a varying amount of time (0, 1, 2, 3 and 4 weeks) at 4°C to determine the appropriate interim storage conditions after harvest and before processing. The highest germination of *Solidago canadensis* (75%), *Shepherdia canadensis* (79%) and *Populus balsamifera* (100%) seeds was observed for the four weeks at 4°C treatment. However, *P. tremuloides* germination was reduced by 22.5% when seeds were kept at 4°C for 3 or 4 weeks relative to the control; the reduction was less (1.5%) when seeds were kept at 4°C for 1 or 2 weeks. No significant difference in mean germination time (MGT) or germination synchrony (SYN) was recorded following the different storage treatments and the control for *Populus tremuloides* or *P. balsamifera*. However, in *Shepherdia canadensis*, the MGT of the seeds in the 3-week treatment was longer, while in *Solidago canadensis*, the 3 or 4 weeks at 4°C treatment improved the SYN relative to the control. The result suggests opportunities exist to store certain boreal seeds after harvest and before processing without reducing their germination characteristics.

Keywords: germination synchrony, interim seed storage, mean germination time, native boreal seeds

Introduction

There is increasing interest across North America in the use of native seeds to restore ecosystem functions. For instance, in boreal Alberta, all mining companies are legally required to conserve biological diversity similar to the undisturbed communities (Alberta Environment, 2010). When higher levels of ecosystem function are required, multi-species plantings are necessary (Lamb, 2018; Pedrini and Dixon, 2020). For many of the native boreal seeds used in afforestation or reforestation programmes, supply is far lower than industry demand. This high demand is likely to be explained by the difficulty of harvesting certain seeds exclusively from the wild. It is also possible that demand is being generated by losses during post-harvest handling (Cobb *et al*., 2020).

Concerns have been raised about the capacity of natural plant populations to continue to provide enough native seeds to support the seed industry into the future. Harvest can be delayed by natural or policy-related causes, which can result in premature or overdue seed collection or failure to process seeds on time. Perhaps the biggest challenge facing this practice is the timing and logistics of deploying an experienced crew who can identify ideal harvest windows and understand the critical seed-handling procedure (Landhausser *et al*., 2019). The best time to harvest trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L.) seeds, for example, is when the capsules are starting to open because of the possibility of the tiny seeds being blown away by the wind (Fung and Hamel, 1993; Day *et al*., 2003). This is particularly true at the late maturity stage, where seeds remain loosely attached to the infructescence. Birds and rodents can easily open matured infructescence and disperse seeds before field harvest (Molnar, 2011).

After harvest, the seed materials go through a series of post-harvest handling stages and storage before propagation. Despite post-harvest handling stages playing a critical role in determining seed viability, germinability or purity, these handling practices are seldom studied. One of the often-overlooked stages of seed production is the storage conditions immediately after collection and before processing. Seeds have a limited amount of time to be extracted from their casings or berries and cleaned before their metabolic functions deplete the seeds of resources. As the seed ages, the loss of viability increases, resulting in seeds with low germination potential (Fotouo-M *et al*., 2015). Seed viability and germination are complex processes and vary greatly between species. Some seeds may be refrigerated for months before cleaning and retain their vigour, while others may lose their germination potential in mere days. For, example, aspen viability is typically quite high (> 90%) if provided with adequate storage conditions (McDonough, 1979; Fechner *et al*., 1981; Robb, 2017). However, the seeds can lose their viability within a few days after harvest due to their tiny size and extreme sensitivity to even minor changes in local temperature and humidity (Fechner *et al*., 1981). Seeds processed immediately after harvest are less prone to postharvest deterioration and germination characteristics tend to improve after harvest. Young (2011) recommended the processing of aspen seeds for storage immediately after harvest since they dry very quickly and cannot survive drastic temperature changes.

Plant species in temperate forests have often been recorded as producing seeds that are “orthodox” and are thus, not damaged by cooling and drying. There are indications where freshly harvested seeds were stored at between 1 and 5°C for < 18 months (short-term storage; Hong and Ellis, 1996) before processing and found more than 90% germination (Smreciu and Gould, 2017). As for longer periods of storage, the seeds can be stored at −18 to −20°C and still maintain their germination potential (Hong and Ellis, 1996; Hong *et al*., 1998). Notwithstanding these findings, there still appear to be serious knowledge gaps regarding our current understanding of the appropriate storage conditions after harvest and before processing of seeds used for post-disturbance restoration of the boreal landscape. When working with species for which seed storage behaviour is not known, the best way to proceed would be to investigate the specific requirements for individual species. This is important because different species have different responses to various storage conditions.

The aim of this study was, therefore, to investigate the appropriate storage conditions for four species that are commonly used in restoration efforts in boreal Alberta, after harvest and before processing without losing their longevity and germination potential.

Materials and methods

Seed materials and treatments

For this case study, we included two tree species (trembling aspen and balsam poplar), one shrub species [Canada buffaloberry (*Shepherdia canadensis* L.)] and one native forb [Canada goldenrod (*Solidago canadensis* L.)]. All seed materials were wild-harvested within the Peace River Region from May to September 2020 (table 1). Seeds of trembling aspen and balsam poplar were harvested from more than 20 individual plants when the infructescence was at the fully ripe stage, but not dispersing seeds. Canada buffaloberry seeds were harvested at a fully-ripe stage, from more than 2000 individual plants. Goldenrod seeds were also collected from 300 individual plants whose pappus were fully exposed, yet not dispersing seeds. Seeds were kept in sealed containers and transported to the facility. Here, the non-extracted seeds were divided into five one-litre portions and stored for either 0, 1, 2, 3 or 4 weeks at 4°C (interim storage treatments). The control seeds (0 weeks) were extracted immediately after harvest, while the rest was placed in labelled paper bags and stored in a 4°C cooler for the duration of interim storage before extraction. After extraction, seeds were dried by placing them on drying trays in a drying rack at ambient conditions until the Equilibrium Relative Humidity of the seeds and the room reached equilibrium (eRH, 15–25%; table 1). The eRH was measured with a HygroPalm HP23-a hand-held meter on quick mode (Rotronic, Bassersdorf, Switzerland). Seeds were then assessed for purity and 100 seed weight (table 2). The pure fraction was then desiccated with activated silica gel at room temperature until it reached the desired moisture content of 4 to 8% (Alberta, 2016). Since these seeds are not always used immediately for restoration following collection, and often need to be stored in the facility for varying amounts of time, we intentionally placed the dried seeds in foil bags and stored them in a –20°C freezer for six months before testing for germination.

Seed germination

Seeds of all treatments were removed from the −20°C storage and germinated using the same procedure. Each treatment consisted of four replicates of 50 seeds. Goldenrod seeds were stratified at 4°C for 12 weeks before incubation in the germination chamber. No stratification was done for the other species. 50 seeds of each replicate were placed in a Petri plate filled with moistened pure silica sand and incubated in a controlled chamber at 25°C, with 12 hours of light and 75% relative humidity. Daily watering with deionised water maintained sufficient moisture within the trays. The germinating seeds were counted every other day for 10 days for trembling aspen and balsam poplar, 50 days for goldenrod and 100 days for buffaloberry. A seed is considered to have germinated once the radical has emerged and has a length equal to that of the seed.

Table 1. Dates and storage conditions for seed collection, extraction and storage of species used in the interim storage study (all dates 2020) on four boreal plant species.

Species	Interim storage period (weeks at 4°C)	Seed collection date	Interim storage end date	Extraction date	–20°C storage date	ERH* (%)
Trembling aspen	0 (Control)	28 May	28 May	28 May	20 Jun	22.40
	1	28 May	04 Jun	04 Jun	20 Jun	24.20
	2	28 May	11 Jun	13 Jun	20 Jun	23.61
	3	28 May	18 Jun	21 Jun	25 Jun	17.86
	4	28 May	25 Jun	28 Jun	01 Jul	24.26
Balsam poplar	0 (Control)	18 Jun	18 Jun	18 Jun	28 Jun	24.42
	1	18 Jun	25 Jun	27 Jun	30 Jun	19.40
	2	18 Jun	02 Jul	04 Jul	09 Jul	20.17
	3	18 Jun	09 Jul	11 Jul	14 Jul	22.20
	4	18 Jun	16 Jul	18 Jul	21 Jul	17.61
Goldenrod	0 (Control)	29 Sep	29 Sep	29 Sep	23 Oct	22.39
	1	29 Sep	06 Oct	07 Oct	23 Oct	24.93
	2	29 Sep	13 Oct	14 Oct	23 Oct	21.44
	3	29 Sep	20 Oct	22 Oct	23 Oct	24.19
	4	29 Sep	27 Oct	29 Oct	03 Nov	23.29
Canada buffaloberry	0 (Control)	12 Jul	12 Jul	12 Jul	12 Jul	16.11
	1	12 Jul	19 Jul	20 Jul	23 Jul	16.36
	2	12 Jul	26 Jul	27 Jul	08 Aug	17.75
	3	12 Jul	02 Aug	03 Aug	08 Aug	23.45

* ERH is the Equilibrium Relative Humidity.

Statistics

Data visualisation and analysis were carried out using the R statistical software (R Core Team, 2020). Four key germination indices (cumulative germination percentage, germination percentage, mean germination time and synchrony) were analysed separately for each species since they germinated at very different rates. The germination pattern between interim storage conditions was determined by plotting the cumulative germination percentage of each species, from the day the test was initiated (0 days) until 100-days later. The germination percentage (GRP) is the number of seeds germinated as per the total number of seeds used in each replicate from the day of germination. The mean germination time (MGT) demonstrates the required time for a seed to germinate after the interim storage treatments. If seeds germinated at the same time, the synchronisation (SYN) index would be 1; if they all germinated at different times, the index would be 0 (Lozano-Isla *et al*., 2019). The GRP, MGT and SYN were calculated using the 'GerminaR' package in R (Lozano-Isla *et al*., 2019). The effects of the initial storage treatments on seed-specific GRP, MGT and SYN were analysed using a generalised linear model (function: *glmer*) with a binomial distribution. The fitted estimates were back-transformed to present for ease of interpretation. Model assumptions were checked with diagnostic plots of fitted and residual values and a histogram of residuals. Residuals conformed to the assumptions of normality and homogeneity of variance, and significance was determined at $\alpha = 0.05$. Treatments were separated with post-hoc (Tukey HSD test) multiple comparison tests using the 'emmeans' function (Lenth *et al*., 2018).

Results

When trembling aspen, buffaloberry and goldenrod seed materials were initially kept for 2, 3 or 4 weeks at 4°C after harvest and before processing, the average total number of seeds extracted, and the total weight were generally greater than for the 'non-stored' control (table 2). As for balsam poplar, more seeds were extracted for the germination test when the materials were initially stored for 1 or 2 weeks at 4°C between harvest and before processing. The purity of trembling aspen seeds was the lowest when seed materials were kept for 2 or 3 weeks at 4°C storage conditions after harvest and before processing (88%, on average). Balsam poplar and buffaloberry recorded the highest mean percentage purity (> 98%) across the five initial storage treatments. Overall, the mean estimated percent purity of goldenrod seeds across the treatments was much lower, ranging from 29.9% when seeds were kept for one week at 4°C to 65.6% when kept for four weeks at the same temperature condition.

Both trembling aspen and balsam poplar showed a similar germination profile with an average of 92% germination reached across the treatments during the first 10 days of germination (figure 1A-B). The cumulative germination of trembling aspen seeds among the treatments varied strongly (i.e., 68–99%). For balsam poplar seeds, the cumulative germination between the different treatments was almost the same (i.e., 95–100%) after 10 days of germination. The effects of the initial storage condition treatments on the cumulative germination rate of buffaloberry seeds were not obvious initially, but we observed an incremental benefit in the three weeks at 4°C storage treatment after the first 10 days, as seeds were then the most rapid to reach 70% germination (figure 1C). The highest cumulative percentage recorded for buffaloberry (60%) occurred in the first 80 days and that of goldenrod (55%) within the first 50 days.

The initial storage condition treatments used in this study affected the GRP ($P <$ 0.0001) of trembling aspen seeds, but not the MGT ($P = 0.125$) or SYN ($P = 0.102$) (figure 2A-C). The GRP of trembling aspen seeds when kept for 1 or 2 weeks at 4°C between harvest and processing was 92 and 99%, respectively; these values were comparable to that in the 'non-stored' control (97%) but significantly greater than those seeds stored for either three weeks at 4°C (81%) or four weeks at 4°C (68%; figure 2A). The mean GRP, MGT and SYN of balsam poplar seeds, however, did not differ ($P = 0.241$) between the initial storage condition treatments (figure 2D-F). As for goldenrod seeds, a longer period of storage (i.e., four weeks at 4°C) after harvest and before processing improved the GRP ($P < 0.0001$) and SYN ($P = 0.018$), as compared to the 'non-stored' control (figure 3D, F). Although initial storage condition treatment did not affect ($P = 0.051$) the germination time of goldenrod seeds, the overall MGT was slightly lower when the seeds were kept for three weeks at 4°C after harvest and before processing (figure 3E).

Table 2. Total number of seeds extracted per litre of harvested seed material, the total weight of extracted seeds (g), the weight of 100 seed samples (g) and purity (%) over the interim storage treatments for four boreal plant species.

Species	Interim storage (weeks at 4°C)	100 seed weight (g)	Total weight (g)	Total number of seeds	% Purity
Trembling aspen	0 (Control)	0.012	5.72	47,443	99.19
	1	0.009	7.80	85,130	94.74
	2	0.011	10.35	97,393	86.78
	3	0.01	10.08	105,550	89.89
	4	0.009	9.36	106,616	94.68
Balsam poplar	0 (Control)	0.041	17.25	42,358	99.77
	1	0.045	20.00	44,272	99.54
	2	0.048	20.61	42,572	98.65
	3	0.046	14.00	30,468	99.77
	4	0.044	13.50	30,483	99.80
Goldenrod	0 (Control)	0.008	23.40	3,047	98.56
	1	0.009	24.50	3,121	99.21
	2	0.007	26.00	3,212	99.84
	3	0.009	28.00	3,821	98.80
Canada buffaloberry	0 (Control)	0.008	0.77	9,724	46.63
	1	0.008	1.08	14,361	29.94
	2	0.007	1.58	22,034	32.73
	3	0.008	3.02	36,932	32.65
	4	0.009	3.86	42,562	65.60

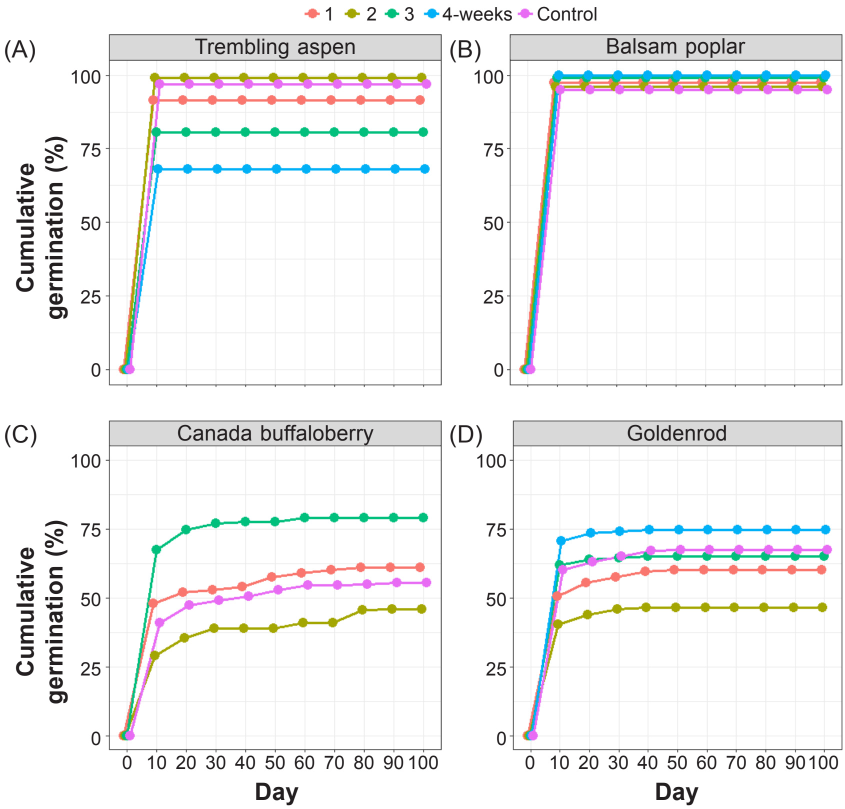

Figure 1. Cumulative germination (%) over 100 days for seeds of (**A**) trembling aspen, (**B**) balsam poplar, (**C**) Canada buffaloberry and (**D**) goldenrod in response to different interim storage treatments (1, 2, 3 or 4 weeks at 4°C), and non-stored control (n = 4).

Discussion

The long-held notion that interim storage of boreal seed materials for an extended period (> 24 hours) and at certain temperatures before extraction can negatively impact germination (Fechner *et al*., 1981; Fairey *et al*., 2001) is challenged by our results, as final germination seems to be unaffected by the initial storage treatment. In the present study, we used 4°C for the initial storage and −20°C for the longer freezer storage as our seeds are considered 'orthodox' which implies that they maintain longevity and germination when stored at low temperatures (De Vitis *et al*., 2020). Seed storage behaviour experiments confirm this, and 0 to 5°C is recommended for short-term storage (< six months) and −18 to −20°C for longer periods (Solberg *et al*., 2020). Germination characteristics generally increased when freshly harvested seeds were kept at 4°C and over periods greater than the non-stored control. The improvement in germination characteristics supports the beneficial effects of drying and cooling orthodox seeds after harvest (Hong and Ellis, 1996; De

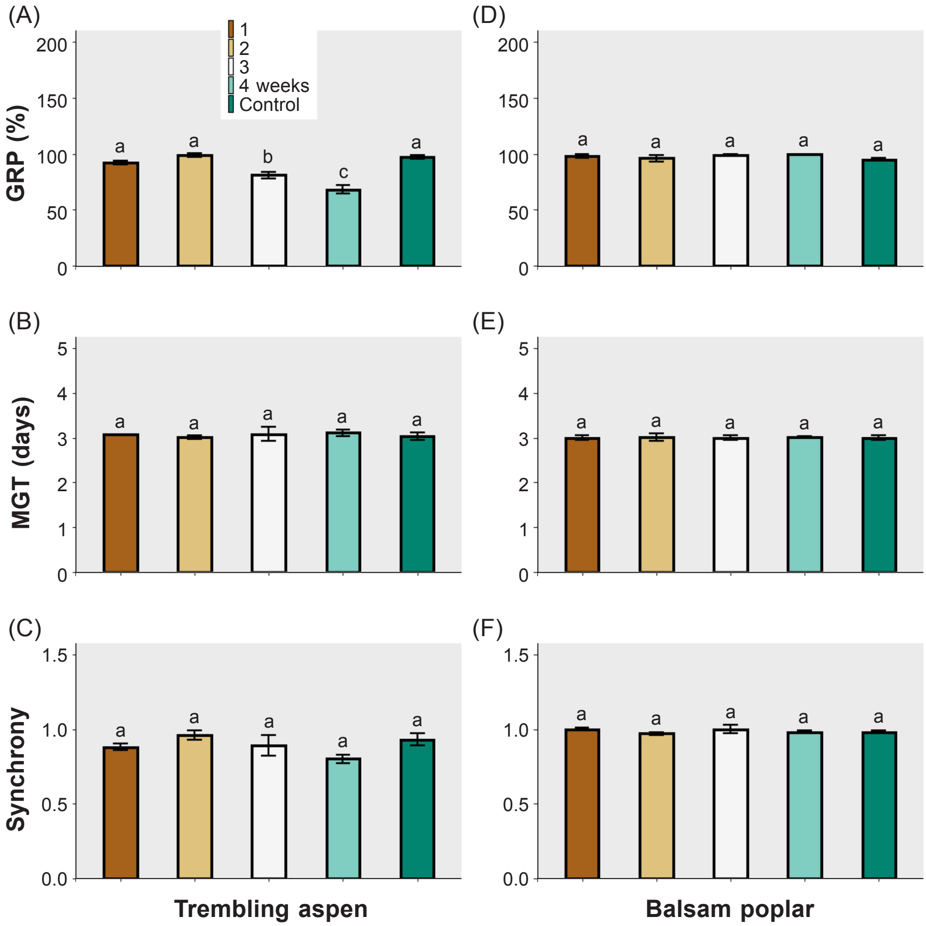

Figure 2. Least square means of germination percentage (GRP), mean germination time (MGT) and synchronisation index (SYN) by species (trembling aspen and balsam poplar) and initial storage condition treatment (1, 2, 3, 4 weeks at 4°C, and 'non stored' control). Error bars represent one standard deviation of the mean (n = 4).

Vitis *et al.*, 2020). Given the narrow harvest window across the study region, it is likely a large fraction of the seeds was not yet mature at the time of harvesting and keeping the seeds for up to four weeks after harvest and before processing likely allowed more seeds to complete their maturation at 4°C. Hong and Ellis (1996) also found that keeping seeds between 0 and 5°C is sufficient to maintain the viability of dry seeds over the short term (< 18 months). Storing the seeds after harvest and before processing might have also prevented "case-hardening", which can occur when seeds with high moisture contents are exposed to rapid drying, making the subsequent extraction processes difficult (Afzal *et al.*, 2020). This phenomenon can reduce seed quality.

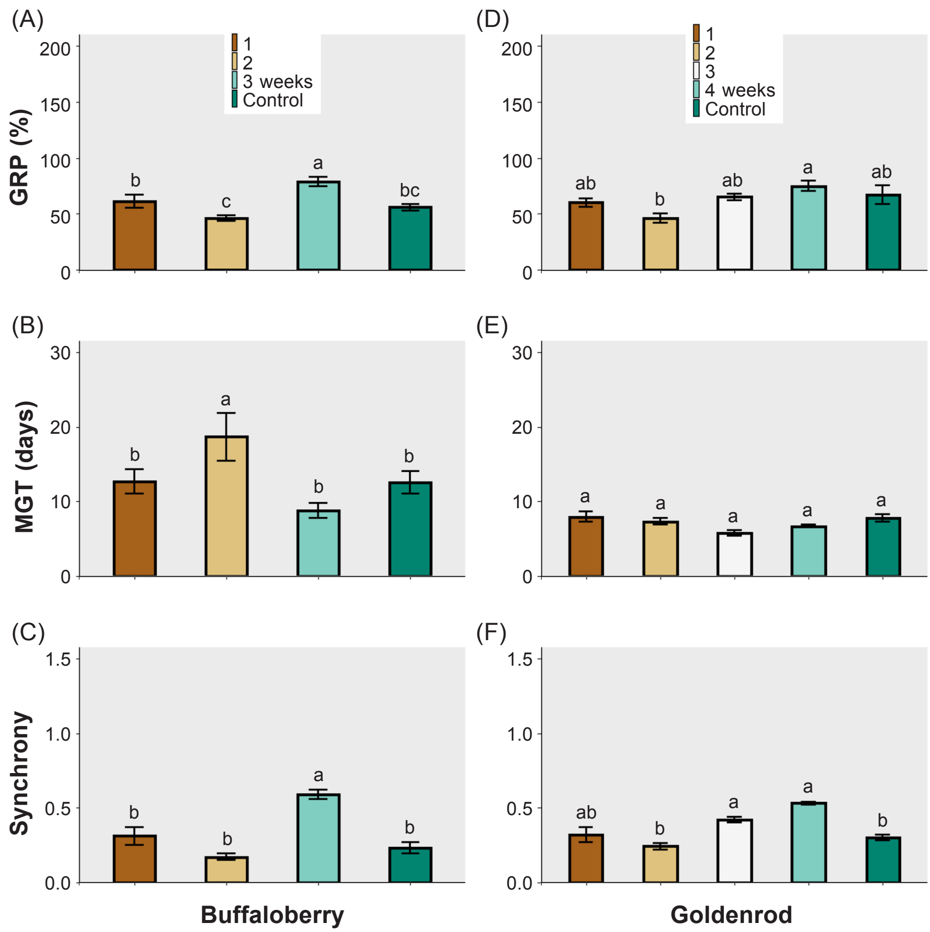

Figure 3. Least square means of germination percentage (GRP), mean germination time (MGT) and synchronization index (SYN) by species (buffaloberry and goldenrod) and initial storage condition treatment (1, 2, 3, 4 weeks at 4°C, and 'non stored' control). Error bars represent one standard deviation of the mean (n = 4).

Leadem (1986) found germination of conifer cones temporarily stored either in covered outdoor cone sheds or in refrigerated coolers at 2°C to be as good or better than the freshly collected cones. Overall, it appeared the initial storage condition treatments improved germination by completing seed maturation, which is an important consideration prior to processing seeds.

The most striking observation was the highest germination percentage recorded in seeds of balsam poplar, buffaloberry and goldenrod after being exposed to the longest duration of storage after harvest and before processing (i.e., four weeks at 4°C). We consider this observation as significant given the very narrow harvest windows exhibited by species that are commonly used in restoration efforts in the studied region (Landhausser *et al*., 2019). Because of the seasonal nature of harvesting in this region, large quantities of seeds are often collected within a short period. Short-term storage after harvest and before processing, thus becomes unavoidable, particularly in the situation where large quantities of seeds need to be collected within a short period and seed extracting machinery has a limited capacity. Studies like this one show that certain boreal seeds can be temporarily stored for varying amounts of time between harvest and processing without losing their longevity or germination performance.

Our results also demonstrate the importance of setting up appropriate storage conditions for individual seed species irrespective of their origin. Although the seeds came from the same ecological habitat, they have strikingly different germination responses to the interim storage treatments. The variations in seed-related characteristics may explain the variation in cumulative mean germination between the species. For instance, we observed that freshly collected trembling aspen seeds maintained a high germination (99%) when infructescence was initially stored in a fridge at 4°C for up to two weeks before processing for storage. However, prolonged storage for three weeks and above is likely to result in an increased incidence of seeds with lower germination (68 – 81%) than those in the control treatment (97%). The overall trend, however, showed the highest GRP in the 1-week-4°C treatment, followed by the control and lowest in the 3-weeks-4°C and 4-weeks-4°C treatments. Trembling aspen seeds, in general, are very tiny and do not exhibit any dormancy, therefore requiring no special treatment before germination (Harrington *et al*., 1999). Though the seeds germinate quickly and completely with little intervention. Several other studies have shown that they can lose their germination potential without prompt extraction and cold storage (Fung and Hamel, 1993; Day *et al*., 2003; Young, 2011). The tiny size and fast-drying ability make immediate processing of the infructescence therefore necessary. However, in the present study, it appears that an optimum interim storage condition for trembling aspen seeds material after harvest will consist of a cold (4°C) storage for up to two weeks. This short period may allow the seed to complete maturation. Practitioners should therefore aim to store trembling aspen seed materials for a maximum of two weeks at 4°C before extraction as this is the condition storage around which aspen seeds attained their greatest GRP (99%), lowest MGT (three days) and largest SYN (0.96).

The highest GRP (79%) was obtained by storing buffaloberry seeds for three weeks at 4°C before extraction and cleaning. We also noticed that this treatment shortened the MGT and improved germination uniformity more than the other treatments. It took an average of five days for buffaloberry seeds to achieve 50% germination, whereas the same number of seeds that were in the control treatment spent nearly 40 days to reach 50% germination. Goldenrod seeds also germinated like the seeds of buffaloberry. The highest GRP (75%) and SYN (0.53) values were obtained in goldenrod seeds that were interimly stored for four weeks at 4°C. Interestingly, about 37% of goldenrod seeds and 40% of buffaloberry seeds did not germinate after incubating for 100 days. As for buffaloberry, seeds that did not germinate may be an indication of a deeper dormancy that was not broken after 12 weeks of cold stratification. When these seeds were acid-scarified (carboxylic acid or gibberellic acid) and cold-stratified, significantly higher germination was observed compared to those that were only cold-stratified (Rosner and Harrington, 2003; Morales *et al*., 2012; Ali *et al*., 2020).

In conclusion, native boreal species often have narrow windows for collection, and collectors may have to decide between cleaning and processing immediately or gathering new seeds. By knowing the optimum time and conditions that native seed material can be stored before extraction, seed collection crews could make informed decisions that allow flexibility in collection and processing times, greatly enhancing seed collection efficiency. We theorise that the longer the seeds can be stored interim without losing their germination characteristics, the greater the chances that more seeds can be collected within the narrow windows by allowing more flexibility in harvesting and processing. This study focused on germination but estimates of seed physical characteristics seem to lend support to this assumption. For most of the species, the largest seed extraction and percent purity occurred when seeds were exposed to one or more weeks of interim storage. Close observation of interim storage treatment and how this practice affects the quantity and quality of seeds harvested will require further study, but at this stage, we can confirm that interim storage can be used as a successful post-harvest handling technique to improve germination in certain boreal species.

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