NRC Research Press

ARTICLE

Reproductive ecology of impoverished pinweed (*Lechea intermedia* var. *depauperata*), a fire-associated narrow endemic from the boreal forest

V.E. Crisfield, D.L. Haughland, and L.A. Pyle

Abstract: Impoverished pinweed (*Lechea intermedia* var. *depauperata* Hodgdon, Cistaceae) is a narrow endemic restricted to the dry, fire-prone Athabasca Plain in northeastern Alberta and northwestern Saskatchewan, Canada. Little is known about the ecology or life history of the taxon that could be used to inform conservation or management decisions. We investigated the reproductive biology of impoverished pinweed to determine whether it exhibits the suite of traits characterizing the temporal disperser syndrome, which is prevalent among Cistaceae species inhabiting fire-prone environments. Specifically, we examined the soil seedbank, characterized seed production, and conducted three sets of germination trials examining the interaction of heat and scarification, burial, and alternate wetting and drying. Our results show that impoverished pinweed is similar to other Cistaceae with respect to seed production, dispersal, and germination, supporting the classification of impoverished pinweed as a temporal disperser. Exposing seeds to temperatures between 125 and 175 °C significantly increased germination as compared with the untreated controls. We discovered an additional cause of seed loss incidentally; here we report the first western Canadian records of *Anthonomus pusillus* Le Conte, a seed-predating weevil. Our results suggest that the temporal and spatial dynamics of impoverished pinweed populations are strongly shaped by fire and the distribution of soil seedbanks.

Key words: Cistaceae, endemic, fire, physical dormancy, seedbank, weevil predation.

Résumé : Le léchéa appauvri (*Lechea intermedia* var. *depauperata* Hodgdon, Cistaceae) est une espèce étroitement endémique restreinte à la plaine d'Athabasca, sèche et sujette au feu, située au nord-est de l'Alberta et nord-ouest de la Saskatchewan, Canada. On en sait peu de l'écologie et du cycle biologique du taxon qui pourrait permettre d'orienter les décisions liées à la conservation ou la gestion. Les auteurs ont examiné la biologie reproductive du léchéa appauvri afin de déterminer s'il présente l'ensemble de traits caractéristiques du mode de dispersion temporelle qui prévaut parmi les espèces de Cistaceae qui habitent des environnements sujets au feu. Spécifiquement, ils ont examiné la réserve de graines du sol, caractérisé la production des graines et réalisé trois séries de tests de germination examinant l'interaction de la chaleur et de la scarification, de l'enfouissement et de l'humectation et de l'assèchement en alternance. Leurs résultats montrent que le léchéa appauvri est semblable aux autres Cistaceae en ce qui concerne la production, la dispersion et la germination de graines, ce qui appuie la classification du léchéa appauvri parmi les espèces à dispersion temporelle. L'exposition des graines à des températures allant de 125 °C à 175 °C augmentait significativement la germination comparativement aux contrôles non traités. Les auteurs ont découvert secondairement une cause supplémentaire de perte de graines ; ils rapportent ici la première consignation dans l'Ouest canadien de la présence d'*Anthonomus pusillus* Le Conte, un charançon prédateur de graines. Leurs résultats suggèrent

Received 15 May 2019. Accepted 27 June 2019.

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Botany **97**: 559–570 (2019) dx.doi.org/10.1139/cjb-2019-0097

que les dynamiques temporelle et spatiale des populations de léchéas appauvris sont fortement façonnées par le feu et la distribution des réserves de graines du sol. [Traduit par la Rédaction.]

Mots-clés : Cistaceae, endémique, feu, dormance physique, réserve de graines, prédation par le charançon.

Introduction

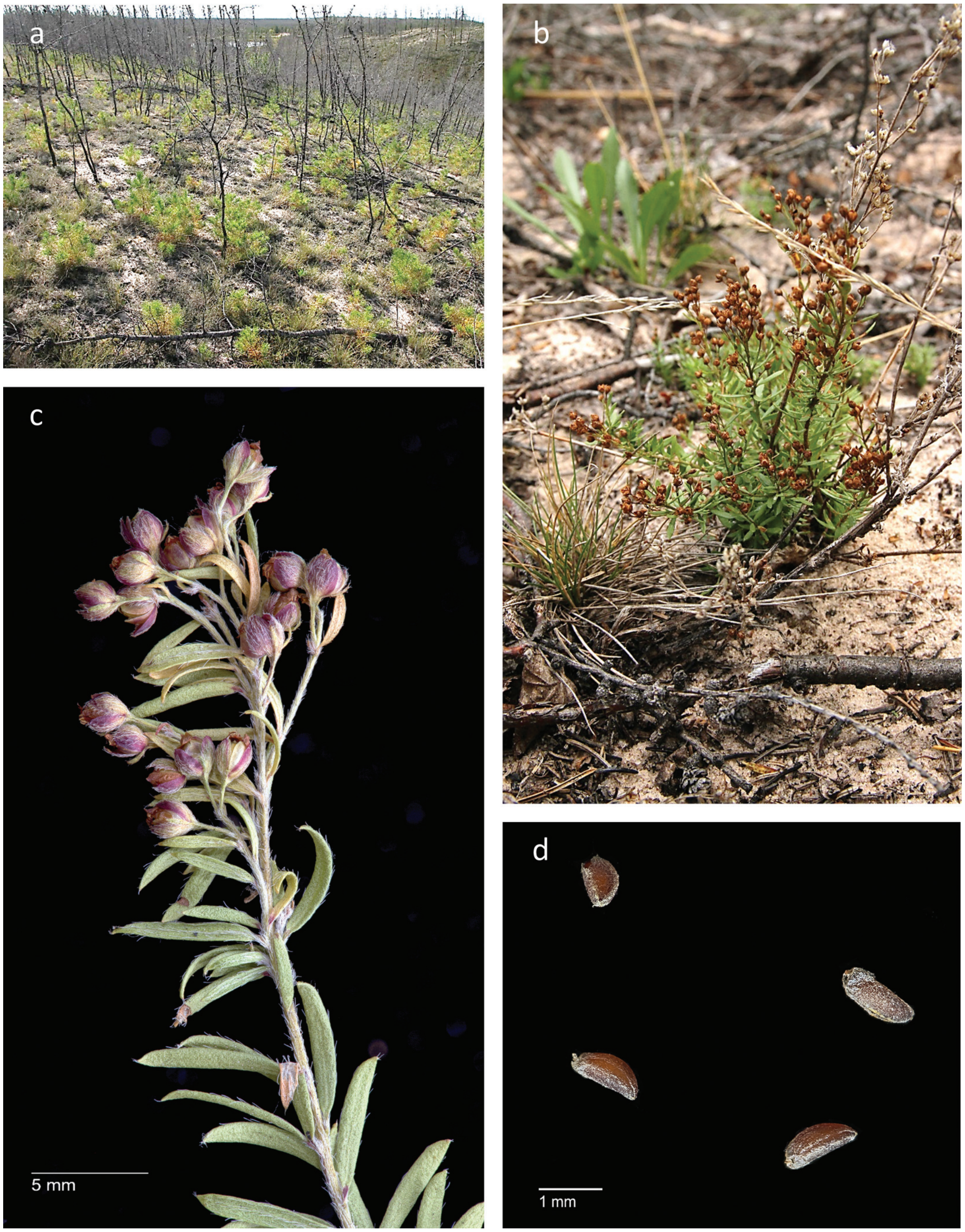
The ecology and life history strategy of a plant are closely related to its seed characteristics and germination ecology (Angevine and Chabot 1979). Dispersal mechanisms, along with the requirements and timing of germination, reflect adaptive responses to environmental factors that optimise establishment. In many ecosystems, persistent seedbanks composed of small, indurate seeds play a critical role in the assembly and succession of plant communities (Thompson et al. 1993). Those seedbanks also are shaped by the ecological legacies of historical disturbance (Bakker et al. 1996), such as fire (Romo and Gross 2011; Brown et al. 2015; Pyle 2018). As a result, information about seeds, seedbanks, and germination requirements provide useful insight into species' ecology and possible responses to disturbance, especially for species that rely entirely on seeds for reproduction and dispersal.

Lechea intermedia var. *depauperata* Hodgdon, commonly known as impoverished pinweed, is a taxonomically-distinct variety (Lemke 2015) of *Lechea intermedia* Legg. ex Britton, or largepod pinweed. This taxon is endemic to the Athabasca Plain south of Lake Athabasca, in northeastern Alberta and northwestern Saskatchewan, where it is found in recently burned jack pine (*Pinus banksiana* Lambert) stands, and occasionally on open, sandy wetland shorelines (Harms 1996; ABMI 2019; EMCLA, S. Nielsen, Dept. of Renewable Resources, University of Alberta, unpublished data; Fig. 1*a*). It is also geographically disjunct from other varieties of *Lechea intermedia* Legg. ex Britton, with the nearest populations occurring in southern Manitoba, over 1000 km southeast of Lake Athabasca (Harms 1996). Only 10 populations of impoverished pinweed have been documented, four in Saskatchewan and six in Alberta, and the plant is listed as "critically imperilled" in both jurisdictions (NatureServe 2018). Saskatchewan populations were originally detected in the 1930s, 1940s, and 1980s; recent efforts to relocate these populations have been unsuccessful (Harms 1996; Lamb et al. 2011). Alberta populations were detected by the Alberta Biodiversity Monitoring Institute (ABMI) and the Ecological Monitoring Committee of the Lower Athabasca (EMCLA) between 2012 and 2014 (ABMI 2019; EMCLA, unpublished data).

Impoverished pinweed is a small, perennial, caespitose forb that reproduces exclusively by seed (Hodgdon 1938; Harms 1996; Fig. 1). It is believed to be short-lived (Hodgdon 1938), although data to support this assertion are lacking. The production, dispersal, and germination of seeds are therefore of paramount importance to its persistence, and furthering our understanding of these characteristics and their interactions with the environment is vital to understanding the long-term population dynamics of the taxon. Currently there is very little information about the reproductive ecology of impoverished pinweed, aside from observations that its seeds have no obvious mechanisms to facilitate long-distance dispersal (Fig. 1*d*), and that they appear to be long-lived, based on successful laboratory germination of 15-year-old seeds (Harms 1996). Studies have been limited to one-time field observations and herbarium study — to our knowledge no field research or germination trials aside from Harms (1996) have been conducted.

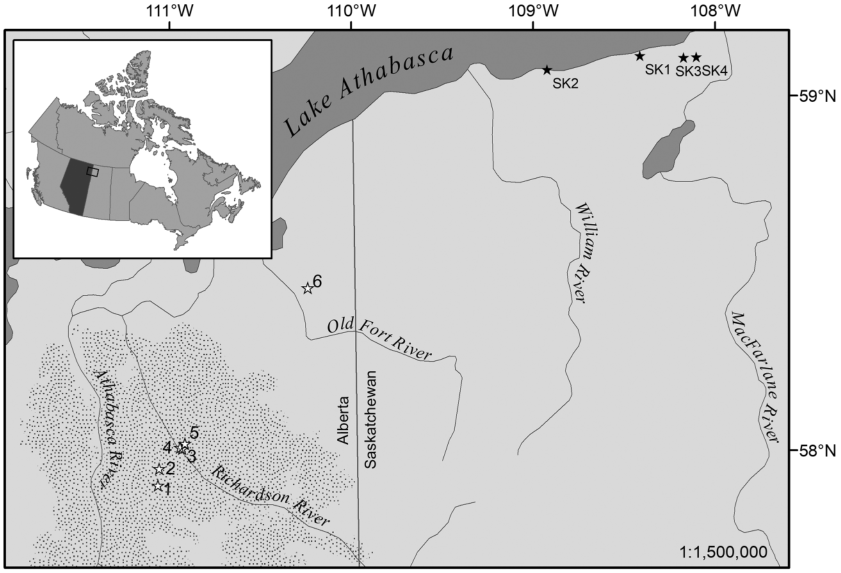
Impoverished pinweed is a member of the Cistaceae, or rockrose family. Species in this family are widely distributed throughout temperate regions, but with a particular concentration in the Mediterranean region (Thanos et al. 1992; Arrington and Kubitzki 2003), where the family originated (Guzman and Vargas 2009). Cistaceae species demonstrate a high degree of phylogenetic conservatism (sensu Harvey and Pagel 1991), with strong affinities for dry, open, and often disturbed sites with nutrient poor substrates (Nelson 1985; Thanos et al. 1992; Barringer 2004; Guzmán and Vargas 2009). Many species are post-fire pioneers (Nelson 1985; Thanos and Georghiou 1988; Thanos et al. 1992; Bastida and Talavera 2002), which produce large annual crops of small, physically dormant seeds (Thanos and Georghiou 1988; Ferrandis et al. 1999; Baskin et al. 2000*b*; Bastida and Talavera 2002). These seeds disperse passively beneath parent plants and persist in the soil seedbank until fire triggers germination, often resulting in the establishment of dense populations during the early stages of post-fire succession (Ferrandis et al. 1999; Bastida and Talavera 2002). This suite of traits (passive seed dispersal, long-lived seeds, physical dormancy, and heat-triggered germination) is characteristic of the "temporal disperser" syndrome described by Keeley (1992). Keeley contrasts temporal dispersers with "spatial dispersers", which disperse their seeds through space, using wind, water, or animals as dispersal vectors. The strategy of spatial dispersers is to cast their seeds widely to maximize the chances of landing in appropriate habitat, where the seeds will quickly germinate. By contrast, temporal dispersers deposit their seeds locally, where they remain over long periods of time, until dormancy is broken by environmental triggers and germination occurs. Rather than moving through space to find suitable habitat, temporal dispersers persist through time, remaining in the seedbank until suitable conditions arise where seeds are already present.

Fig. 1. Representative impoverished pinweed habitat at the site of Population 4 (*a*), mature plant in situ at Population 5a (*b*), mature fruiting stems (*c*), and seeds (*d*).



Temporal dispersers persist in the seedbank by way of physical dormancy; their seeds have a hard, impermeable endocarp that must be broken before germination can occur. In Cistaceae, the structures responsible for physical dormancy are a bixoid chalazal plug and an impermeable layer of lignified palisade cells near the endocarp's exterior (Baskin et al. 2000*b*). Mechanisms demonstrated to release physical dormancy include chemical or physical scarification, heat, fluctuating temperatures, and drying (Thanos et al. 1992; Baskin and Baskin 2001). Other potential triggers have been suggested, including soil microbial activity (Gogue and Emino 1979; Gopinathan and Babu 1985), abrasion by soil particles (Went 1955), and alternate wetting and drying of seeds (Thanos et al. 1992); however, the effectiveness of microbes and abrasion have been disputed (Baskin and Baskin 2000), and the effects of alternate soaking and drying do not appear to have been tested in physically dormant seeds. Heat associated with fire has been shown to stimulate germination in many species with physical dormancy, including several species in the Cistaceae (Thanos et al. 1992; Herranz et al. 1999; Moreira

Fig. 2. Locations of impoverished pinweed populations in Alberta (1–6) and Saskatchewan (SK1-SK4). Grey stippling represents the boundaries of the Richardson Burn. Data: Harms (1996); Government of Canada (2011*a*, 2011*b*); Government of Alberta 2015; ABMI (2019).



et al. 2010). No additional dormancy mechanisms (e.g., physiological dormancy) have been documented in Cistaceae species (Thanos et al. 1992), and their seeds germinate readily when physically scarified (Thanos and Georghiou 1988; Thanos et al. 1992; Herranz et al. 1999; Baskin et al. 2000*b*).

The temporal disperser syndrome has been documented in a range of Mediterranean-type ecosystems, and the effect of heat on germination has been well studied for many plant species in these regions (e.g., Keeley 1991; Tarrega et al. 1992; Luna et al. 2007; Moreira and Pausas 2012). By contrast, there has been little focus on the phenomenon of temporal dispersers in the boreal forest, in spite of the important role of fire in shaping these ecosystems. Work on post-fire regeneration of boreal plants has focused primarily on the regeneration of trees (Greene et al. 1999; Purdy et al. 2002; Johnstone and Chapin 2006; Brown et al. 2015) and on community composition (Azeria et al. 2011; Pinno and Errington 2016; Whitman et al. 2018), with little attention given to seed germination patterns of understorey species (but see Granström and Schimmel 1993 and Baskin et al. 2000*a*).

Based on the prevalence of the temporal disperser syndrome within the Cistaceae, the phylogenetic conservatism displayed by species in this family, and the observed association between impoverished pinweed and recently burned sites, we hypothesised that the reproductive requirements and patterns of impoverished pinweed are similar to other Cistaceae species. While the documentation of the temporal disperser syndrome in this family has been limited to Mediterranean species, it may be an ancestral trait that developed early in the evolution of the Cistaceae in the fire-prone ecosystems of the Mediterranean region, and which has been retained in extant taxa throughout the family. If this is the case, we would expect to see abundant seed production, relatively localised seed dispersal, and dormancy-breaking mechanisms associated with heat. In this study we report on the first reproductive ecology studies of impoverished pinweed, with an emphasis on the spatial distribution of the soil seedbank, seed production, germination requirements, and potential responses to fire. We believe that these factors will, in part, explain the spatial and temporal distribution of impoverished pinweed populations, and provide insight into how future disturbances and environmental change might impact long-term population dynamics in this rare and geographically restricted taxon.

Materials and methods

Study location

Field data collection was conducted along the Fort Chipewyan winter road in northeastern Alberta, in the vicinity of the Richardson River, where five of the six Alberta populations are located (Fig. 2). The sixth, a more northern population, was excluded from our study as it can only be accessed by helicopter, whereas the winter road is accessible by all-terrain vehicle in the summer. All Alberta populations are found within the Athabasca Plain Subregion of the Boreal Forest Natural Region of Alberta, which is characterised by rapidly-drained, coarse-textured Brunisolic soils and jack pine dominated forests (Natural Regions Committee 2006). The five study populations occur within the boundaries of the Richardson Burn; a wildfire that burned over 575 000 ha of forest in northeastern Alberta in the summer of 2011 (Pinno and Errington 2016). All five populations are found in burned, xeric upland sites, characterised by high light levels, sandy soils, low soil moisture, abundant exposed mineral soil, and relatively sparse understorey vegetation.

The five study populations were numbered 1–5 with 1 being furthest south and 5 being furthest north (Fig. 2). These populations were initially detected in summers 2013 and 2014 and are assumed to have established following the Richardson Burn. We had initially sampled a sixth population, but later concluded that owing to its close proximity (~150 m) to Population 5, it should be treated as an subpopulation of Population 5 rather than a separate population. For the purposes of this study we refer to this subpopulation as Population 5a.

We collected field data in late August of 2015 and 2017. Field methods were constrained by the remoteness of the study sites and the associated logistical challenges of transporting equipment and samples to and from field sites, as well as time limitations. Additionally, because of the rarity of impoverished pinweed, we were conservative in our choice of field methods, limiting field activities to those that would not detrimentally affect populations. The location of one of the five study populations (Population 2) within a protected area further restricted data collection at this population. The resulting datasets for this study are by necessity small, and not all variables were assessed at all populations.

Seed collection and extraction

Seeds were collected from both soil and aerial seedbanks at Populations 1, 2, 3, 5, and 5a in summer 2015. The soil seedbank was sampled to characterise seed densities inside and outside of impoverished pinweed populations. We collected samples using a 10 cm deep × 5 cm wide soil corer. In most cases, three soil samples were collected from within each population, and three from adjacent, unoccupied areas (i.e., 15–125 m from the boundary of each population) with similar habitat characteristics. In the case of Population 5a, only one sample was collected within the population, owing to the population's very small spatial extent (1.5 m^2). One of the samples from Population 3 became contaminated with additional seeds (from outside of the sample) during processing and was discarded. The remaining 27 samples were included in the analyses.

Mature, intact fruiting stems (Fig. 1*c*) were also collected from several plants in each of the five populations, for use in germination trials (next section). These stems, which persist for one or more growing seasons following maturation, represent the aerial seedbank.

Seed extraction

Seeds were found to be too heavy/dense to be extracted from the soil samples by flotation, and dormancy precluded using germination-based assessment methods for quantifying the soil seedbank. Seeds were thus extracted manually, using the following procedure: we spread out a shallow layer of soil (5–10 mL) in a Petri dish and examined it under a dissecting microscope; all impoverished pinweed seeds were removed. This process was repeated until the full volume of each soil sample was examined. Seeds of impoverished pinweed are visually distinctive (Fig. 1*d*) and were easily detectable under a microscope, and with the small amount of material examined at one time, we are confident that detection issues did not influence our results.

Seeds from the aerial seedbank were extracted using a sieving process. Fruit were removed from the stems by hand, very gently ground with a mortar and pestle to break up the capsules, then rinsed for one minute through 850 μm, 500 μm, and 125 μm sieves to separate the seeds from chaff. Sieved material was rinsed into drying bowls and placed in a 32 °C oven for 48 h to allow water to evaporate.

Germination trials

Trials were conducted to determine what mechanisms might promote germination in impoverished pinweed. In our preliminary tests we observed very low germination (~4%) in unmanipulated seeds, while seeds that were mechanically scarified using a scalpel achieved germination nearing 100% (V. Crisfield and L. Robb, unpublished data), suggesting that germination is chiefly controlled through physical dormancy. Treatments were thus selected based on their potential to break physical dormancy, as well as their ecological relevance in the environment of the Athabasca Plain. The following treatments were tested:

1. Heat and scarification

   These treatments were tested in a full-factorial design. Temperature treatments consisted of nine different heat treatments between 50–250 °C in 25 °C increments, and one untreated reference. The range of temperatures tested was chosen to reflect temperatures during fire documented in the literature (Beadle 1940; Smith and Sparling 1966; Ryan 2002; D. Thompson, personal communication, 2016), within the limitations of the available equipment. Seeds were placed in glass Petri dishes in an oven (Fisher Scientific Isotemp 100L FA; ThermoFisher Scientific, Ottawa, Ontario, Canada) for 45 s, and immediately transferred out of the hot Petri dishes upon removal. Scarification was applied under a dissecting microscope to half of the seeds prior to heat treatments, using a scalpel to nick a small opening in the seed coat, while avoiding the embryo. Applying scarification to half the seeds allowed us to determine whether a lack of germination associated with a particular temperature treatment was attributable to a failure of the treatment to break dormancy, or whether the treatment was lethal to seeds.
2. Burial

   This treatment used seeds extracted from the soil seedbank, to determine whether abrasion by sand might be sufficient to scarify seeds and break dormancy. We assumed that seeds extracted from soil samples would have been subject to some level of abrasion, either at the soil surface, from wind blowing sand particles across the surface, from freeze–thaw cycles, or from movement downwards through the soil profile.

3. Wet–dry

   This treatment assessed the affects of alternate wetting and drying on germination. Seeds were given 2 mL of water every four days, allowing the filter paper (see below) to dry thoroughly in between waterings.

4. Control

   Seeds extracted manually from the aerial seedbank and not subject to scarification or any other treatments were used as a control, out of concern that the sieving process might have resulted in abrasion sufficient to artificially increase germination.

With the exception of the burial treatment, all treatments used seeds extracted from the aerial seedbank. All treatments consisted of five replicates of 10 seeds. Seeds were selected using a dissecting microscope to ensure that only mature, filled, and undamaged seeds were used. Seeds were germinated on a double layer of filter paper in plastic Petri dishes at room temperature (20 °C), in ambient light conditions, for the duration of germination trials. All treatments aside from the wet–dry treatment were watered as needed to keep filter papers moist throughout the trials. Germinants were counted every day for the first 10 days of the trial, and every two days thereafter, with germination defined as the emergence of a radicle. Trials were ended after 28 days, and no follow up viability tests were conducted as preliminary trials suggest viability is close to 100% (V. Crisfield and L. Robb, unpublished data).

Seed production

In the summer of 2017, we collected fruiting stems from two randomly selected plants from within Populations 1, 3, 4, and 5. The number of fruit per plant was counted in the lab, and approximately 10% of the fruit from each plant were dissected to quantify seed production per fruit. During fruit dissection we found a small species of weevil occupying several fruit collected from one of the plants collected at each of Populations 3 and 5. The weevil and infested fruit were imaged using a scanning electron microscope (Zeiss Evo MA10), and specimens were sent to a Curculionoidea (weevil) taxonomist at the Canadian Museum of Nature for further identification. In addition, we examined all pressed impoverished pinweed specimens collected from the study sites for additional evidence of weevils or weevil damage.

Statistical analyses

Soil seedbank

To analyse the distribution of seeds in the soil seedbank, we first converted seed abundance into density (number of seeds per square metre to a sample depth of 10 cm) for each sample. We then examined whether collection location (inside or outside of pinweed populations) influenced seed density, using a generalised linear mixed model set to a Poisson distribution, to account for zero inflation in the dataset. Populations was included as a random (blocking) factor.

Germination trials

Analyses of germination trials focused on assessing the effects of the various treatments on seed germination. Three different analyses were run, each driven by a different research question. First, we assessed potential responses to fire by analysing how heat and scarification affect germination. Next, we examined whether additional dormancy-breaking mechanisms (burial and alternate wetting and drying) also stimulated germination. Finally, we compared two groups of untreated seeds, one extracted manually from fruits, the other extracted from sieving, to determine whether the extraction methods might have affected trial results. Methods for each of these analyses are described below. Owing to counting errors at the beginning of germination trials, some of the replicates only had nine seeds, and germinant counts for each replicate were thus converted into proportions based on the total number of seeds in each replicate.

Heat × scarification

We tested the effect of heat and scarification on germination with a 2-way ANOVA, using a linear mixed effects model created with the R package *lme4* (Bates et al. 2015). Population was included as a random (blocking) factor. Residuals of the model were inspected for the assumptions of normality and heteroscedasticity. We also conducted post-hoc pairwise contrasts for each treatment pair. Least squared means were generated using *lsmeans* (Lenth 2016), and all contrasts were Bonferroni corrected.

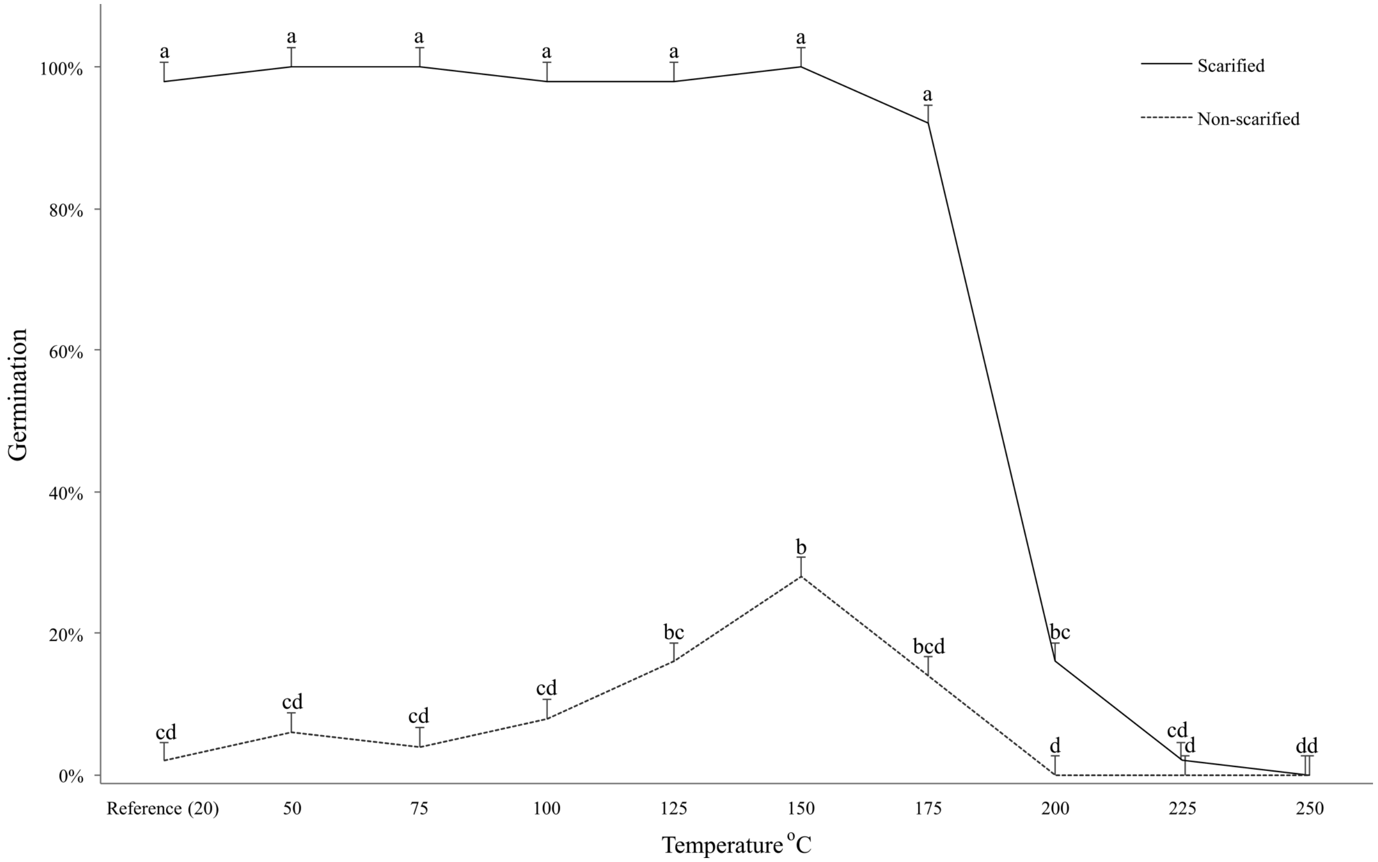
Burial and alternate wetting and drying

To assess the effectiveness of the wet–dry and burial treatments for stimulating germination, we compared these two treatments with the control treatment using a generalised linear model (GLMM) set to a binomial distribution. The binomial link was chosen based on the nature of the data (germination success vs. failure).

Potential effects of sieving

To assess whether the sieving process affected germination levels, we compared germination of the unheated, unscarified reference treatment from the heat × scarification test, to the control treatment, which used seeds extracted manually from the aerial seedbank. The unheated, unscarified reference treatment seeds that

Fig. 3. Germination (LS mean % ± SE) of impoverished pinweed seeds that were scarified or non-scarified then exposed to 10 different heat treatments. Contrasts were conducted using ANOVA and Bonferroni corrected; letters distinguish significant differences. Standard error bars for 225 °C and 250 °C treatments were offset horizontally for visual clarity.



were extracted by sieving but were not otherwise subjected to any treatments; therefore, a difference in germination between the two groups might indicate that the sieving process influenced results of germination tests. We used a GLMM set to a binomial distribution for this analysis, for the same reasons described above.

All statistical analyses were conducted in R version 3.3.1 (R Core Team 2017).

Results

Soil seedbank

Seed density was strongly localized within impoverished pinweed populations ($\chi^2 = 486.6$; df = 3; $P < 0.001$). Mean seed density within populations was 19.9 seeds per sample, equating to 10 792 seeds·m^{-2}, whereas the mean density outside of impoverished pinweed populations was 0.07 seeds per sample, or 36 seeds·m^{-2}. All of the out-of-population samples combined yielded only a single seed. Seed densities within pinweed populations were highly variable, ranging from zero seeds in three samples to a maximum of 114 seeds in the sample from Population 5a.

Germination trials

Heat and scarification treatments

Germination was significantly affected by temperature ($F_{[9,80]} = 83.54$; $P < 0.001$), scarification ($F_{[1,80]} = 259.56$; $P < 0.001$), and the interaction between the two ($F_{[9,80]} = 76.00$; $P < 0.001$). Scarified seeds had very high germination (nearly 100%) at temperatures lower than 200 °C (Fig. 3), and germinated very quickly (data not shown). At temperatures ≥200 °C germination declined rapidly. Unscarified seeds generally had much lower germination, which varied according to the temperature treatments and peaked in the range of 125–175 °C. Germination was very low for treatments <100 °C and >200 °C. Germination rates were also considerably slower in unscarified seeds (data not shown).

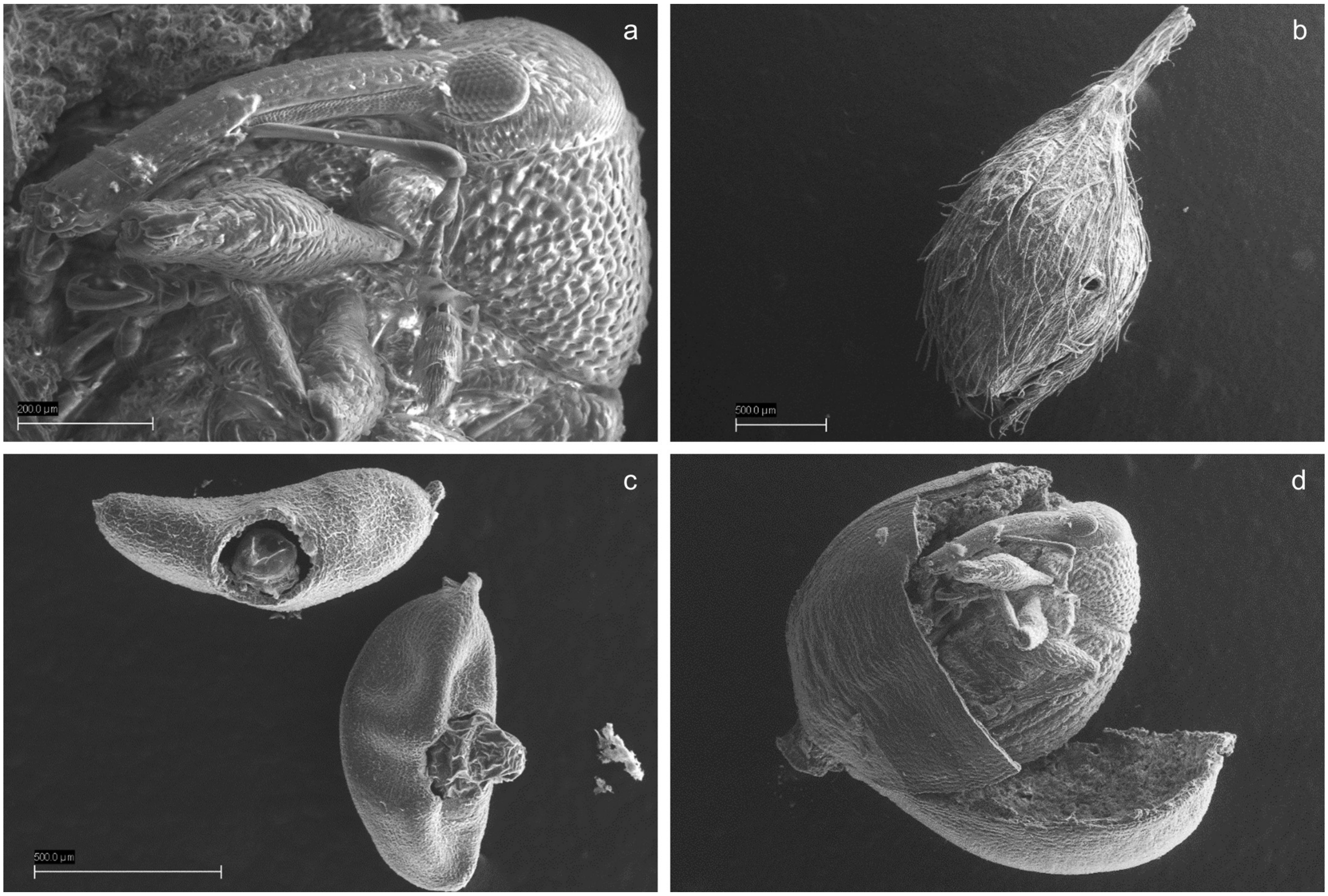
Other dormancy breaking mechanisms

Neither the burial nor the wet–dry treatment differed significantly from the control treatment ($\chi^2 = 4.46$, df = 2, $P = 0.108$). The alternate wetting and drying treatment did not result in any germination at all, and only 3 of 50 seeds in the burial treatment germinated.

Effects of sieving on germination

Germination levels of sieved seeds were identical to those of manually extracted aerial seedbank seeds ($\chi^2 = 0$, df = 1, $P = 1$), indicating that the sieving process is highly unlikely to have influenced the results of the germination trials.

Fig. 4. Scanning electron microscope images showing (*a*) *Anthonomus pusillus* adult; (*b*) hole on the side of an infested impoverished pinweed fruit, presumably resulting from egg laying; (*c*) *A. pusillus* larvae in impoverished pinweed seeds; and (*d*) fruit occupied by mature *A. pusillus* individual. Imagery reproduced with permission from the Royal Alberta Museum.



Seed production

Reproductive output averaged 97.9 (±113.8, SD) fruit per plant (n = 8 individuals), and ranged widely among samples, from a low of four to a maximum of 289 fruit per plant. The reproductive maximum of the fruit was 6 fertilized ovules (2 ovules for each of 3 carpels); however, average seed production was 3.7 (±1.15) seeds per fruit (n = 58 fruit), ranging from 1 to 6, for a mean of 421 seeds per plant. The weevil species found in the fruit was identified as *Anthonomus pusillus* Le Conte, 1876 (Curculionidae; R. Anderson, personal communication, 2018). Based on SEM imagery (Fig. 4) and further dissection of the infested fruit, it appears that this weevil predates on capsule contents and seeds during larval development (Fig. 4*c*). Non-dehisced fruit with adult weevils were found with all their seeds consumed (Fig. 4*d*), and in other cases, open fruit were found with signs of larvae damage, including holes through the capsule and perianth (Fig. 4*b*) and partially consumed seeds (Fig. 4*c*). Of the seven pressed specimens collected in 2015 from Populations 1, 4, and 5, weevil impacts were evident on one specimen collected from Population 1.

Discussion

The reproductive traits of impoverished pinweed conform to the characteristics of the temporal disperser syndrome, lending support to our hypothesis that this syndrome may be an ancestral trait in the Cistaceae. Impoverished pinweed clearly has a close association with fire, as evidenced by the positive germination response to heat treatments, and the occurrence of most populations within recently burned sites. The association with burned sites might have additional explanations beyond heat-stimulated germination: the taxon might be shade intolerant, unable to compete in established or dense plant communities, and (or) reliant on open mineral seedbeds. Thus, fire might be important not only for stimulating germination, but also for creating the environmental conditions needed for successful establishment and persistence of impoverished pinweed.

The results from our germination trials showed a clear, significant response pattern to heat, with maximum germination associated with the 150 °C treatment. This suggests that soil heating associated with low to moderate fire temperatures might promote germination in impoverished pinweed, whereas temperatures ≥200 °C are generally lethal. Soil surface temperatures during fire are complex and mediated by multiple variables, including topography, soil type, soil moisture, and weather, among others (Campbell et al. 1995; Davies 2013), and soil temperatures during fire in jack pine stands can range from as low as 60 °C to over 1000 °C (Beadle 1940; Smith and Sparling 1966; Ryan 2002; D. Thompson, personal communication, 2016). The range of fire severities and types (crown vs. ground) observed in the Richardson Burn (Pinno and Errington 2016) suggest a wide range of surface temperatures during fire, some perhaps cool enough to promote impoverished pinweed germination, others possibly hot enough to destroy entire soil seedbanks. Germination responses to scarification were in line with results from similar studies on other Cistaceae species (Thanos et al. 1992; Herranz et al. 1999), confirming that physical dormancy is the only dormancy mechanism controlling germination of impoverished pinweed seeds.

While the results of germination trials suggest that fire plays an important role in the establishment of impoverished pinweed, observations over three field seasons indicate that populations continue to recruit new individuals 4–6 years after fire (V.E. Crisfield, D.L. Haughland, and L.A. Pyle, unpublished data), raising the question of what mechanisms are promoting continued germination. Our results indicate that abrasion is unlikely to play a role, and Baskin and Baskin (2000) provide compelling arguments against the adaptive utility of abrasion as a dormancy breaking mechanism. Alternate wetting and drying appeared to be a promising avenue for investigation given the rapidly drained soils in the Athabasca Plain, but this treatment also proved ineffective. Populations might be sustained in part by a small proportion of soft-coated, non-dormant seeds, as evidenced by the germination of a small number of untreated seeds in our trials. This phenomenon has been observed in other species with physically dormant seeds (Thanos and Georghiou 1988; Thanos et al. 1992; Herranz et al. 1999), and is thought to be a means by which these populations maintain themselves in the short term. Owing to the high seed production observed in impoverished pinweed, even a small proportion of non-dormant seeds may be enough to sustain populations. Other possible mechanisms include daily solar heating (Probert 2000; but see Moreira and Pausas 2012) and daily temperature fluctuations (Probert 2000; Baskin and Baskin 2001).

The soil seedbank of impoverished pinweed was highly localized, with only a single seed found outside the boundaries of current populations, indicating that the seeds are mostly dispersed in the vicinity of parent plants, and that seed dispersal across space is probably not a major component of the taxon's life history strategy. It follows that the distribution of impoverished pinweed populations, both extant and in the seedbank, are probably inherently disjunct across the landscape. Persistent seedbanks are cryptic pools of diversity that often are highly dissimilar from the above-ground plant community, especially in forests (Hopfensperger 2007). Thus, it is likely that additional cryptic, dormant populations of impoverished pinweed are present in the soil and emerge periodically when exposed to a disturbance of the appropriate severity, adding an element of temporal fluctuation to the taxon's population dynamics. This would be an expected pattern for a temporal disperser, and might partially account for the difficulties associated with relocating known populations in Saskatchewan (Harms 1996; Lamb et al. 2011).

The incidental discovery of the weevil *Anthonomus pusillus* constitutes the first record of this species in western Canada (Webster et al. 2016). Other observations of this species suggest an association with the Cistaceae (Webster et al. 2016), and its presence in impoverished pinweed capsules points to a potentially interesting ecological relationship. While predation by *A. pusillus* presumably reduces the reproductive success of impoverished pinweed to some degree, we saw no evidence during field investigations that this is having detrimental impacts at the population level. Given the patchy distribution, rarity, and small population size of impoverished pinweed, we hypothesize that the weevil might be sustained primarily by the regionally co-occurring sand heather *Hudsonia tomentosa* Nutt., and only predates on pinweed secondarily. Additional fieldwork would be required to test this hypothesis.

The temporal disperser syndrome has rarely been documented in boreal plants; indeed, to our knowledge the only other boreal species that is known to display similar germination responses to fire is *Geranium bicknellii* Britton (Granstrom and Schimmel 1993). Reproductive strategies in boreal plant communities are typically characterised by seeds with physiological dormancy (Baskin and Baskin 2001), relatively small, transient and depauperate soil seedbanks (Johnson 1975; Fenner 1985; Archibold 1989), and a tendency towards clonal expansion over establishment by seed (Archibold 1989; Økland 1995; Chavez and Macdonald 2010). The above suggests that the temporal disperser syndrome might be relatively uncommon in the boreal forest compared with other reproductive strategies. However, in the environment of the Athabasca Plain, which is unusually dry and warm relative to other habitats in the western Canadian boreal forest (Natural Regions Committee 2006), the temporal disperser syndrome may be more adaptive than it would be in other boreal plant communities. After fire, establishment by seed from persistent seedbanks is more commonly associated with dry sites and short fire intervals, whereas in moister forest types with longer fire intervals, re-sprouting from vegetative organs is favoured (Archibold 1989). The low productivity of the dry forests in the Athabasca Plain also results in relatively shallow organic layers, which often are removed by fire, exposing an abundance of mineral seedbeds that are optimal for seed germination and establishment. As such, despite their northern latitude, the dry, sunny conditions of the Athabasca Plain might promote dormancy and germination patterns more typical of hot, dry environments (Baskin and Baskin 2001), rather than those of more "typical" boreal forest communities.

Two spatially patchy factors, soil seedbank distribution and fire severity, likely interact with fire frequency to influence the distribution of impoverished pinweed across the landscape and through time.

With little ability to disperse seeds effectively across space, impoverished pinweed is highly dependent on conditions where viable seedbanks exist, and changes to these conditions could have detrimental effects on the taxon. Our results demonstrate that its seeds are vulnerable to severe fires that generate high soil temperatures. Further, although some species produce seeds that persist for decades to centuries (Darlington and Steinbauer 1961; Spira and Wagner 1983), the longevity of impoverished pinweed seeds in the soil is unknown, and may have been shaped by the fire regime with which it evolved. As such, changes in the frequency or severity of fires, resulting for example from climate change or from movement of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) into the forests of the Athabasca Plain, could have significant impacts on long term population dynamics of impoverished pinweed. Conversely, our understanding of the relationship between impoverished pinweed and fire could be used to inform potential conservation measures: for example, low severity, controlled burns where seedbanks are known or thought to exist might be a tool that can help to promote the persistence of populations over time.

Acknowledgements

The authors would like to thank Dr. Robert Anderson at the Canadian Museum of Nature for identification of *Anthonomus pusillus* specimens. Jacqueline Dennett and Tim Chipchar provided valuable advice that informed our field methods. Lindsay Robb from the Alberta Tree Improvement and Seed Centre provided insight into seed germination strategies. Ian Kriston produced the SEM imagery presented in this manuscript, and Michelle Mark and Taylor Lund assisted with processing soil samples. The Royal Alberta Museum provided financial and logistical support.

References

Alberta Biodiversity Monitoring Institute (ABMI). 2019. Terrestrial field data. Datasets T01C (Site Capability), T01E (Site Disturbance) and T15 (Vascular Plants). Alberta Biodiversity Monitoring Institute, Edmonton, Alberta, Canada. Available from http://www.abmi.ca [accessed 9 January 2019].

Angevine, M.W., and Chabot, B.F. 1979. Seed germination syndromes in higher plants. *In* Topics in plant population biology. *Edited by* O.T. Solbrig, S. Jain, G.B. Johnson, and P. Raven. The MacMillan Press Ltd., London, UK. pp. 188–206.

Archibold, O.W. 1989. Seed banks and vegetation processes in coniferous forests. *In* Ecology of soil seed banks. *Edited by* M. Allessio Leck, V. Thomas Parker, and R.L. Simpson. Academic Press, Inc., San Diego, Calif. pp. 107–122.

Arrington, J.M., and Kubitzki, K. 2003. Cistaceae. *In* Flowering plants: dicotelydons. The families and genera of vascular plants, volume 5. *Edited by* K. Kubitzki and C. Bayer. Springer, Berlin, Germany. pp. 62–70.

Azeria, E.T., Bouchard, M., Pothier, D., Fortin, D., and Hébert, C. 2011. Using biodiversity deconstruction to disentangle assembly and diversity dynamics of understorey plants along post-fire succession in boreal forest. Global Ecol. Biogeogr. **20**: 119–133. doi:10.1111/j.1466-8238.2010.00580.x.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., and Thompson, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Bot. Neerl. **45**(4): 461–490. doi:10.1111/j.1438-8677.1996.tb00806.x.

Barringer, K. 2004. New Jersey pinweeds (*Lechea*, Cistaceae). J. Torrey Bot. Soc. **131**(3): 261–276. doi:10.2307/4126957.

Baskin, C.C., and Baskin, J.M. 2001. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, Calif.

Baskin, C.C., Milberg, P., Andersson, L., and Baskin, J.M. 2000*a*. Germination studies of three dwarf shrubs (*Vaccinium*, Ericaceae) of Northern Hemisphere coniferous forests. Can. J. Bot. **78**(12): 1552–1560. doi:10.1139/b00-129.

Baskin, J.M., and Baskin, C.C. 2000. Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles. Seed Sci. Res. **10**: 409–413. doi:10.1017/S0960258500000453.

Baskin, J.M., Baskin, C.C., and Li, X. 2000*b*. Taxonomy, anatomy and evolution of physical dormancy in seeds. Plant Spec. Biol. **15**(2): 139–152. doi:10.1046/j.1442-1984.2000.00034.x.

Bastida, F., and Talavera, S. 2002. Temporal and spatial patterns of seed dispersal in two Cistus species (Cistaceae). Ann. Bot. **89**: 427–434. doi:10.1093/aob/mcf065.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Beadle, N.C.W. 1940. Soil temperatures during forest fires and their effect on the survival of vegetation. J. Ecol. **28**(1): 180–192. doi:10.2307/2256168.

Brown, C.D., Liu, J., Yan, G., and Johnstone, J.F. 2015. Disentangling legacy effects from environmental filters of postfire assembly of boreal tree assemblages. Ecology, **96**(11): 3023–3032. doi:10.1890/14-2302.1.

Campbell, G.S., Jungbauer, J.D., Bristow, K.L., and Hungerford, R.D. 1995. Soil temperature and water content beneath a surface fire. Soil Sci. **159**(6): 363–374. doi:10.1097/00010694-199506000-00001.

Chavez, V., and Macdonald, S.E. 2010. Understory species interactions in mature boreal mixedwood forests. Botany, **88**(10): 912–922. doi:10.1139/B10-062.

Darlington, H.T., and Steinbauer, G.P. 1961. The eighty-year period for Dr. Beal's seed viability experiment. Am. J. Bot. **48**(4): 321–325. doi:10.1002/j.1537-2197.1961.tb11645.x.

Davies, G.M. 2013. Understanding fire regimes and the ecological effects of fire. *In* Fire phenomena and the Earth system: an interdisciplinary guide to fire science. 1st ed. *Edited by* C.M. Belcher. John Wiley & Sons, Chichester, West Sussex, UK. pp. 97–124.

Fenner, M. 1985. Seed ecology. Chapman and Hall, New York, N.Y.

Ferrandis, P., Herranz, J.M., and Martínez-Sánchez, J.J. 1999. Effect of fire on hard-coated Cistaceae seed banks and its influence on techniques for quantifying seed banks. Plant Ecol. **144**: 103–114. doi:10.1023/A:1009816309061.

Gogue, G.J., and Emino, E.R. 1979. Seed coat scarification of *Albizia julibrissin* Durazz by natural mechanisms. J. Am. Soc. Hortic. Sci. **104**: 421–423.

Gopinathan, M.C., and Babu, C.R. 1985. Structural diversity and its adaptive significance in seeds of *Vigna minima* (Roxb.) Ohwi & Ohashi and its allies (Leguminosae-Papilionoideae). Ann. Bot. **56**(6): 723–732. doi:10.1093/oxfordjournals.aob.a087063.

Government of Alberta. 2015. Historical wildfire perimeters. [Shapefile] Retrieved from: https://wildfire.alberta.ca/resources/historical-data/spatial-wildfire-data.aspx.

Government of Canada. 2011*a*. Boundary Files – 2011 Census. [Shapefile] Retrieved from: https://www12.statcan.gc.ca/census-recensement/2011/geo/bound-limit/bound-limit-2011-eng.cfm.

Government of Canada. 2011*b*. Water File – Lakes and Rivers (polygons) – 2011 Census. [Shapefile] Retrieved from: https://open.canada.ca/data/en/dataset/448ec403-6635-456b-8ced-d3ac24143add.jsonld.

Granström, A., and Schimmel, J. 1993. Heat effects on seeds and rhizomes of a selection of boreal forest plants and potential reaction to fire. Oecologia, **94**: 307–313. doi:10.1007/BF00317103.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. **29**(6): 824–839. doi:10.1139/x98-112.

Guzmán, B., and Vargas, P. 2009. Historical biogeography and character evolution of Cistaceae (Malvales) based on analysis of plastid *rbcL* and *trnL-trnF* sequences. Org. Divers. Evol. **9**: 83–99. doi:10.1016/j.ode.2009.01.001.

Harms, V.L. 1996. COSEWIC status report on impoverished pinweed (*Lechea intermedia* var. *depauperata*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont.

Harvey, P.H., and Pagel, M.D. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, Oxfordshire, UK.

Herranz, J.M., Ferrandis, P., and Martínez-Sánchez, J.J. 1999. Influence of heat on seed germination of nine woody Cistaceae species. Int. J. Wildl. Fire, **9**(3): 173–182. doi:10.1071/WF00014.

Hodgdon, A.R. 1938. A taxonomic study of *Lechea*. Rhodora, **40**(470): 30–131.

Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos, **116**(9): 1438–1448. doi:10.1111/j.0030-1299.2007.15818.x.

Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. **53**(24): 2933–2941. doi:10.1139/b75-323.

Johnstone, J.F., and Chapin, F.S. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems, **9**: 14–31. doi:10.1007/s10021-004-0042-x.

Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. Bot. Rev. **57**: 81–116. doi:10.1007/BF02858766.

Keeley, J.E. 1992. Temporal and spatial dispersal syndromes. *In* Plant–animal interactions in Mediterranean-type ecosystems. *Edited by* C.A. Thanos. *In* MEDECOS VI Proceedings, University of Athens, Athens, Greece. pp. 251–256.

Lamb, E.G., Mischkolz, J., and Guedo, D. 2011. The distribution and abundance of the endemic vascular plant taxa of the Athabasca Sand Dunes of northern Saskatchewan. University of Saskatchewan Department of Plant Sciences. Available from www.npss.sk.ca/docs/2_pdf/Athabasca_Occupancy_Survey_2011.pdf.

Lemke, D.E. 2015. *Lechea*. *In* Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 20+ volumes. Oxford University Press, New York and Oxford. Vol. 6, pp. 389–397.

Lenth, R.V. 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Luna, B., Moreno, J.M., Cruz, A., and Fernández-González, F. 2007. Heat-shock and seed germination of a group of Mediterranean plant species growing in a burned area: an approach based on plant functional types. Environ. Exp. Bot. **60**: 324–333. doi:10.1016/j.envexpbot.2006.12.014.

Moreira, B., and Pausas, J.G. 2012. Tanned or burned: the role of fire in shaping physical seed dormancy. PLoS ONE, **7**(12): e51523. doi:10.1371/journal.pone.0051523.

Moreira, B., Tormo, J., Estrelles, E., and Pausas, J.G. 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Ann. Bot. **105**: 627–635. doi:10.1093/aob/mcq017.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. *Compiled by* D.J. Downing and W.W. Pettapiece. Government of Alberta Publ. No. T/852, Edmonton, Alta.

NatureServe. 2018. *Lechea intermedia* var. *depauperata*. NatureServe Explorer. Available from http://explorer.natureserve.org [accessed 12 December 2018].

Nelson, S.D. 1985. The autoecology of *Hudsonia tomentosa* in Northern Alberta. Ph.D. thesis, University of Alberta, Department of Botany, Edmonton, Alta.

Økland, R.H. 1995. Persistence of vascular plants in a Norwegian boreal coniferous forest. Ecography, **18**: 3–14. doi:10.1111/j.1600-0587.1995.tb00114.x.

Pinno, B.D., and Errington, R.C. 2016. Burn severity dominates understory plant community response to fire in xeric jack pine forests. Forests, **7**: 83. doi:10.3390/f7040083.

Probert, R.J. 2000. The role of temperature in the regulation of seed dormancy and germination. *In* Seeds: the ecology of regeneration in plant communities. *Edited by* M. Fenner. CABI Publishing, Wallingford, Oxfordshire, UK. pp. 261–292.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**(1): 289–306. doi:10.14214/sf.564.

Pyle, L. 2018. Influence of management and disturbance history on germinable seed bank composition and legume recruitment in Alberta's Aspen Parkland and Mixedgrass Prairie. Ph.D. thesis, University of Alberta, Department of Agriculture, Food and Nutritional Science, Edmonton, Alta. doi:10.7939/R3RJ4999T.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Romo, J.T., and Gross, D.V. 2011. Preburn history and seasonal burning effects on the soil seed bank in the Fescue Prairie. Am. Midl. Nat. **165**(1): 74–91. doi:10.1674/0003-0031-165.1.74.

Ryan, K.C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. Silva Fenn. **36**(1): 13–39. doi:10.14214/sf.548.

Smith, D.W., and Sparling, J.H. 1966. The temperatures of surface fires in jack pine barren. I. The variation in temperature with time. Can. J. Bot. **44**(10): 1285–1292. doi:10.1139/b66-144.

Spira, T.P., and Wagner, L.K. 1983. Viability of seeds up to 211 years old extracted from adobe brick buildings of California and northern Mexico. Am. J. Bot. **70**(2): 303–307. doi:10.1002/j.1537-2197.1983.tb07871.x.

Tarrega, R., Calvo, L., and Trabaud, L. 1992. Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio, **102**(2): 139–147. doi:10.1007/BF00044730.

Thanos, C.A., and Georghiou, K. 1988. Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. Plant Cell. Environ. **11**: 841–849. doi:10.1111/j.1365-3040.1988.tb01910.x.

Thanos, C.A., Georghiou, K., Kadis, C., and Pantazi, C. 1992. Cistaceae: a plant family with hard seeds. Isr. J. Bot. **41**: 251–263.

Thompson, K., Band, S.R., and Hodgson, J.G. 1993. Seed size and shape predict persistence in soil. Funct. Ecol. **7**(2): 236–241. doi:10.2307/2389893.

Webster, R.P., Anderson, R.S., Webster, V.L., Alderson, C.A., Hughes, C.C., and Sweeney, J.D. 2016. New Curculionoidea records from New Brunswick, Canada with an addition to the fauna of Nova Scotia. ZooKeys, **573**: 367–386. doi:10.3897/zookeys.573.7444.

Went, F.W. 1955. The ecology of desert plants. Sci. Am. **192**(4): 68–75. doi:10.1038/scientificamerican0455-68.

Whitman, E., Parisien, M.-A., Thompson, D.K., and Flannigan, M.D. 2018. Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest. Forests, **9**: 151. doi:10.3390/f9030151.