

RESEARCH ARTICLE



Jack pine of all trades: Deciphering intraspecific variability of a key adaptive trait at the rear edge of a widespread fire-embracing North American conifer

Emmanuelle Pelletier | Guillaume de Lafontaine 

Canada Research Chair in Integrative Biology of the Northern Flora, Département de biologie, chimie et géographie, Centre for Northern Studies, Centre for Forest Research, Université du Québec à Rimouski, Rimouski, Québec, Canada

Correspondence

Guillaume de Lafontaine, Département de biologie, chimie et géographie, 300 allée des Ursulines, Rimouski QC, G5L 3A1 Canada.
Email: guillaume_delafontaine@uqar.ca

Abstract

Premise: Understanding mechanisms fostering long-term persistence of marginal populations should provide key insights about species resilience facing climate change. Cone serotiny is a key adaptive trait in *Pinus banksiana* (jack pine), which shows phenotypic variation according to the fire regime. Compared to range-core populations within the fire-prone boreal forest, low and variable serotiny in rear-edge populations suggest local adaptation to uncommon and unpredictable wildfire regime. We assessed environmental/physiological factors that might modulate intraspecific variation in cone serotiny.

Methods: We experimentally subjected closed cones to incrementing temperatures, then tested seed germination to determine whether and how various ecological factors (cone age, branch height, tree size, tree age) are related to cone dehiscence and seed viability in jack pines from rear-edge and range-core populations in eastern Canada.

Results: Cones from rear-edge populations dehisce at a lower opening temperature, which increases with cone age. Cones from range-core stands open at a more constant, yet higher temperature. Cones from rear-edge stands take between 13 and 27 years to reach the level of serotiny achieved at the range core. At the rear edge, seed viability is steady (51%), whereas it decreases from 70% to 30% in 20 years at the range core.

Conclusions: We inferred the mechanisms of a bet-hedging strategy in rear-edge populations, which ensures steady recruitment during fire-free intervals and successful postfire regeneration. This capacity to cope with infrequent and unpredictable fire regime should increase the resilience of jack pine populations as global changes alter fire dynamics of the boreal forest.

KEYWORDS

bet-hedging strategy, boreal biome, eco-evolutionary dynamics, fire disturbance, intraspecific trait variation, marginal populations, Pinaceae, *Pinus banksiana*, rear edge, serotiny

In the face of global change, natural populations can either migrate to newly suitable environments or adapt locally to their altered ecosystem to avoid extirpation (Davis and Shaw, 2001; de Lafontaine et al., 2018). These responses are exacerbated in marginal populations, which are already at the limit of the climatic or environmental tolerance of a species and often at the edge of its distribution (Nadeau and

Urban, 2019). Marginal environmental conditions that are currently restricted to the warm limit of species distribution (i.e., rear edge) may become increasingly widespread throughout the species range under a warmer climate (Rehm et al., 2015). Hence, peripheral rear-edge populations are the first to encounter new conditions triggered by global warming and thus the most imminently threatened

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(Nadeau and Urban, 2019). They may also be reservoirs of unique genetic variation (de Lafontaine et al., 2013) and thus important contributors for the long-term conservation of genetic diversity, phylogenetic history, and evolutionary potential (Hampe and Petit, 2005). Understanding how the eco-evolutionary dynamics at the rear edge can uphold long-term persistence of peripheral rear-edge populations will provide key insights about species resilience during climate change (Lesica and Allendorf, 1995; Hampe and Petit, 2005; Kawecki, 2008; Rehm et al., 2015).

Intraspecific trait variation reflects differences in genotypes and phenotypic plasticity across varying environments (Moran et al., 2016). Local adaptation increases genetic divergence among populations over generational timescales as a result of natural selection to contrasting environments (Lenormand, 2002; Kawecki and Ebert, 2004). Plasticity allows individuals to rapidly adjust phenotypes according to changes in local conditions, dampening adaptive evolution by buffering selective pressures. However, the extent of trait plasticity is ultimately under genetic control, and heterogeneous environments might foster adaptive plasticity (Ghalambor et al., 2007; Chevin and Lande, 2011; Chevin and Hoffmann, 2017). Hence, whether genetic or plastic, intraspecific trait variation driving demographic trajectories is instrumental to understanding population responses to rapid environmental alteration brought about by ongoing global changes (Moran et al., 2016; Kelly, 2019), especially for marginal populations, where intensified responses, high demographic stochasticity, and spatially structured trait variation are expected (Valladares et al., 2014; Banitz, 2019).

The extent of intraspecific trait variation can differ across ecological gradients in response to environment heterogeneity (Westerband et al., 2021). For instance, some fire-adapted species can exhibit variation in serotiny—a heritable fitness-related trait—in different disturbance regimes (Pausas, 2015; Lamont et al., 2020). Serotiny is the retention of mature seeds in closed cones or fruits for more than a year, leading to the buildup of a canopy seed bank through delayed seed dispersal (Enright et al., 1998). The opening of the cones/fruits is triggered by wildfires (pyriscence), drought periods (xeriscent) or both, depending on the species (Lamont, 1991; Nathan et al., 1999; Espelta et al., 2011). Of 95 pine species (*Pinus* sp.) examined by Lamont et al. (1991), 22 are serotinous, but only six are considered obligate pyriscent, meaning cone opening is strictly contingent on fire. Hence, most serotinous species have a dual life-history strategy, bearing pyriscent structures enabling postfire regeneration as well as nonserotinous cones/fruits that open at maturity, which allows continuous interfire recruitment (Lev-Yadun, 1995; Whelan et al., 1998; Nathan et al., 1999; Goubitz et al., 2004; Hernández-Serrano et al., 2013). The percentage of closed mature cones/fruits in individuals of many serotinous species (i.e., apparent serotiny, sensu Lamont, 2021) has been shown to decrease in populations where fire frequency is low (Givnish, 1981; Muir and Lotan, 1985; Gauthier et al., 1996; Schoennagel et al., 2003;

Hernández-Serrano et al., 2013; Lamont et al., 2020). This dual life-history strategy within individuals showing high but incomplete serotiny is often considered as bet-hedging in environments where fire interval is unpredictable and/or on average longer than the mean longevity of the species (Enright et al., 1998). Diversified bet-hedging is a reproduction strategy that optimizes the long-term individual fitness by sacrificing mean fitness to reduce fitness variance between years in unpredictable environments (Philippi and Seger, 1989; Olofsson et al., 2009; Childs et al., 2010). Individuals “hedge their bets” by simultaneously expressing multiple phenotypes conferring fitness advantage in different conditions (Simons, 2011). Accordingly, in fire-prone species, those individuals adept at producing both serotinous and nonserotinous cones/fruits should have an advantage in environments where the fire-return interval is long and unpredictable (Goubitz et al., 2004).

Jack pine (*Pinus banksiana* Lamb.; Pinaceae) is the North American boreal tree species best adapted to wildfires (Rowe and Scotter, 1973). Mature cones of this obligate pyriscent species generally remain closed until the resin layer on their outer surface is melted by the high temperatures reached in wildfires (Cameron, 1953). Massive postfire seed release triggers a surge in recruitment thanks to rapid establishment on a mineral substrate, rich in resources and without competition (Cayford et al., 1967; Lamont et al., 2020). Because it is shade-intolerant, jack pine is eventually replaced by more competitive species such as black spruce (*Picea mariana*) or balsam fir (*Abies balsamea*) as stands senesce during prolonged absence of fire (>220 years; Le Goff and Sirois, 2004). Serotiny has been extensively studied in Australia, South Africa, and in Mediterranean pines, but factors driving its variability remain poorly investigated in jack pine (but see Gauthier et al., 1993a). Indeed, reduced serotiny was reported in some jack pine stands where the frequency of lethal wildfire is low and unpredictable (Gauthier et al., 1993b, 1996), a noticeable trend at the rear-edge of the species distribution (Radeloff et al., 2004). For instance, Pelletier et al. (2022) reported lower yet more variable serotiny within rear-edge jack pine populations from eastern Canada compared to range-core populations. Furthermore, these uneven-aged stands at the rear edge are in demographic equilibrium with steady regeneration, whereas younger range-core stands are single cohorts lacking interfire recruitment. Pelletier et al. (2022) argued that, unlike range-core jack pine populations, rear-edge populations locally rely on a bet-hedging evolutionary strategy to ensure both steady recruitment during long fire-free intervals and eventual successful postfire regeneration. The variation in serotiny in rear-edge populations could thus represent an adaptive solution to the infrequent and unpredictable fire regime.

Nevertheless, other confounding factors potentially influencing dehiscence of serotinous cones/fruits have been reported. For instance, studies have shown serotiny to decrease with increasing cone age in other serotinous pine species (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz

et al., 2017). The rationale is that older serotinous structures eventually open as their enclosure senesce and die (necriscence; Lamont, 1991), which could lead to the release of fewer viable seeds (Causley et al., 2016). This type of opening occurs when the maintenance costs of serotiny in older cones come in competition with younger cone cohorts, especially for water allocation (Martín-Sanz et al., 2017). A possible loss of serotiny in older jack pine cones has been suggested from field observations (Gauthier et al., 1993a) but was never tested empirically. Cone height above the ground is another factor related to serotiny in lodgepole pine (*Pinus contorta*). Lower branches bear a higher percentage of opened cones compared to upper branches likely because radiative thermal energy transferred from the ground upward can accumulate heat within cones closer to the ground (Crossley, 1956). Field measurements suggest a limited positional effect in jack pine cones (Gauthier et al., 1993a), but lifelong exposure to higher radiative energy in cones closer to the ground could lower their opening temperatures compared to cones from upper branches. Tree age and size could also matter. In lodgepole pine, serotinous cones do not appear before trees reach 15–60 years, which contributes to a rapid stand densification after fire (Critchfield, 1980; Schoennagel et al., 2003). Fewer closed cones were also associated with younger trees in jack pine, but this association may be related to diameter at breast height (DBH) rather than age per se (Gauthier et al., 1993a). However, the opposite effect was reported for Aleppo pine (*Pinus halepensis*) for which serotiny decreases with increasing tree size (Goubitz et al., 2004; Martín-Sanz et al., 2016). This promotes the rapid buildup of a seed bank ensuring stand replacement where frequent fires bring an immaturity risk (Keeley et al., 1999).

Although multiple factors potentially affect seed release in jack pine, whether they actually contribute to modulate intraspecific variation in serotiny in contrasting fire regimes remains unknown. To address this knowledge gap, we experimentally subjected closed cones to incrementing temperatures (i.e., cumulative heat exposure; temperature \times time), then tested seed germination to determine whether and how various ecological factors are related to cone dehiscence and seed viability in jack pine from rear-edge and range-core populations in eastern Canada. Assuming that the energy required for cone opening is ultimately related to serotiny, we expect that cones from rear-edge populations require less cumulative heat exposure than those from the core of the range. We then hypothesized that (1) older cones open at lower temperature and bear fewer viable seeds than younger cones; (2) cones that are closer to the ground in the field require less energy than cones from upper branches to open; and (3) cones from younger and/or smaller trees open at lower cumulative heat exposure than those from older/larger trees. While we worked under the null hypothesis that these responses are immutable in jack pine, our interest is actually to explore differences between range-core populations and rear-edge populations. Indeed, assessing determinants of cone dehiscence and their

consequences on seed viability relative to intraspecific variation in serotiny should provide key insights on eco-evolutionary dynamics of marginal stands.

MATERIALS AND METHODS

Study sites and field sampling

During the growing season of 2019, we sampled 24 jack pine stands from the core ($N = 7$) and the rear edge ($N = 17$) of the species distribution in eastern Québec, Canada (47–51°N; 68–70°W; Figure 1). Range-core sites represent haphazard examples of typical boreal jack pine stands that were easily accessible by roads. These are located on well-drained sandy glacial deposits topped by a shallow organic horizon within the boreal forest, dominated by black spruce, balsam fir, and paper birch (*Betula papyrifera*). We investigated the rear edge more comprehensively. In this area, most sites are located on rock outcrops within the northern temperate forest, mainly composed of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and balsam fir. These peripheral rear-edge stands are smaller, more isolated, and occupy less of the terrestrial landscape than those in the core of the range (Pelletier et al., 2022). According to the Canadian fire regime zonation system (Erni et al., 2020), the rear edge has a very low fire activity with virtually no natural wildfire (e.g., natural fire rotation period >1600 years in preindustrial forests of this area; Elzein et al., 2020), whereas range-core sites are located in fire units prone to recurrent lightning-ignited wildfires (Figure 1). On average, serotiny is lower and more variable within rear-edge populations compared to those from the core of the range (Pelletier et al., 2022).

At each site, 10 randomly chosen mature jack pines were sampled. Three cone-bearing branches from different measured heights (lower, middle, and upper parts of the tree crown) were cut using an extendable tree pruner pole. If the upper parts of the crown were unreachable, we only collected the branch closest to the ground. All sampled branches ($N = 492$) were kept in opened paper bags at room temperature until further laboratory treatments. For each tree, DBH was recorded, and a core was sampled using a Pressler increment borer as close to the ground as possible. Detailed methods used to estimate stand-scale serotiny are reported elsewhere (Pelletier et al., 2022). Briefly, at each site, up to 100 mature jack pine individuals were assigned to one of six serotiny classes (based on the relative abundance of closed cones), and average class value was reported as a percentage reflecting apparent stand-scale serotiny.

Laboratory experiment

At the laboratory, three fully closed cones of contrasted ages were sampled from each branch ($N = 1381$ cones). Specifically, for each sampled branch, the mature closed cone

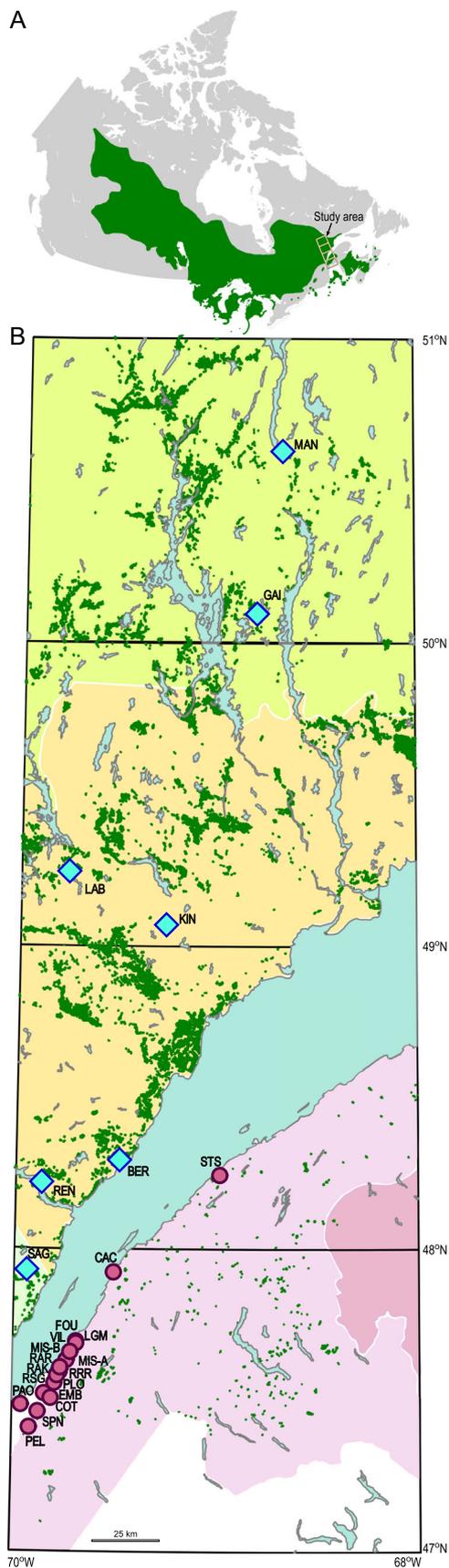


FIGURE 1 Study sites and biogeographic setting of jack pine (*Pinus banksiana*). (A) Transcontinental range of jack pine and sampling area in eastern Québec. (B) Rear-edge (purple dots) and range-core

nearest to the branch tip (the youngest mature cone), the one closest to the trunk (the oldest cone), and one roughly in the middle of the branch were collected. Cone age was determined by cutting the branch at the insertion point, sanding the surface until late and early wood rings were clearly visible, and counting growth rings using a stereomicroscope (Olympus SZ61, Tokyo, Japan). To estimate a minimal age of individual trees, core samples were dried, mounted, and sanded before tree rings were counted. For samples that failed to intersect the pith, minimal tree ages were adjusted by adding the estimated number of missing rings using a geometric pith locator (Applequist, 1958).

Cone opening experiment (heating experiment) was carried out according to a completely randomized design. Each cone was placed in a 100 mL glass beaker randomly positioned on a sheet pan in the middle of a forced convection laboratory oven (JeioTech ON-12GW, Seoul, South Korea) preheated to 48°C. After 1 h, we removed the sheet pan from the oven while (1) the oven was set to a higher temperature and (2) cone opening level was assessed. The opening level refers to the relative abundance of opened scales on each individual cone (level 1: 1–25% opening, level 2: 26–50% opening, level 3: 51–75% opening, and level 4: 76–100% opening; Figure 2). The above cycle was repeated so that the oven temperature was iteratively increased by 3°C increment every hour, when cone opening level was recorded. Each cone was thus heated in the oven for a total run of 6 h with 1 h at 48°C, 51°C, 54°C, 57°C, 60°C, and 63°C. The cone opening experiment took 33 days to complete since the oven can accommodate up to 48 randomly assigned cones per 6-h run.

At the end of each daily run of the cone opening experiment, all cones were heated at 80°C overnight to fully open all scales on every cone. The seeds from these fully opened cones were then manually extracted, and individual seeds were assessed as being filled or empty by applying pressure to the seed unit using forceps. For each cone, the total number of seeds and the number of filled seeds (i.e., containing an embryo) were recorded. The filled seeds of each cone were batch-weighed using an analytical balance and stored in small kraft envelopes until assayed for germination. Individual seed mass was estimated by dividing the total mass by the number of filled seeds recovered from each cone. For the germination assay, at most 20 seeds from one cone were uniformly distributed on a filter paper in a 9-cm petri dish ($N = 1381$ dishes). The filter papers were dampened with 3 mL of primary grade pure water and kept moist throughout the experiment. In total, 23,404 seeds were set to germinate in growth chambers at an optimal temperature of 20°C with 75%

(blue diamonds) sites. Green polygons indicate jack pine stands >4 ha according to Québec's ecoforest data map sheets 21 N, 22 C, 22 F and 22 K from south to north (MFFP, 2020). Background colors represent different fire regime units (FRUs; Erni et al., 2020): purple, FRU 4 (0.03 fire-Mha⁻¹·yr⁻¹); yellow, FRU 11 (0.33 fire-Mha⁻¹·yr⁻¹); light green, FRU 10 (0.64 fire-Mha⁻¹·yr⁻¹).

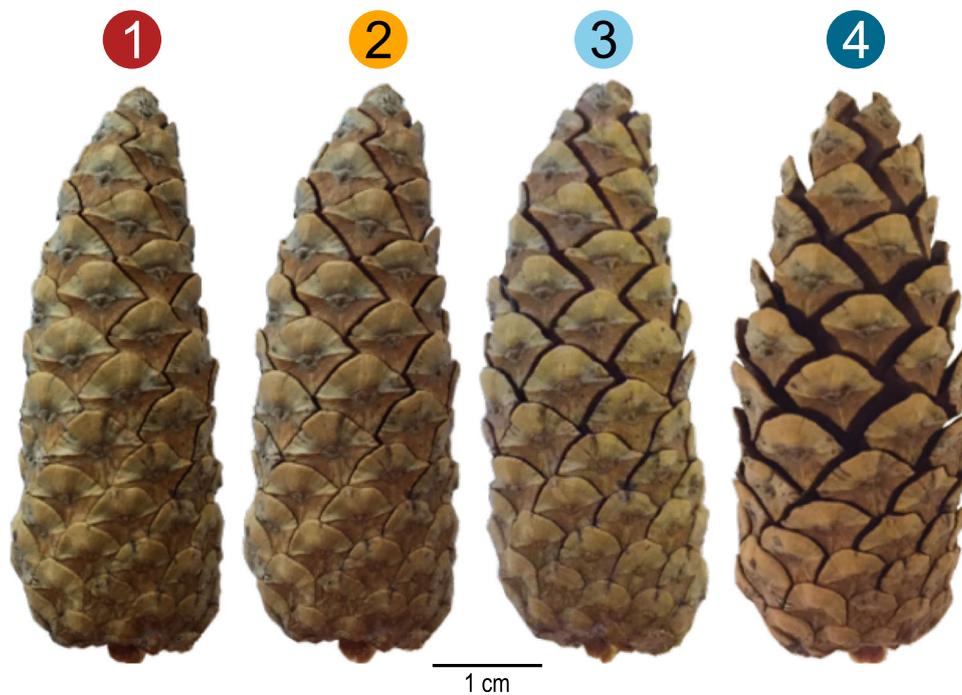


FIGURE 2 Levels of jack pine (*Pinus banksiana*) cone opening during the heating experiment: 1 = 1–25% of the scales are opened, 2 = 26–50% of the scales are opened, 3 = 51–75% of the scales are opened, and 4 = 76–100% of the scales are opened.

relative humidity and a luminous flux of 22,000 lux during 16 h of daylight and 0 lux during 8 h of night. Every day, germinated seeds (radicle >2 mm long) were counted and removed from the petri dishes. The experiment ended when no new seeds had germinated on a given day (i.e., 27 days).

Statistical analyses

The opening levels after each 1-h cycle in oven were used to generate four nonindependent response variables for statistical analyses. For simplicity, the response variable of the heating experiment is expressed as the temperature at which cones reach a given opening level. But because the cones were also exposed to every lower-temperature iteration for 1 h, the response variable (cone opening temperature) actually reflects the cumulative heat exposure (temperature \times time) required to open the cone at the given level. All statistical analyses with cone opening temperature as the response variable were conducted individually for each opening level (levels 1–4). Because the observations are not independent, repeating these tests for each opening level merely reflects whether the relationship assayed between a given ecological factor and cone opening temperature is stable during the various stages of cone opening. A simple linear regression model was used to test the assumption that stand-scale serotiny (estimated from field observations) is actually related to cone opening temperature (assayed in the laboratory heating experiment). Difference between rear-edge and range-core sites in terms of cone opening temperature or mean stand-scale serotiny was assessed

using Welch's two-sample *t*-test. We determined whether putative explanatory variables (cone age, branch height, tree age, and DBH) are related to cone opening temperature using a linear mixed model with the study sites and individual trees as a random factors [Model formula = Opening temperature \sim Cone age + DBH + Branch height + Tree age + (1|Site) + (1|Tree)] with lmer() function in the R package lmerTest (Bates et al., 2015; Kuznetsova et al., 2017). We used a type III analysis of variance (ANOVA) with Satterthwaite's method to provide inferences on the parameters of the linear mixed model (function anova() in R package car; Fox and Weisberg, 2019). We then analyzed explanatory variables with a significant *P*-value individually, separating our data set between geographical regions (rear-edge and range-core). Simple linear regression models were computed to assess whether explanatory variables had a significant effect on cone opening temperature within each region. Because available data are relatively sparse for cones >20 years old, all statistical analyses involving cone age relied on a comprehensive subset including cones \leq 20 years old ($N = 1353$ cones).

For each cone, germination percentage (number of germinated seeds/total number of seeds assayed) and germination velocity ($\sum n_i/d_i$, where n_i is the number of seeds that germinated on day d_i ; Maguire, 1962) were computed. Next, Welch's two-sample *t*-tests were used to assess the differences in mean number of seeds per cone, percentage of filled seeds per cone, individual seed mass, number of germinated seeds per cone, germination percentage, and germination velocity between rear-edge and range-core sites. Finally, simple linear regression model

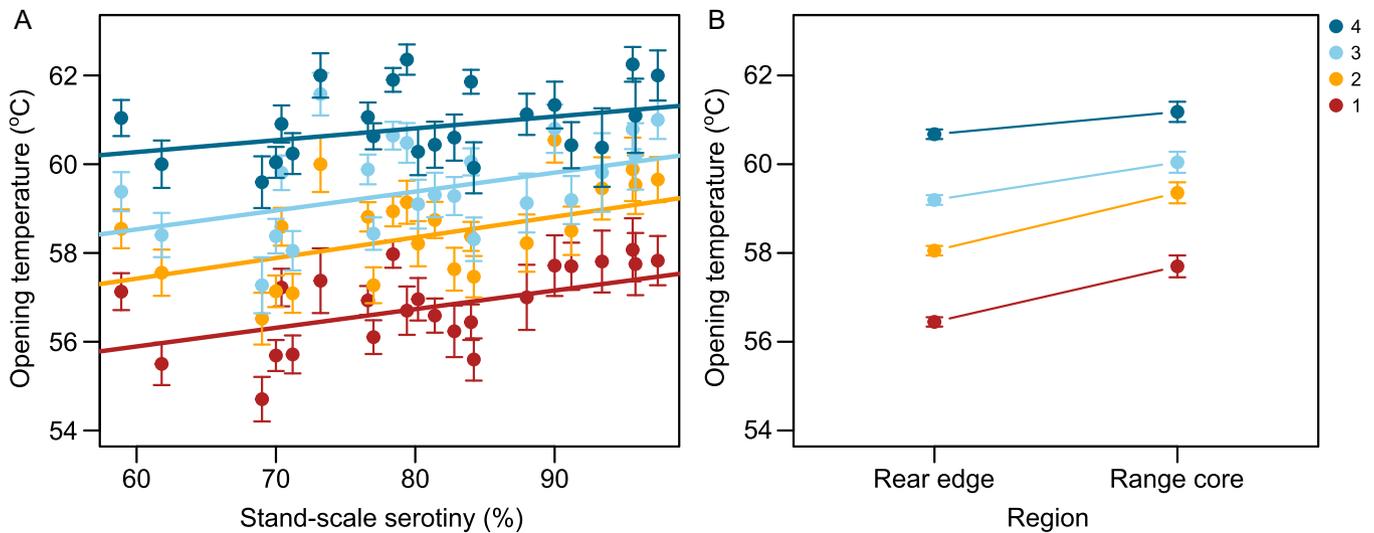


FIGURE 3 Cone opening temperature at the four opening levels as a function of stand-scale serotiny (A) and comparison of mean opening temperature at the four opening levels between rear-edge and range-core jack pine (*Pinus banksiana*) stands (B). Solid lines indicate significant statistical tests (linear regressions or *t*-tests); means \pm SE are shown. Colors for cone opening levels: red, 1; yellow, 2; light blue, 3; dark blue, 4.

was fitted to test for an association between cone age and percentage of germination for seeds from the rear edge and from the core of the range.

All statistical analyses were performed using R version 4.1.1 (R Core Team, 2021). A significance level of $\alpha = 0.05$ was used for all statistical tests. Assumptions of normality and homogeneity of the residuals were ascertained in all models using Shapiro-Wilk's test, Levene's test, and diagnostic plots.

RESULTS

Stand-scale serotiny estimated in the field was positively associated with cone opening temperature in the laboratory oven for each level of cone opening. Cones sampled in stands with a higher degree of serotiny needed more cumulative heat to dehisce compared to those from less serotinous stands (Figure 3A; $P < 0.001$ for levels 1, 2, and 3; $P = 0.016$ for level 4). In the field, cones from rear-edge stands were significantly less serotinous than those from range-core stands (74.9% vs. 93.1%, $P < 0.001$; see also Pelletier et al., 2022). Correspondingly, mean opening temperature was significantly lower for cones collected in rear-edge stands than for those from the core of the range at all opening levels (Table 1, Figure 3B). The linear mixed model suggested that cone age and DBH of parental tree had significant effects on cone opening temperature, while branch height and tree age did not (Table 2). Separate analyses of the relationship between cone age and opening temperature in each region (rear edge vs range core) revealed that cone opening temperature was positively associated with cone age at the rear edge (Figure 4A; $P < 0.001$ for levels 1, 2, and 3, and $P = 0.02$ for level 4), but there was no significant relation in the core of the range

TABLE 1 Comparison of the mean opening temperature (T) necessary to reach the four opening levels between cones collected in rear-edge and range-core sites along with *P*-values, *t*-values and degrees of freedom (df) for each *t*-test.

Cone opening level	$T_{\text{rear-edge}}$ (°C)	$T_{\text{range-core}}$ (°C)	<i>P</i>	<i>t</i> _{df}
1	56.4	57.7	<0.001	4.67 ₂₆₁
2	58.0	59.4	<0.001	5.03 ₂₅₂
3	59.2	60.0	0.001	3.53 ₂₀₀
4	60.7	61.2	0.047	2.00 ₁₃₁

(Figure 4B; $0.30 < P < 0.88$). In other words, older cones required greater cumulative heat to dehisce compared to younger cones, but only at the rear edge. For each cone opening level, the crossing point between intersecting linear regression models of the rear edge and the range core provides an estimate of the age at which cones from rear-edge stands should reach an opening temperature similar to those from the core of the range. We found that this should occur when cones from rear-edge stands reach 13–27 years old, depending on the opening level considered (estimated age at which rear-edge cones behave as range-core cones is 27.2, 25.6, 13.1, and 15.7 years for opening levels 1, 2, 3, and 4, respectively; Appendix S1). Cone opening temperature was positively associated with DBH both at the rear edge (Figure 5A; $P = 0.19$ and 0.002 for opening levels 1 and 2, $P < 0.001$ and 0.003 for levels 3 and 4) and at the core (Figure 5B; $P = 0.03$, 0.03 , 0.27 , and 0.092 for levels 1 to 4, respectively) for most, but not all, opening levels. Consistent with mixed models, no univariate relationship was found between branch height or tree age and cone opening temperature (Appendix S2; $P > 0.05$ for all opening levels).

Results from seed output and germination assay are reported in Table 3. The mean number of seeds per cone and the mean percentage of filled seeds per cone were significantly higher at the rear edge compared to the core of the range. However, the mean mass per seed was greater in

the range core. Considering the mean number of seeds per cone \times mean percentage of filled seeds per cone \times mean mass per filled seed, jack pines at the rear edge invest ca. 35% more in seed output per cone than trees in the range core (0.031 g vs. 0.023 g). The higher individual seed mass did not translate into increased germination potential at the core of the range. Indeed, the number of germinated seeds per cone, germination percentage, and germination velocity were similar between the two regions. Germination percentage did not vary with cone age at the rear edge (Figure 6A; $P = 0.75$), but there was a significant negative relationship in range core stands (Figure 6B; $t_{190} = 3.93$, $P < 0.001$). Hence, seed viability declines with increasing age since maturation but only in the core of the species range, not at the rear edge.

TABLE 2 ANOVA of the linear mixed model for each opening level with their respective sum of squares (SS), denominator degrees of freedom (DENdf), F - and P -values and for each variable. Sites and individual trees were included as a random factors. Significant P -values are in boldface.

Cone opening level	Fixed effect	SS	DENdf	F	P
1	Cone age***	231.2	1096	21.01	<0.001
	DBH*	40.8	120	4.65	0.033
	Branch height	0.9	51.6	0.11	0.744
	Tree age	2.8	88.2	0.32	0.570
2	Cone age***	240.0	1069	28.10	<0.001
	DBH**	75.7	118	8.86	0.004
	Branch height	15.9	48	1.86	0.179
	Tree age	<0.1	83	<0.01	0.952
3	Cone age***	115.4	948	15.35	<0.001
	DBH**	55.1	153	7.33	0.008
	Branch height	3.0	64	0.39	0.532
	Tree age	0.9	109	0.12	0.731
4	Cone age*	23.5	682	3.66	0.056
	DBH*	24.1	132	3.76	0.054
	Branch height	0.3	41	0.04	0.839
	Tree age	2.1	89	0.33	0.566

DISCUSSION

In this study of various ecophysiological factors potentially driving seed release and viability in jack pine from the rear edge and the core of its distribution, we assessed whether and how these factors might contribute to the variable level of cone serotiny observed in jack pine stands from regions marked by contrasted fire activity (Pelletier et al., 2022). The study relies on the assumption that the energy required for cone opening in laboratory heating experiments represents a good proxy of cone serotiny observed in the field. Indeed, our results show that the cumulative heat exposure necessary to open cones (i.e., estimated by the response variable “cone opening temperature”) is positively associated with stand-scale serotiny. Closed cones from populations with a higher level of serotiny thus require more cumulative heat to open compared to closed cones sampled in stands where serotiny is low and variable. This result indicates that our cone heating experiment testing how

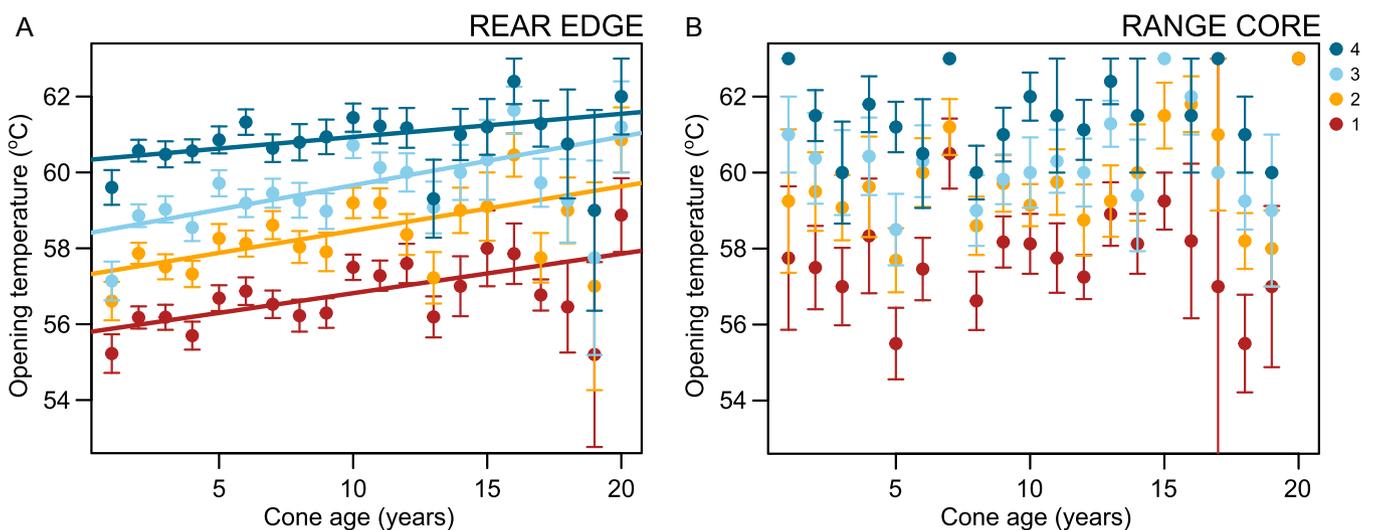


FIGURE 4 Cone opening temperature at the four opening levels as a function of cone age at the rear edge (A) and the core (B) of jack pine (*Pinus banksiana*) distribution. Solid lines indicate significant linear regression models at the rear edge; no significant linear regression model was found in the core of the range. Means \pm SE are shown. Colors for cone opening levels: red, 1; yellow, 2; light blue, 3; dark blue, 4.

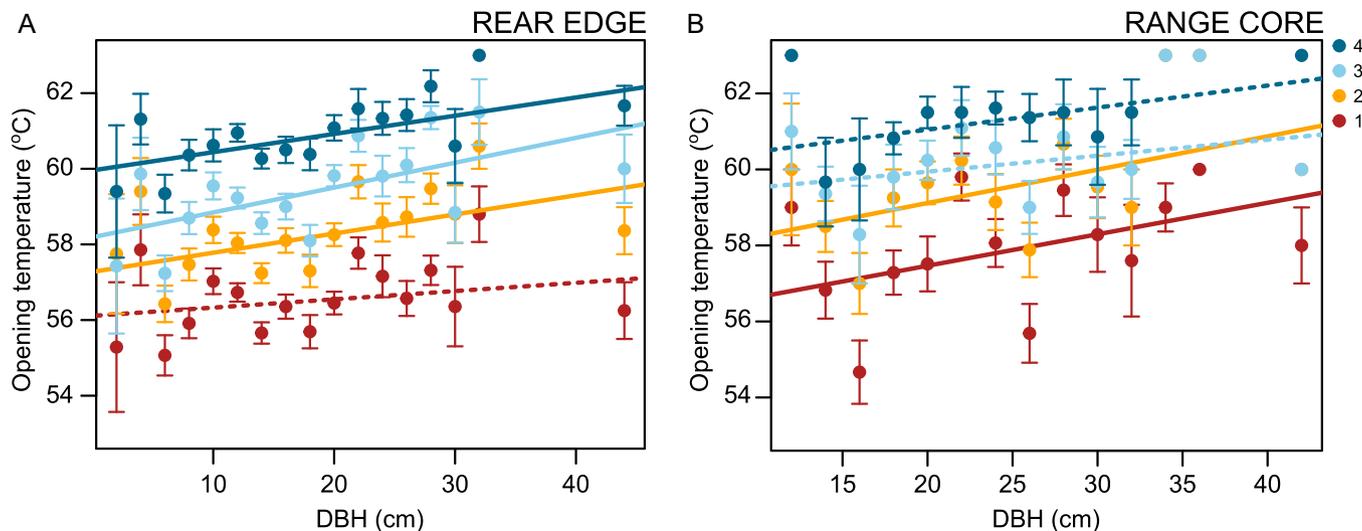


FIGURE 5 Cone opening temperature at the four opening levels as a function of diameter at breast height (DBH) at the rear edge (A) and the core (B) of jack pine (*Pinus banksiana*) distribution. Solid lines are significant linear regression models, broken lines are not. Means \pm SE of 2-cm DBH classes are shown instead of a scatterplot of raw data to simplify visualization. Colors for cone opening levels: red, 1; yellow, 2; light blue, 3; dark blue, 4.

TABLE 3 Comparison of mean number of seeds per cone, mean percentage of filled seed per cone, mean mass per seed (g), number of germinated seeds per cone, germination percentage and germination velocity between rear-edge and range-core sites, along with p -values, t -values and degrees of freedom (df) for each t -test.

Variable	Rear edge	Range core	P	t_{df}
Mean N of seeds/cone***	23.56	18.62	<0.001	5.10 ₂₈₆
Mean % of filled seeds/cone***	55.10	44.94	<0.001	6.10 ₂₆₇
Mean mass/seed***	0.0024	0.0028	<0.001	5.17 ₃₁₇
N germinated seeds/cone	8.45	8.33	0.806	0.25 ₂₃₉
Germination %	50.77	52.96	0.370	0.70 ₂₄₃
Germination velocity	1.13	1.14	0.845	0.20 ₂₃₈

ecophysiological factors relate to the thermal energy required to open cones can be scaled up to provide key insights about the intraspecific variability in serotiny observed in the field.

As expected, we found a significant difference in cone opening temperature between the two study regions (rear edge vs range core). Closed cones from rear-edge jack pine sites in the temperate forest, where wildfires are infrequent and highly unpredictable, require less cumulative heat to open than those from range-core sites in the fire-prone boreal forest. This result reflects the difference in stand-scale serotiny observed in nature, whereby serotiny at the rear-edge is lower and more variable compared to range-core populations (Pelletier et al., 2022; present study) and lends further support to the idea that marginal rear-edge populations are locally adapted to infrequent/unpredictable wildfires. Such adaptive response is in fact possible because

serotiny is a heritable trait in many pine species (Perry and Lotan, 1979; Wymore et al., 2011; Ledig et al., 2013; Hernández-Serrano et al., 2014; Castellanos et al., 2015) including jack pine, where heritability is notably high (Rudolph et al., 1959; Teich, 1970; Pike, 2011). Furthermore, cone serotiny in pine species shows phenotypic variation within and/or among natural populations according to fire regime (Givnish, 1981; Gauthier et al., 1993b, 1996; Schoennagel et al., 2003; Radeloff et al., 2004; Hernández-Serrano et al., 2013; Romero and Ganteaume, 2020; Pelletier et al., 2022). Finally, genomewide association studies exploring the genetic architecture underlying serotiny in pines have uncovered many putative adaptive genes across the genome, suggesting a complex genetic basis (Parchman et al., 2012; Budde et al., 2014; Feduck et al., 2015). Taken together, these findings have rightfully led many authors to argue that variation in serotiny represents an evolutionary response to the natural selection pressure exerted by fire regimes (Enright et al., 1998; Pausas, 2015; Lamont et al., 1991, 2020). However, this conclusion is likely to be toned down if cone opening is in part driven by multiple environmental factors unrelated to the fire regime such as age, size, and position (Lamont et al., 2020).

For instance, we hypothesized that cones located closer to the ground in the field would require less energy to dehisce than cones from higher in the canopy. The rationale behind this positional hypothesis was that a long-lasting exposure to higher radiative heat from the ground eventually reduces resin bond strength in cones from lower branches making them more likely to open at lower temperature. However, results from our heating experiment indicate that branch height is not related to the opening temperature. In contrast, field observations showed that lower branches of lodgepole pine bear a greater proportion of opened cones compared to upper branches (Crossley,

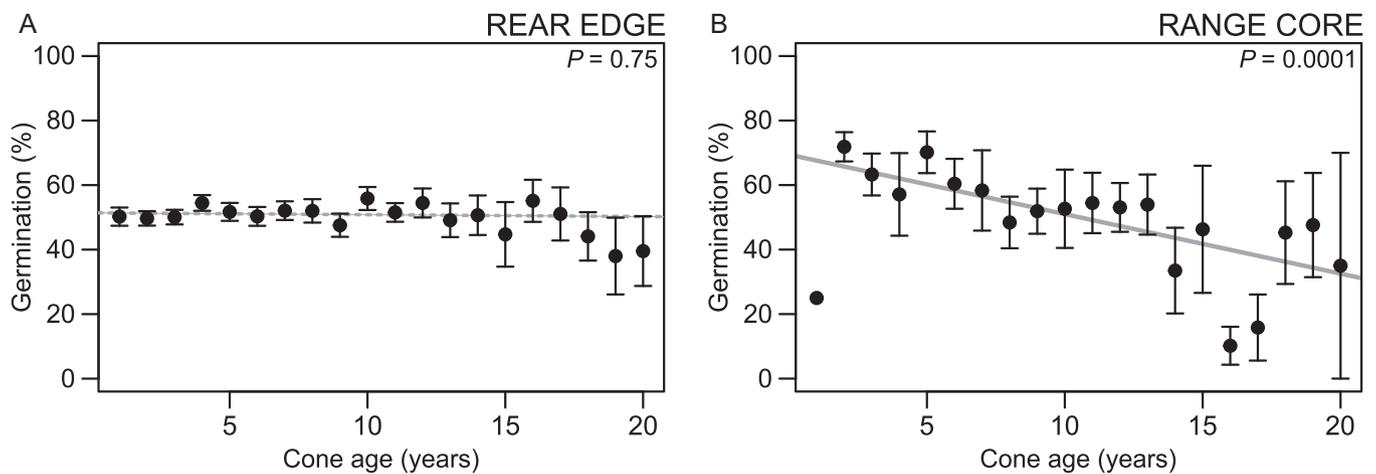


FIGURE 6 Germination percentage as a function of cone age at the rear edge (A) and the core (B) of jack pine (*Pinus banksiana*) distribution. The linear regression model is significant in the range core (solid grey line) but not at the rear edge (broken grey line); means \pm SE are shown.

1956). This pattern could reflect a more direct positional effect whereby radiative heat reaches opening temperatures in situ rather than the lingering effect of a lifelong exposure to radiative heat as tested here. Still, we did not observe a disproportionate number of opened cones in the lower branches of jack pines on our sampled sites (E. Pelletier and G. de Lafontaine, personal observations). Although we did not formally test the positional hypothesis in the field, we had no problem finding closed cones from very low branches (e.g., 0 to 1.5 m) to include in our experiment. Gauthier et al. (1993a) found that the proportion of serotinous cones was slightly reduced on branches below 2.6 m, but only for trees with a DBH \geq 10 cm. These equivocal results also tend to dismiss the existence of a direct positional effect caused by ground-radiated heat in jack pine because the relationship collapses for smaller individuals.

Our results support the contention that tree size, not tree age, modulates serotiny. Indeed, opening temperature of the cones from both regions (rear edge/range core) was positively related to the DBH, but not the age of jack pine individuals. Thus, in agreement with our hypothesis, cones from smaller trees require less cumulative heat exposure to dehisce, but contrary to our hypothesis, this relationship is independent of tree age. Gauthier et al. (1993a) reported a tendency for smaller/younger jack pine trees (DBH < 7 cm; tree age < 32 years) to bear fewer serotinous cones relative to larger/older individuals. Such delayed serotiny might contribute to a rapid postfire stand densification, thanks to continuous seedling establishment during the first few decades after fire (Critchfield, 1985; Lamont et al., 1991). Our results partly agree with this hypothesis, although we did not find an effect of tree age. We thus advocate for an effect of low resource availability rather than tree juvenility to explain cone opening at lower temperature in small individuals. Redmond et al. (2019) found no trade-off between reproduction and vegetative growth (i.e., increased cone production in years of high vegetative growth) for the

pinon pine (*Pinus edulis*). Despland and Houle (1997) reached a similar conclusion in jack pine. Thus, tree size should be roughly proportional to the amount of resources available for cone production. Larger trees, regardless of their age, might have more resources to allocate to the production of serotinous cones than smaller trees that fail to develop full serotiny. The opposite pattern was found in Aleppo pine, for which there is a trade-off between vegetative growth and cone production (Climent et al., 2008) and where serotiny decreases with tree height (Goubitz et al., 2004; Martín-Sanz et al., 2016). These findings might reflect an adaptation of Mediterranean pines to a recurrent, low-severity fire regime, incurring a risk of being burned before enough seeds for postfire recruitment accumulate in the canopy seed bank (Lamont et al., 1991; Keeley et al., 1999). By contrast, in the boreal forest, the likelihood of severe, stand-replacing fire increases as fuel accumulates in dense stands with large trees (Terrier et al., 2017; Thompson et al., 2017). It would thus seem advantageous for jack pine to produce serotinous cones that require gradually more thermal energy to dehisce (i.e., higher melting point of the resinous compound or thicker resin layer) as trees become larger (Crossley, 1956; Lamont et al., 1991).

Based on previous studies on other pine species, we expected serotiny to decrease with cone age due to the maintenance costs of older, senescent cones (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz et al., 2017). We found that dehiscence is indeed related to cone age but, contrary to our hypothesis, opening temperature increased with cone age, meaning serotiny should increase with time since cone maturity. However, and quite interestingly, this relationship differs between regions. Cones at the rear edge require increasing amount of cumulative heat to break up their resin bound as they age. Cones from range-core sites, on the other hand, reach a level of serotiny at maturity that then remains constant. We estimate that it takes between 13 and 27 years for cones from rear-edge stands to reach this

same level of serotiny. This result suggests that cones in rear-edge populations become more serotinous as they age, which should allow for continuous seed dispersal opportunities to arise between fire events. Indeed, the opening of young cones at lower temperature increases the odds of seed dispersal without fire during many years after cone maturation. After 13–27 years, the cones that remained closed eventually reach a level of serotiny comparable to those of jack pines from the boreal forest. These highly serotinous cones then incorporate the aerial seed bank to insure successful regeneration over the long term in case of wildfire (Lamont et al., 1991). This mechanism is not relevant in the boreal forest, where crown fires are likely to occur during the average lifespan of jack pines. As such, our data contribute to explaining the lower yet more variable degree of serotiny found within rear-edge jack pine populations compared to range-core populations (Pelletier et al., 2022). However, they do not support the maintenance cost hypothesis invoked for Mediterranean pines, which states that older cones open by senescence as a result of intraindividual competition for water allocation with younger cone cohorts (Tapias et al., 2001; Espelta et al., 2011; Martín-Sanz et al., 2017). Unlike jack pine, these pine species are moderately serotinous and prone to open their cones without fire by desiccating during drought (Nathan et al., 1999; Pausas, 2015). The effect of cone age on serotiny might starkly differ on a physiological level in such species that are not obligate pyriscent.

Under the maintenance cost hypothesis, we expected that seed viability would decrease with cone age. Consistent with the results of the cone opening experiment, those from our germination assay do not support the maintenance cost hypothesis. Indeed, germination percentages and germination velocity were similar between the rear edge and the range core, ruling out the possibility that lower stand-scale serotiny at the rear edge reflects cone opening by senescence, releasing fewer viable seeds (i.e., necrisence; Lamont, 1991). Quite the opposite, cones from rear-edge stands hold more seeds, include fewer empty seeds, and disperse lighter seeds compared to cones from the boreal forest. All things considered, jack pines at the rear edge invest ca. 35% more in viable seed output per cone than trees in the range core. Cones releasing a greater number of viable, albeit lighter seeds should translate into higher dispersal capacity, which increases the odds of encountering suitable microhabitats for recruitment (Howe and Smallwood, 1982). More seed dispersal might be advantageous at the rear edge when seeds are released without fire because suitable microsites are scattered within mature stands, but not so much in the boreal forest where large wildfires expose extensive tracts of mineral seedbed, rich in resources and devoid of competition (Cayford et al., 1967; Lamont et al., 2020).

A few studies have investigated seed viability over time in jack pine and reached conflicting conclusions. For instance, some authors have reported a decrease in seed viability associated with cone age in jack pine (Roe, 1963;

Popovich et al., 1970; Jeffers, 1985), whereas others did not (Despland and Houle, 1997). Our results help reconcile these contradictory findings by pointing out that the relationship between seed viability and cone age is variable. On the one hand, germination percentage does not vary according to cone age at the rear edge. In this area, where a fraction of the seed output is readily dispersed due to lower serotiny in young cone cohorts, cones gradually become fully serotinous while maintaining a steady level of seed viability (i.e., 51% germination; Figure 6A, Table 3), which contributes to consolidate long-term regeneration capacity in case of fire. On the other hand, germination percentage decreases with cone age in the core of the range. In this fire-prone area, cones are fully serotinous from the outset, and seed viability reaches its highest level at cone maturation (intercept of the linear regression model indicates 70% germination; Figure 6B). Because the latest mature cone cohort immediately integrates the aerial seed bank, it might be advantageous for jack pine in fire-prone areas to continuously maximize seed viability of the latest cone cohort in case of wildfire, at the cost of gradually reducing seed viability in older cones, while still maintaining a low proportion of viable seeds (down to 30% germination after 20 years, Figure 6B; see also Roe [1963] for similar results). In fire-prone areas, more empty seeds and decreasing seed viability over time could represent a strategy to reduce seed predation (Perea et al., 2013). Seed foragers benefit from massive postfire seed release events because their energy intake increases while effort and time costs decrease, although plants incur a higher cost of reproduction (Crawley, 2000). Deceptive seeds (empty or dead) might contribute to overall jack pine fitness in fire-prone areas by increasing the proportion of viable seeds that escape postdispersal predation.

At the rear edge of jack pine distribution, where fire occurrence is uncommon and uncertain, cones become increasingly serotinous without losing seed viability as they age. Individuals in these marginal populations can thus rely on a reproductive strategy implying continuous regeneration throughout their lives (iteroparity) instead of a single massive reproduction event (semelparity) as is generally the case for jack pine (Enright et al., 1998; Nevoux et al., 2010). This syndrome entails a diversified bet-hedging strategy whereby individuals optimize long-term fitness in stochastic environments by sacrificing mean fitness to reduce temporal variance in fitness (Simons and Johnston, 1997; Olofsson et al., 2009; Childs, 2010; Simons, 2011). In the low and unpredictable fire environment of the rear edge, young cones can open without fire after reaching maturity, insuring a steady release of seeds with high dispersal capacity for interfire recruitment. While seed viability is not different on average between rear-edge and range-core cones, it is lower in younger cones from the rear edge (ca. 50% germination) than in younger cones from the core (up to 70% germination). Eventually, older rear-edge cones that have remained closed become as serotinous as cones from fire-prone areas, at which point they become part of the

long-term aerial bank. In the unlikely event of a wildfire, these older cones will release seeds that retained their full viability (ca. 50% germination), which is higher than in old cones from the core (30% germination at 20 years). Jack pine individuals from rear-edge populations thus warrant at least some postfire regeneration, albeit with a lower average fitness compared to their conspecifics from the core of the range that end up with a larger aerial seed bank. Weak serotiny has previously been discussed as a bet-hedging strategy in other fire-prone species, allowing for site exploration and recruitment both interfire and postfire (Enright et al., 1998; Whelan et al., 1998; Nathan et al., 1999; Cramer and Midgley, 2009). This adaptation was invoked where interfire recruitment is possible and fire intervals are long and variable (Tonnabel et al., 2012), such as in rear-edge jack pine stands (Pelletier et al., 2022).

Intraspecific variation in serotiny is often viewed as an adaptive solution to the infrequent and unpredictable fire regime (Pausas, 2015; Lamont et al., 1991, 2020). However, confounding factors affecting dehiscence of serotinous structures might potentially obfuscate the evolutionary importance of this variation (Martín-Sanz et al., 2016). In this study, we elucidated some physiological and environmental factors modulating intraspecific variation in serotiny in jack pine from contrasting fire regimes. We inferred a hypothetical mechanism driving the bet-hedging strategy seemingly observed in marginal jack pine stands at the rear edge of the species distribution (Tonnabel et al., 2012; Pelletier et al., 2022). The genetic basis of this dual life-history strategy remains to be investigated, but our findings suggest rapid evolutionary adaptation is possible in peripheral populations of a widespread boreal conifer as a consequence of local conditions that contrast with those generally found in the boreal forest. This study adds to a growing body of literature emphasizing the need to take into account the possibility of local adaptation and intraspecific trait variability for populations eco-evolutionary responses to global change (Hoffmann and Sgrò, 2011; Violle et al., 2012; Franks et al., 2014; Valladares et al., 2014; Moran et al., 2016; de Lafontaine et al., 2018; Des Roches et al., 2018; Westerland et al., 2021). Understanding the eco-evolutionary dynamics at the edge of species distribution is fundamental to accurately assess the resilience of natural ecosystems in the face of climate change and to design efficient conservation strategies.

AUTHOR CONTRIBUTIONS

E.P. and G.d.L. conceived the ideas, designed methodology, collected and analyzed the data; E.P. wrote the manuscript under the supervision of G.d.L. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data are available on Figshare repository (Pelletier and de Lafontaine, 2022; <https://doi.org/10.6084/m9.figshare.21539931>).

ORCID

Guillaume de Lafontaine  <http://orcid.org/0000-0001-6889-1733>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. For each cone opening level, the crossing point between intersecting regression lines of the rear edge (solid line) and the range core (broken line) models provides an estimate of the age at which cones from rear-edge jack pine (*Pinus banksiana*) stands reach an opening temperature similar to those from the core of the range.

Appendix S2. Cone opening temperature at the four opening levels as a function of branch height (A) and tree age (B) in jack pine (*Pinus banksiana*).

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