RESEARCH ARTICLE

Prescribed Fire Increases Seedling Recruitment in a Natural Pitch Pine (*Pinus rigida*) Population at its Northern Range Limit

Joshua Frans Van Wieren[1,2,3]

[1]Department of Biology
Carleton University
1125 Colonel By Drive
Ottawa, ON, Canada

Andrew M. Simons[1]

[2]Thousand Islands National Park
Parks Canada Agency
2 County Rd. 5
Mallorytown, ON, Canada

[3] Corresponding author: josh.vanwieren@pc.gc.ca; (613) 923-5261 ext. 113

Associate editor: Paula Fornwalt

Natural Areas Journal 39:308–318

ABSTRACT: Disturbances, including wildfire, play an important role in forest maintenance, and have been modified over time. Determining the importance of historical disturbance can be complex, especially if disturbance regimes differ over a species' range. *Pinus rigida* (pitch pine) is associated with wildfire in the core of its range; however, the association becomes less certain toward its range margins, including at the northeast extent of its range in the Thousand Islands Ecosystem (TIE), Ontario, where the species is rare. To test for fire dependence of seedling recruitment in a natural pitch pine population at this range limit, we compared the efficiency of prescribed fire to mechanical and control treatments. We used a Before–After Control–Impact (BACI) design at two sites in the TIE, controlling for the effects of canopy cover, understory cover, and depth to mineral soil. Pitch pine seedlings were observed for the first time in decades in the TIE following treatment; only fire had a significant positive effect on recruitment. Our results suggest that prescribed fire is effective in increasing pitch pine seedling recruitment even in a marginal natural pitch pine population. We discuss what mechanisms might explain these results, as well as restoration considerations including the potential for modified mechanical disturbance treatments where prescribed fires might not be feasible.

Index terms: Fire-adapted conifers, fire history, prescribed burn, restoration ecology, seedling regeneration

INTRODUCTION

Natural disturbances such as fire, wind, insect attacks, drought, and ice storms play a key role in the development, structure, and function of many forests and influence the persistence of disturbance-dependent species (Attiwill 1994). Wildfire is known to create a patchwork of different ecological communities across a landscape (Davis et al. 2003) and generally influences vegetation composition, structure, and pattern by decreasing competition and preparing seedbeds and soil conditions suitable to particular species (Van Sleeuwen 2006). Organisms from microbes (Graham et al. 2014) to trees (e.g., Cayford et al. 1983) exhibit adaptations leading to successful regeneration only after fires.

Disturbance regimes have been extensively altered, with wildfire suppression in the 19th and 20th centuries providing perhaps the best-studied example. Suppression has led to an increase of shade-tolerant species that change light, moisture, and soil dynamics (e.g., Carleton 2000; Nowacki and Abrams 2008). In the continued absence of fire, competition for light and moisture increases at the understory level (Parker et al. 2009) and canopy competition can lead to decreased regeneration of shade-intolerant species (Nowacki and Abrams 2008). Additionally, soil duff layers can increase over time in the absence of fire, which obstructs access to the mineral soil that is beneficial to some species for seedling growth (Waldrop and Brose 1999).

Given the influence that disturbance regimes can have on forest ecosystems, it is important that land management be based on an understanding of these disturbance processes. Hobbs and Norton (1996), for example, suggest that effective ecological restoration depends on the development of mitigation methods based on an understanding of the processes leading to degradation and decline. It is thus imperative that conservation managers understand how to implement disturbance restoration actions in forests where natural disturbances have been altered. However, it can be difficult for managers to determine what mitigation is required to maintain disturbance dependent forests (Ne'eman et al. 2004).

Pitch pine (*Pinus rigida* Miller) is a predominantly fire-adapted coniferous tree found throughout the eastern United States from Maine to Georgia, reaching its northern range limit in southern Ontario and Quebec in Canada (Gucker 2007). Like many other pine (*Pinus*) species and fire-adapted species in general, pitch pine is negatively affected by both canopy and understory competition and increased depth to mineral soil (Ledig and Little 1979; Welch et al. 2000). Canopy competition can cause mortality in seed trees and reduce light availability for seedlings (Welch et al. 2000). Understory competition is also known to affect pitch pine seedlings by increasing light competition in particular (Gucker 2007). Increased duff and litter layers decrease access to mineral soil and chances for successful regeneration (Ledig and Little 1979).

Pitch pine often occurs in ecosystems with frequent fire (Gucker 2007) and its regeneration has long been considered to be associated with fire (Buchholz and Good 1982). Apparent adaptations include development of thick bark that protects mature trees from fire (Little 1953) and epicormic sprouting from dormant buds along the main trunk, which enable pitch pine to recover from crown loss after fires (Ledig and Little 1979). Furthermore, even if all foliage of an individual tree is destroyed by the heat of a fire, the crown will still produce new needles (Ledig and Little 1979); seedlings are also able to recover from fires through basal buds insulated in or against mineral soil (Little and Somes 1956).

A striking fire adaptation of pitch pine is the presence of serotinous cones (Givnish 1981). There is evidence for strong adaptation to fire including serotiny at the core of its range (Ledig and Little 1979) in the New Jersey Pine Plains. Frequency of serotiny generally decreases among populations from that point in all directions (Ledig and Fryer 1972), including in the marginal natural populations found in Ontario, Canada, that lack cone serotiny (Vander Kloet 1981). However, if cone serotiny is a response to particular fire regimes it cannot be taken as a general indicator of fire adaptation. Furthermore, northern pitch pine populations—including those found at the northeastern range margin of the species within the Thousand Islands Ecosystem (TIE)—exhibit adaptations to promote range expansion and rapid colonization (e.g., smaller seeds, more seeds per cone) and may be a leading edge of a range expansion from refugia along the Atlantic Coast (Ledig et al. 2015). If populations in the TIE are adapted to rapid colonization, they may have colonized areas after glaciation with limited competition. It is thus unclear whether this population will respond favorably to fire, although evidence points to some influence of fire. First, the TIE population has been experiencing a sharp decline since at least the 1970s (Lynch 2008), a period in which there was strong fire suppression in the area (SLINP 1993). There has been an almost complete lack of observation of seedlings at the TIE over the past 50 y and, although absence of proof is not proof of absence, undetected recruitment is unlikely because these sites are small and heavily monitored. Second, the expression of fire adaptations such as thick bark and epicormic sprouting exhibited in the TIE suggest at least a historical role of fire in TIE populations. Finally, there is evidence of at least two instances of stand regeneration following fire in the TIE (Rogeau 2007; Srutek et al. 2008). Therefore, despite the lack of serotiny, which is only one of several putative fire adaptations, the relative importance of fire in maintaining the TIE pitch pine population remains unknown. Additional anecdotal observations, such as a fire that completely destroyed pitch pine at a TIE site (Vander Kloet 1981) point to the need for further study.

Some understanding of pitch pine's response to fire has been gained through restoration projects that have been implemented throughout the core of the species' range, with fewer implemented toward the range margins. Prescribed fire has been applied extensively to various pitch pine populations in the United States since the 1930s (e.g., Little 1953; Welch et al. 2000). Canopy thinning has also been used, although less frequently than fire, to both restore pitch pine and reduce fuel loads (Clark and Patterson 2003). No mechanical treatments and only one experimental prescribed fire (Srutek et al. 2008) have been implemented in the TIE. Pitch pine populations in the TIE occur in unique forest communities with unique fuel types and microclimates (Witzke 1996). Consequently, pitch pine populations in the TIE may respond differently than core populations to treatments, and warrant region-specific approaches.

The purpose of this study is to determine whether a restoration approach is effective for pitch pine recruitment where there has been a complete lack of seedling recruitment in undisturbed sites over many decades, and what restoration technique has the greatest effect on increasing pitch pine seedling recruitment in the TIE. Specifically, we test the hypothesis that pitch pine is fire-adapted at recruitment. We thus predict that prescribed fire will (1) lead to recruitment, and (2) result in greater seedling numbers relative to a mechanical treatment and control. To this end, we assessed pitch pine seedling recruitment at a prescribed fire plot, a mechanical treatment plot, and a control plot at each of two sites in the TIE, using a Before–After Control–Impact (BACI) design.

METHODS

Study Species

Pitch pine is often a dominant species in pine barrens throughout much of its range, where it can sometimes be a climax species (Abrams and Orwig 1995). However, it is most often an early successional species replaced by hardwoods in the absence of fire (Westveld et al. 1956). Most populations found in the TIE occur on the Frontenac Arch, a narrow portion of Precambrian shield that connects the Adirondack mountain range in New York State with the Canadian Shield in Canada. Pitch pine in the TIE is found predominantly on rock outcrops and populations are currently described as over-mature and declining with little to no recruitment (Witzke 1996). Most pitch pine populations in the TIE are being outcompeted by hardwood species in the canopy and by shade-tolerant seedlings and shrub species in the understory (SLINP 1993).

Study Area

To determine what restoration technique is the most effective at promoting pitch pine seedling recruitment in the TIE, we compared the results of two different treatments and a control at two locations (hereafter referred to as "sites") in the TIE: Georgina Island (Georgina) and Mallorytown Landing (Mallorytown; Figure 1). Both sites were in similar ecosites (Lee et al. 1998) to ensure comparable species compositions, tree sizes, and soil conditions. They were characterized by dry rocky ridges interspersed with dips containing deeper soils. Georgina pitch pine are found in "Dry-fresh mixed woodland ecosites" and Mallorytown pitch pine stands are found in "Dry-fresh pitch pine coniferous woodland ecosites" (note: this community is derived

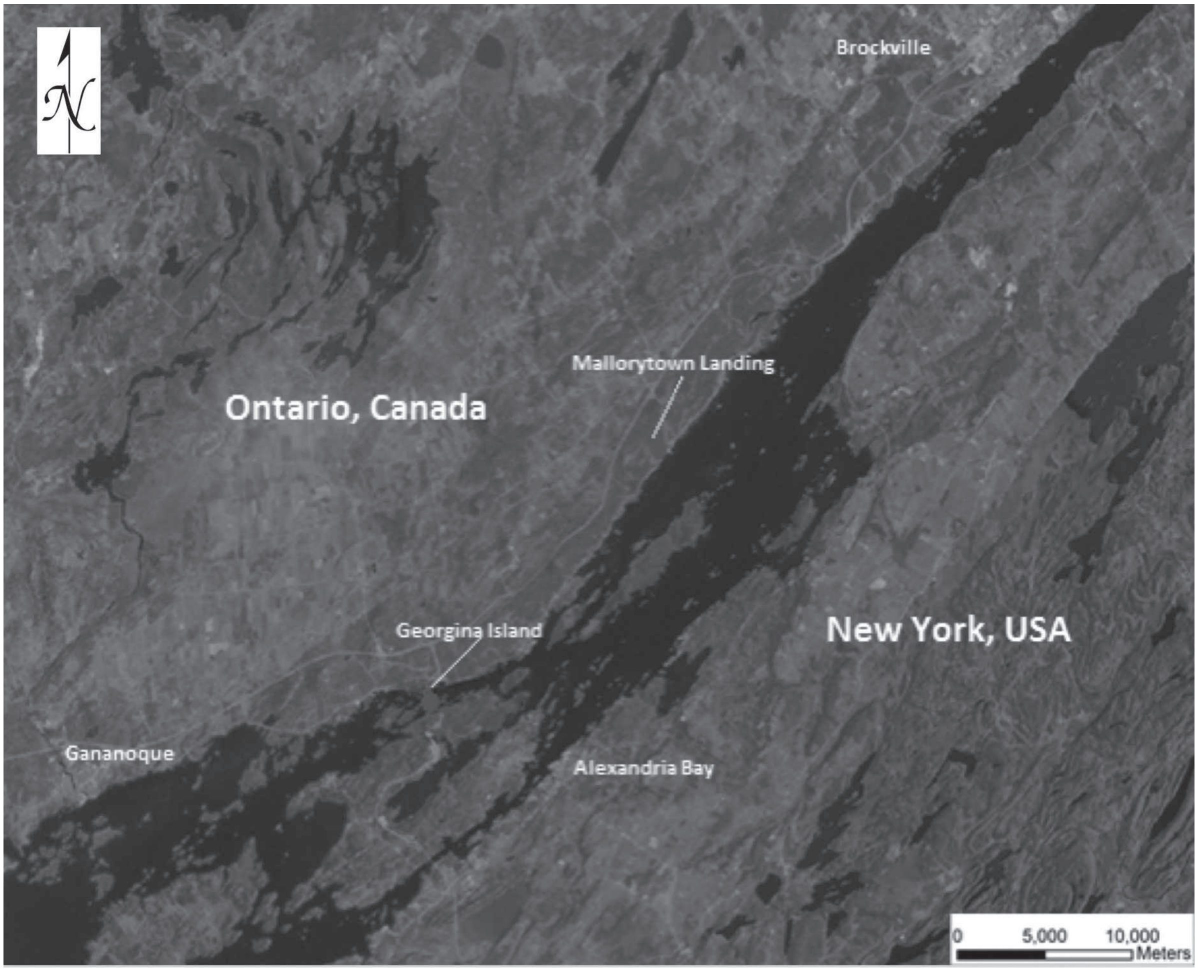

Figure 1. Study sites at Georgina Island and Mallorytown Landing, where a control, prescribed fire, and mechanical treatment were included at both sites.

from the "Dry-fresh white pine coniferous woodland ecosite," which was the closest fit in the manual; Lee et al. 1998). Both sites contained mixed conifer–deciduous stands; however, Mallorytown had a stronger maple (*Acer* spp.) presence whereas Georgina had a stronger oak (*Quercus* spp.) presence. Both sites have been protected as part of Thousand Islands National Park for at least 50 y. Mallorytown may have been used as pasture in the early 1900s, whereas no historical anthropogenic impacts are known on Georgina.

Study Design

A Before–After Control–Impact (BACI) design was utilized to test the effect of different treatments on the number of pitch pine seedlings. A BACI design allows a test of the impact (in our case, two impacts) while controlling for any natural changes that may have occurred (Smith et al. 1993) and provides control for both spatial and temporal variation (Parker and Wiens 2005). The BACI design overcomes limitations on the ability to control natural variation at the sites. In our study, one prescribed fire treatment, one mechanical treatment, and one control plot were included at each site. Plot sizes are constrained by the dimensions of the natural pitch pine stands: Georgina plot sizes were 80 × 50 m, 50 × 40 m, and 60 × 50 m, and Mallorytown plot sizes were 40 × 40 m, 30 × 40 m, and 40 × 40 m in fire, mechanical, and control plots, respectively. Data for the BACI analysis were collected in all plots within 1 y before the treatment and 1 y following the treatment. In addition, site-wide seedling censusing was performed for a further 2 y at both TIE sites. Many BACI studies only include one or two study sites because impacts are not planned, or treatments can only be applied in a few locations (due to logistical or resource constraints; Smith et al. 1993). Similarly, our study was limited by necessity to two sites because of logistical constraints on implementing prescribed fires, and because pitch pine is a rare tree with few stands in Canada (Vander Kloet 1973).

Treatment Types

Prescribed fires were hand ignited using drip torches in an "S" pattern across the entire burn plot and allowed to self-extinguish where safely possible, following standards of the Field Guide to the Canadian Forest Fire Behaviour Prediction System (FBP; Taylor et al. 1997) under guidance of a Parks Canada Fire Behaviour Analyst. The prescription for Mallorytown was slightly more moderate as a precaution for the presence of residential housing within 300 m of the prescribed fire. Some canopy thinning took place at Mallorytown to increase the fuel load to a level deemed comparable to that found at Georgina, as recommended by a Parks Canada Fire Behaviour Analyst, using the fuel load classifications outlined in the FBP, to ensure complete burn coverage of the treatment plot. The Georgina fire was ignited in August of 2009 and Mallorytown was ignited in August of 2011. Although the treatment areas were quite small, this is typical of wildfire in the TIE; a fire is limited by the lack of continuous surface fuel in this heterogeneous landscape. Thus, it is not unusual for fire to be in the range of only 30 × 30 m to 70 × 70 m in the TIE (Rogeau 2007).

Mechanical treatments involved removing 85% of all competing canopy trees including all size ranges down to trees one m in height, while leaving all pitch pines standing. Although percent removal, canopy cover, and basal area are not equivalent, this treatment was based on a rough estimate of canopy cover reduction in a fire, and on the finding that removal of 85% of the basal area led to an increase in pitch pine regeneration (Barden and Woods 1976). The majority of trees were removed using chainsaws; however, some large white pines (*Pinus strobus* L.) were girdled and left standing as snags to provide wildlife habitat. Shrubs and small trees less than one m in height were cut as close to the base of the trunk as possible using a trimmer with a metal blade attachment. All woody debris from tree and shrub reductions was removed from the sites or dragged into large piles to minimize the impact on the study site. The soil was then exposed by blowing most debris from the surface using a power sweep tool. Finally, the entire site was scarified using a soil cultivator to increase access to mineral soil and attempt to remove remaining competing herbaceous and woody species.

Sampling Design

All variables were measured in 2 × 2-m quadrats placed every 10 m along two parallel transects in both treatments and the control at both sites within one y before and after the treatments. The total sample size was 18 fire and control plots and 14 mechanical plots. Fewer mechanical plots were included because some of the original quadrats were compromised after the mechanical treatments were completed. It is important to note that our study design assumes independence between each of these quadrats. Ideally all the quadrats along a transect or both transects at a site would have been averaged and used as individual sample units. However, that would have required having more pitch pine stands than were available and implementing more fire and mechanical treatments than were operationally feasible.

Variables Measured

The response variable and three covariates were measured in each 2 × 2-m quadrat. The response variable was the number of pitch pine seedlings and the covariates were canopy cover, understory cover, and depth to mineral soil. To determine understory cover, the percent area covered in the quadrat by all herbaceous plants and any woody plant less than 4 cm in diameter at breast height (dbh) were included. All plants were identified to species save grasses and sedges, which were grouped together. The percentage of each species was then combined to determine an overall percent cover. Quadrats were surveyed in mid-May for spring ephemeral species and from July to August to capture everything else, without double-counting spring ephemerals if present. Canopy cover was estimated visually as percentage of the sky obstructed by canopy from the vantage point of the center of each 2 × 2-m quadrat. A quadrat with 80% canopy cover would have only 20% of the sky visible from its centroid. To determine the depth to mineral soil, we measured the distance between the forest floor and mineral soil using a soil auger to extract a soil core from the center of the quadrat. The start of mineral soil was defined as the top of the A horizon (Lee et al. 1998). Since soil depths can vary even within a site due to rocky outcrops and dips and rises in the terrain, depth to mineral soil was measured in each of the 2 × 2-m quadrats.

Analysis

To evaluate the relative importance of treatment on pitch pine seedling recruitment, we included all three covariates and compared 15 models in a multi-model inference framework (MMI). We analyzed our data using a two-factor Poisson mixed-model analysis of covariance (ANCOVA) using R 3.0.2. Since each covariate is known to influence pitch pine regeneration, an ANCOVA was ideal because it allowed us to test the effect of both treatments on the response variable, while controlling for the effect of the covariates. To facilitate the BACI design, time (before and after) was included in each model as a categorical factor variable. As a result, each model assessed the differences among treatments in their effect on the change in the response variable from the before to after values. We included site as a random effect in the ANCOVA to control for any differences between the two sites that might confound our results.

We ranked models in the MMI framework based on their Akaike Information Criterion (AIC) values (i.e., $\Delta AIC < 2.0$) and calculated the associated model weights (w_i; Burnham and Anderson 2002). To determine which variable(s) were most strongly supported in determining pitch pine seedling recruitment, we calculated model-averaged estimates of the coefficients for each of the variables in the top models. The advantages of this approach are that it includes an assessment of model selection uncertainty, and objectively determines which model and combination of variables are best supported by the data. A limitation of the design is that if more than one model is selected on the basis of strong AIC values, effects exclusive to a particular model may in fact be driven by correlation with effects not included in this model. Under these circumstances, we considered an additional post hoc ANOVA to partition the competing effects and their interaction.

RESULTS

Model Selection

Over decades of its management history, no pitch pine recruitment has been observed in the TIE in the absence of fire. Here, seedlings were observed, and exclusively in the treatment sites. Although only 15 seedlings were observed in quadrats the year directly following treatment—and thus used in the BACI models—a total of 0, 79, and 6 seedlings were observed in the control, fire, and mechanical plots, respectively, over the 3-year period following treatment (Figure 2).

The BACI models that solely included treatment (fire and mechanical) and depth to mineral soil in determining an increase in pitch pine regeneration the year following treatment had the greatest support in the initial ANCOVA analysis (Table 1). Treatment had an Akaike weight (w_i) of 0.509 and depth to mineral soil was 0.331, in combination accounting for 84% of the total w_i. All other models, including any with canopy and understory cover included, were >4ΔAIC from the top model. The model-averaged partial regression coefficients were 0.202, 0.065, and −0.012 for the fire treatment, mechanical treatment, and depth to mineral soil, respectively (where both treatments and a decrease in the depth to mineral soil had a positive effect on pitch pine seedling numbers; Table 2). Fire and depth to mineral soil were the only two variables whose standard error did not overlap with zero.

Since both the treatment and depth to mineral soil models demonstrated good predictive ability in determining pitch pine seedling recruitment in the initial analysis, a post hoc test was completed to test for an interaction effect between the two models. This post hoc test shows an interaction effect between treatment and depth to mineral soil (Figure 3). The model containing treatment and depth to mineral soil as well as the interaction between the two had the highest r^2 value (Table 3). Only the fire treatment has a regression coefficient that does not overlap with zero in this model. The interaction effect between fire and soil appears to confound the relative importance of both parameters in determining pitch pine seedling recruitment. When the interaction is not controlled for in the model, the regression coefficients are fairly close (see hashed line in Figure 3). However, when the interaction is included in the model, the regression coefficients for both fire and soil deviate from each other and increase from their original values (see solid line in Figure 3).

Table 1. AIC model selection statistics of ANCOVA models where T = treatment, S = depth to mineral soil, C = canopy cover, and U = understory cover. Response variable is number of pitch pine seedlings.

Model	AIC	Δi	w_i
T	166.769	0	0.509
S	167.631	0.861	0.331
C	170.772	4.003	0.069
TS	171.525	4.756	0.047
CS	172.192	5.423	0.034
TC	175.365	8.596	0.007
U	178.768	11.998	0.001
TU	179.178	12.409	0.001
TCS	179.588	12.818	0.001
US	180.315	13.546	0.001
CU	183.569	16.800	0.000
TUS	183.872	17.103	0.000
CUS	184.556	17.787	0.000
TCU	187.329	20.560	0.000
TCUS	191.501	24.731	0.000

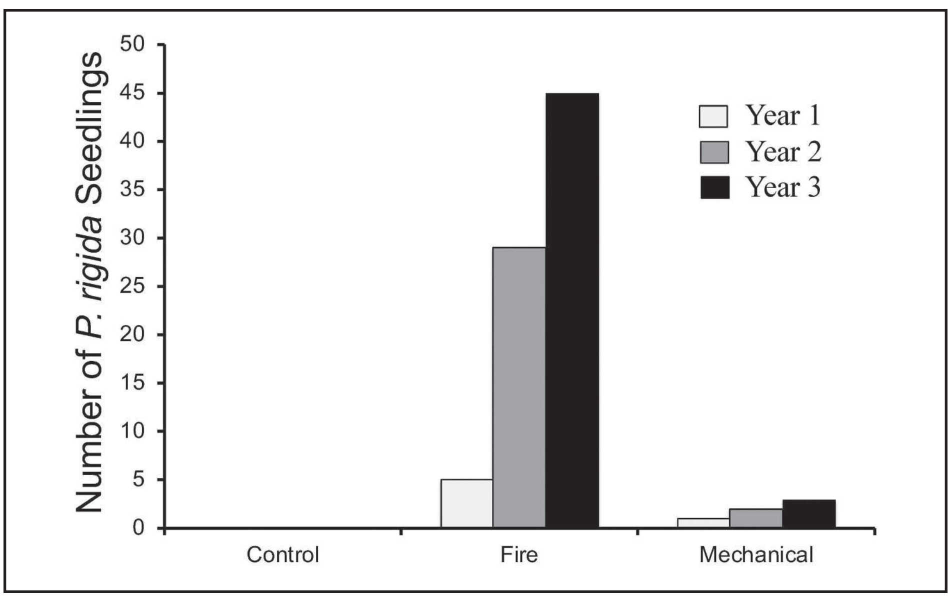

Figure 2. Pitch pine seedling numbers observed at the level of experimental study plots (i.e., not restricted to quadrats) in the 3 y post-treatment.

General Responses of Vegetation Community and Soil Depth to Treatments

The covariates showed a variable response one year following the treatments. Percent canopy cover significantly decreased following both the fire (df = 95, $P < 0.0001$)

Table 2. Model-averaged estimates of the variable coefficients and standard error, calculated using the two models with strongest support.

Parameter	β	SE	df	*P*-value
Fire	0.202	0.072	95	0.006
Mechanical	0.065	0.077	95	0.401
Depth to Mineral Soil	−0.012	0.004	96	0.006

and mechanical treatments (df = 95, $P < 0.0001$; Figure 4). Percent understory cover was not significantly affected by either the fire (df = 95, $P = 0.362$) or mechanical (df = 95, $P = 0.093$) treatments (Figure 5). Finally, depth to mineral soil decreased significantly in the fire treatment (df = 95, $P = 0.013$) but not in the mechanical treatment (df = 95, $P = 0.149$; Figure 6).

DISCUSSION

Adaptation to fire in pitch pine appears to be strong at the core of its range (Ledig and Little 1979), diminishing among populations toward range margins (Ledig and Fryer 1972). Although genetic population differentiation in important plant life-history characters is pervasive (e.g., Wagner and Simons 2009), this is dependent on population history. Given Ontario pitch pine appear to be at the northern edge of post-glaciation range expansion and exhibit adaptations typical of rapid colonization (Ledig et al 2015), the expectation for the extent of fire-dependent recruitment is unclear.

The results of our study support the retention of some fire dependence in the marginal populations studied. The strong predictive ability of the treatment model and the relative strength of the fire treatment regression coefficient both suggest that prescribed fire results in the greatest increase in pitch pine seedling recruitment compared to mechanical or no treatment. The post hoc test provides additional support, suggesting that fire may be most effective at increasing pitch pine regeneration in ways other than altering habitat conditions: controlling for the interaction between the fire treatment and depth to mineral soil increased the relative effect size of the fire treatment. It is also important to note the consistency with which fire had a positive effect on pitch pine regeneration: regardless of which variables were included, fire was consistently positively associated with pitch pine regeneration. Although the efficacy of fire to increase pitch pine regeneration is well supported in parts of its range (e.g., Welch et al. 2000), this study represents only the second and third prescribed fires for pitch pine in Canada and is the first study to determine that fire is more effective than a mechanical disturbance technique.

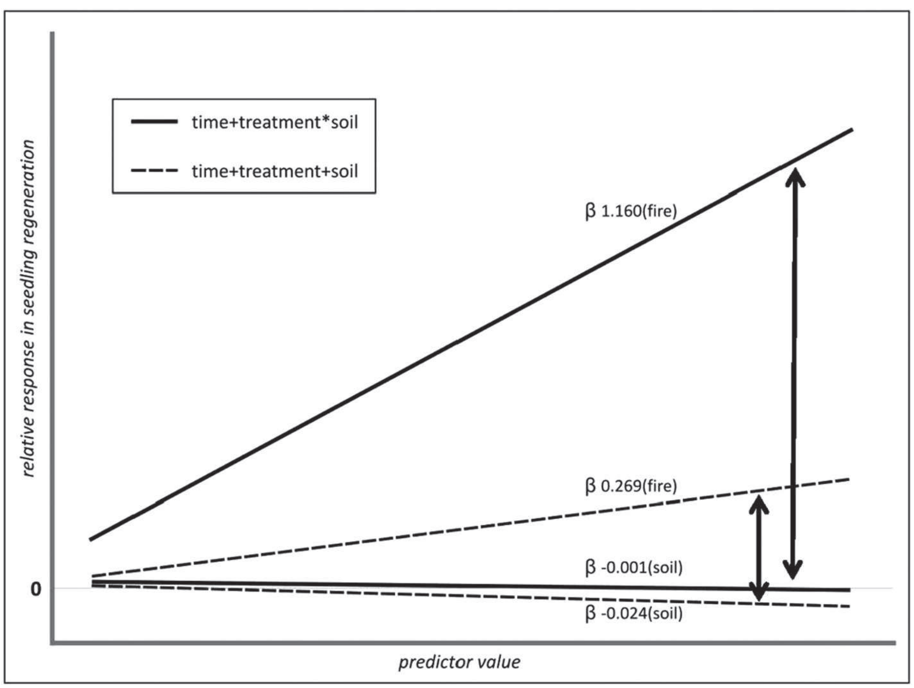

Figure 3. Change in relative importance of fire compared to depth to mineral soil (soil) for an ANCOVA model that includes a treatment*soil interaction term versus a model that does not. β refers to the partial regression parameter for each ANCOVA model.

As expected (Fulé et al. 2012), the mechanical and fire treatment significantly decreased canopy cover (see fire treatment photos in Figure 7), increasing light penetration to the understory. Surprisingly, though, neither treatment decreased the percent understory cover. Although herbaceous and shrub species replaced within one y the understory removed by the treatments, a window of reduced understory directly following treatments may have provided an establishment opportunity for pitch pine seedlings.

Depth to mineral soil was the only measured variable that fire significantly improved that the mechanical treatment did not. In many locations fire smoldered and burned through the duff and litter layers exposing bare mineral soil, ideal for pitch pine seedling germination and growth (Little and Moore 1952). In contrast, the mechanical treatment did not decrease the depth to mineral soil, possibly because the treatment mixed, rather than removed, the litter or duff layers. The test that included the interaction between treatment and depth to mineral soil had the highest r^2 value, suggesting that fire could be modifying the effect of depth to mineral soil on pitch pine regeneration. It has been argued that fire may create a variety of favorable chemical and physical conditions for pitch pine

Table 3. **β values for each parameter in the original treatment + depth to mineral soil tests and post hoc interaction tests, where F = fire treatment, M = mechanical treatment, T = treatment, S = depth to mineral soil, and * represents an interaction test; r^2 values are provided as indicators of the amount of variation explained by each model.**

Model	Parameter	β	r^2	SE	df	P-value
S+T	F	0.269	0.191	0.120	94	0.028
	M	0.143		0.126	94	0.262
	S	−0.024		0.011	94	0.033
S+T+S*T	F	1.160	0.318	0.322	92	0.001
	M	0.171		0.305	92	0.576
	S	−0.001		0.026	92	0.980
	S*F	−0.125		0.037	92	0.001
	S*M	−0.006		0.030	92	0.848
S*T	S*F	−0.038	0.174	0.019	94	0.049
	S*M	−0.026		0.011	94	0.015

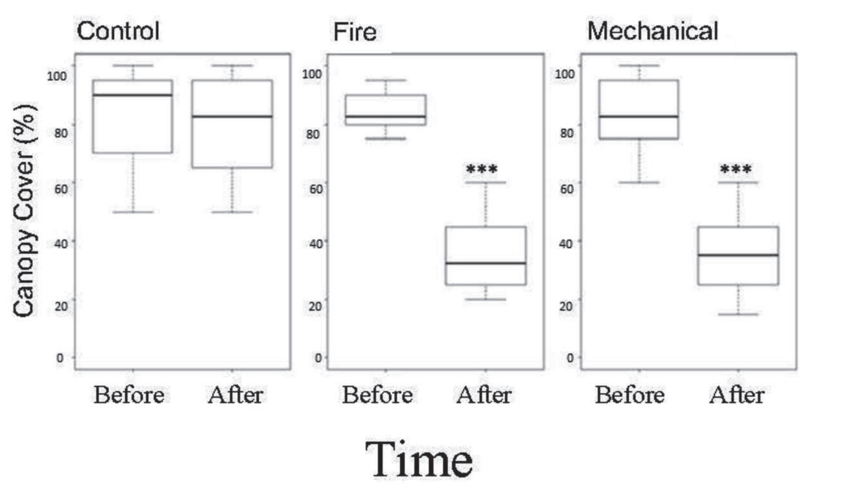

Figure 4. Canopy cover in control, fire treatment and mechanical treatment before and after treatments. *** = $P < 0.001$ using ANCOVA.

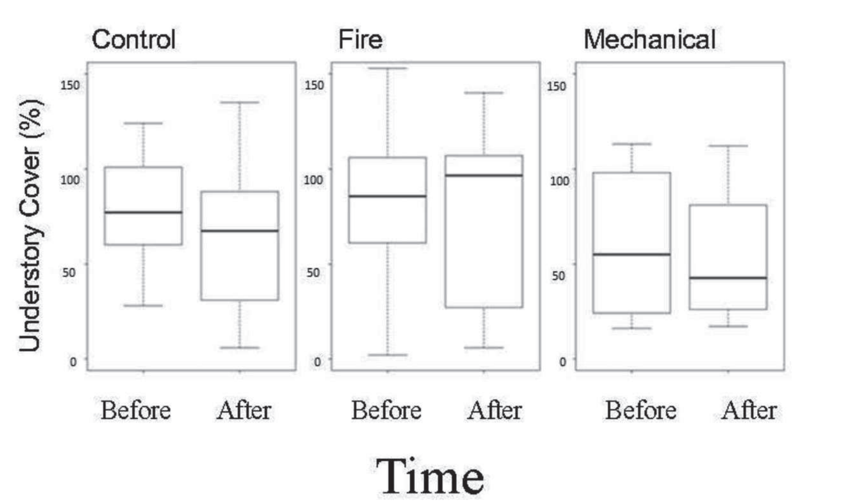

Figure 5. Understory cover in control, fire treatment and mechanical treatment before and after treatments.

recruitment (Groeschl et al. 1993; Certini 2005; Jonsson et al. 2006). However, it is interesting to note that remarkable increases in understory vascular plant species were observed in the prescribed fire (49 new species) and mechanical (35 new species) treatments, with only two new species observed in the control plot.

It is important to recognize the limitations of the present study. The focus was on initial seed germination and early seedling survival; data collection over a longer time period would allow stronger inferences about stand regeneration. Sample size in our study was constrained both by the small number and size of pitch pine stands in Canada, and by the obvious limitations on implementing prescribed fires. However, we obtained a seedling sample size sufficient for statistical inference in a before–after control–impact study. Furthermore, given the complete absence of seedlings in undisturbed areas of the TIE over at least the past 50 y, we would argue that the observation of 85 seedlings in the fire and mechanical treatment plots and zero seedlings in the control quadrats during the two y subsequent to the treatment and BACI analysis is itself a result. This study is also limited in the inferences that can be drawn about the biological mechanisms leading to increased recruitment, such as increased allocation to reproduction either through potentially adaptive plasticity (cf. Simons 2014) in cone or seed production (González-Ochoa et al. 2004; Peters and Sala 2008; Haymes and Fox 2012), which

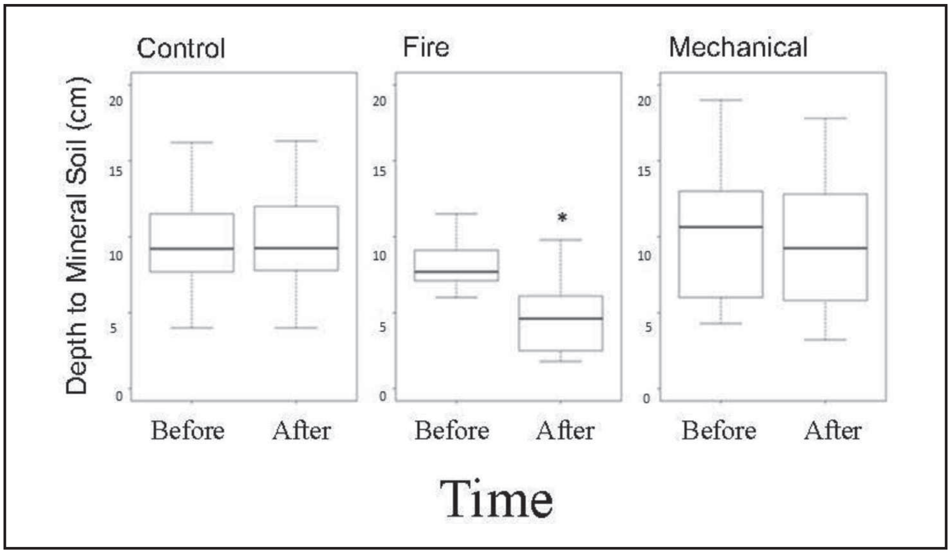

Figure 6. Depth to mineral soil in control, fire treatment and mechanical treatment before and after treatments. * = $P < 0.05$ using ANCOVA.

would require before–after counts, or increased growth rates (Escudero et al. 2000; Hille and den Ouden 2004) in response to disturbance.

Study is also needed to further investigate abiotic mechanisms, such as soil chemistry, underlying the greater effectiveness of fire than mechanical treatments at increasing regeneration. It is important to consider whether mechanical treatment could be improved to facilitate restoration at sites where prescribed fire is not feasible (e.g., logistical, cost, or safety concerns). It is possible that mechanical treatments lack either seed input or conditions suitable to seed germination or early seedling survival. Therefore, post-treatment seedling plantings might enhance the effectiveness of mechanical treatments, coupled with continued thinning of competing hardwoods. Although the two TIE sites differed slightly in hardwood species composition, no information on competitive interactions could be gleaned. If natural recruitment is a goal in mechanical restoration sites, experimenting with additional soil scarification techniques may be beneficial. Other possibilities could be explored, such as mechanical treatment followed by prescribed fire to reduce mortality of mature pitch pine seed trees.

Determining the fire regime in TIE and other marginal populations of pitch pine may be difficult (Rogeau 2007) but understanding the historical disturbance regime is important to help guide land management. For example, fire suppression may have led to the crossing of a threshold (Hobbs and Norton 1996), in which fuel loads increase to a point where fire intensity is more severe than mature pitch pine can survive (Van Sleeuwen 2006). This could be significant for *P. rigida*, since more-intense fires may cause extreme smoldering, which can disrupt basal sprouting (Windisch 1999). If individual pitch pine trees become less fire-adapted with age (Windisch 1999), increased periods between fires may reduce the ability of pitch pine stands to respond favorably to fire. In three plots defined internally by Parks Canada Agency at the Georgina site, 80% (n = 29) of the adult trees (dbh > 4 cm) were killed within one y of the fire and 93% had died two y after the fire. There appears to be a tradeoff between treating sites with prescribed fires severe enough to destroy shade-tolerant hardwoods and root systems of competing shrubs, while retaining some pitch pine seed trees (Srutek et al. 2008). Even though remaining seed trees generated successful recruitment, it is possible that with lower adult tree mortality rates, regeneration may have been even better.

CONCLUSIONS

Overall, we found that fire was more effective than mechanical disturbance at increasing initial pitch pine seedling recruitment at the species' extreme northeast range margin. Our results imply that fire has a significant effect on pitch pine seedling recruitment beyond a reduction in canopy cover and possibly beyond or in conjunction with depth to mineral soil. Pitch pine at the core of its range exhibits strong fire adaptations that increase seedling regeneration after fires, whereas TIE populations exhibit fewer adaptations. Consequently, the effectiveness of fire to increase seedling regeneration compared to mechanical disturbance demonstrated in our study suggests it is possible that pitch pine in the TIE have retained fire-adapted traits beneficial to establishing seedlings that are triggered by fire events.

ACKNOWLEDGMENTS

We thank the Thousand Islands National Park fire crew, Parks Canada Fire Program staff (especially Derek Bedford, Marie-eve Foisy, Victor Kafka, and Raymond Quenneville), for expertise and logistical support in conducting prescribed fires, and Sheldon Lambert, Jeff Leggo, Harry Szeto, Paul Zorn, and Doug Bickerton for additional support. Excellent suggestions were furnished by two anonymous reviewers. Funding was provided by the Parks Canada Agency and through an NSERC DG to AMS.

Joshua Frans Van Wieren obtained a Bachelor degree in Environment and Resource Studies from the University of Waterloo before obtaining his Master's degree in Biology (evolutionary ecology) at Carleton University. Joshua is Park Ecologist with Parks Canada at the Thousand Islands National Park, with responsibilities including ecological restoration, ecosystem monitoring, prescribed fires, species at risk recovery, and medicinal plant mapping with the Mohawk Nation at Akwesasne, and has special interests in citizen science.

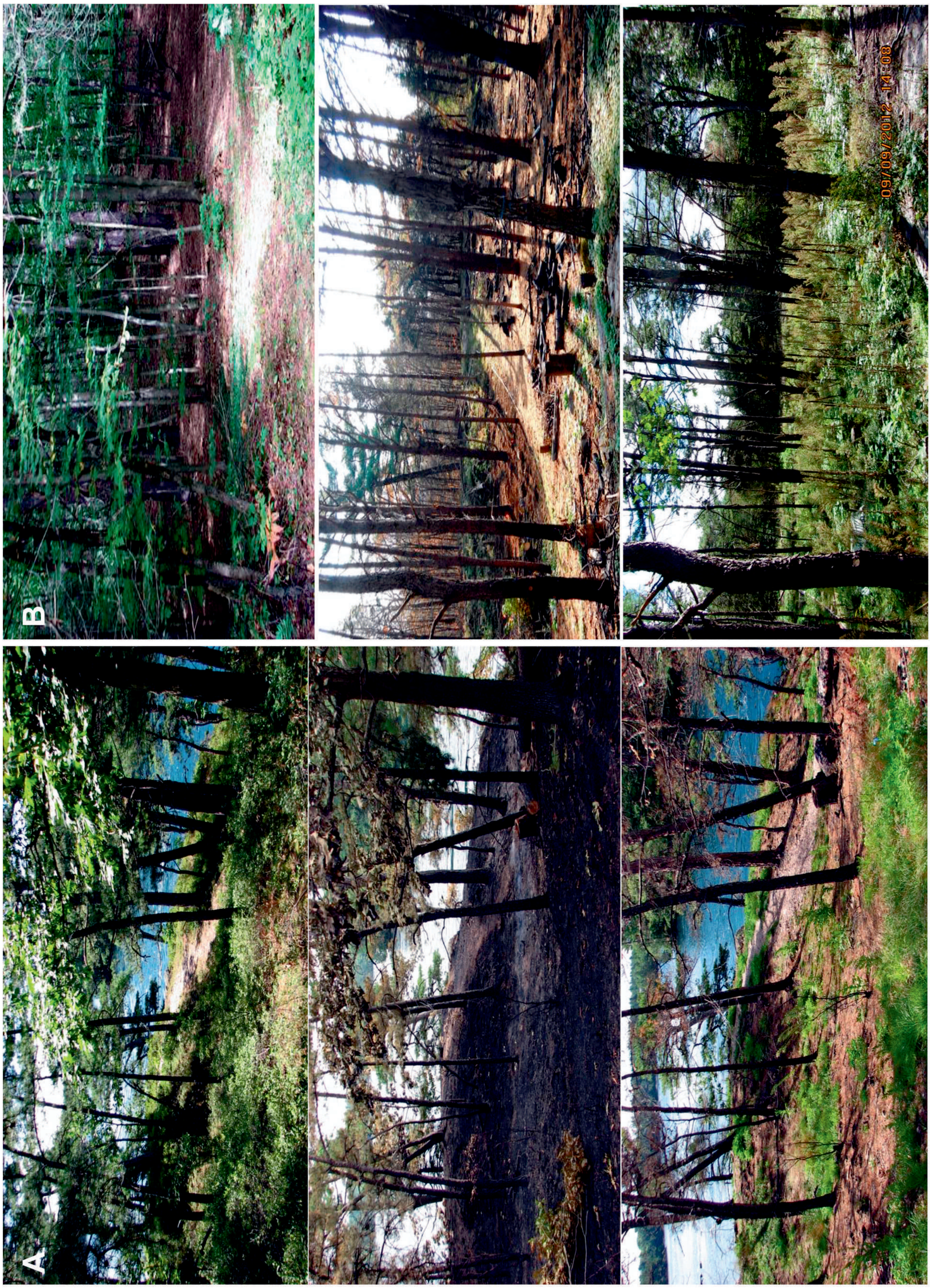

Figure 7. (A) From top to bottom, Georgina Island prescribed fire treatment one year before the fire, one day after the fire, and one year after the fire; (B) from top to bottom, Mallorytown Landing prescribed fire treatment one year before the fire, two months after the fire, and one year after the fire.

Andrew M. Simons holds degrees in Biology from the University of Guelph (BSc), McGill University (MSc), and Dalhousie University (PhD), and conducted post-doctoral research at North Carolina State University. Andrew is Professor of Biology at Carleton University, where he has been since 2000; the common thread of his research program is the evolutionary ecology of organismal response to environmental variation—from adaptive tracking, phenotypic plasticity, to the evolution risk aversion, or "bet-hedging" strategies—using a wide range of tools from dendrochronology to evolutionary genetics.

LITERATURE CITED

Abrams, M.D., and D.A. Orwig. 1995. Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. Oecologia 101:353-360.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management 63:247-300.

Barden, L.S., and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. Forest Science 22:399-403.

Buchholz, K., and R.E. Good. 1982. Density, age structure, biomass and net annual above-ground productivity of dwarfed *Pinus rigida* Mill. from the New Jersey Pine Barren Plains. Bulletin of the Torrey Botanical Club 109:24-34.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, NY.

Carleton, T.J. 2000. Vegetation responses to the managed forest landscape of central and northern Ontario. Pp. 178–197 *in* A.H. Perera, D.L. Euler, and I. Thompson, eds., Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario. University of British Columbia Press, Vancouver, BC.

Cayford, J.H., D.J. McRae, R.W. Wein, and D.A. Maclean. 1983. The ecological role of fire in jack pine forests. Pp. 183–199 *in* R.W. Wein and D.A. Maclean, eds., The Role of Fire in Nothern Circumpolar Ecosystems. Wiley & Sons, New York, NY.

Certini, G. 2005. Effects of fire on properties of forest soils: A review. Oecologia 143:1-10.

Clark, K.H., and W.A. Patterson III. 2003. Fire Management Plan for Montague Plain Wildlife Management Area. Department of Natural Resources Conservation, University of Massachusetts, Amherst. Available from <https://www.umass.edu/nebarrensfuels/publications/pdfs/montague_fireplan.pdf>.

Davis, R.J., J. Wilkinson, and D. Heaman. 2003. Fire management efforts in Ontario's protected areas: A synopsis. Pp. 421–427 *in* C.J. Lemieux and J.G. Nelson, eds., Proceedings of the 2003 Parks and Research Form of Ontario. Available from <http://casiopa.mediamouse.ca/wp-content/uploads/2010/05/PRFO-2003-Proceedings-p421-427-Davis-Wilkinson-and-Heaman.pdf>.

Escudero, A., Y. Nunez, and F. Perez-Garcia. 2000. Is fire a selective force of seed size in pine species? Acta Oecologica 21:245-256.

Fulé, P.Z., J.E. Crouse, J.P. Roccaforte, and E.L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? Forest Ecology and Management 269:68-81.

Givnish, T.J. 1981. Serotiny, geography, and fire in the Pine Barrens of New Jersey. Evolution 35:101-123.

Gonzalez-Ochoa, A.I., F.R. Lopez-Serrano, and J. de las Heras. 2004. Does post-fire forest management increase tree growth and cone production in *Pinus halepensis*? Forest Ecology and Management 188:235-247.

Graham, J.K., M.L. Smith, and A.M. Simons. 2014. Experimental evolution of bet hedging under manipulated environmental uncertainty in *Neurospora crassa*. Proceedings of the Royal Society B 281:20140706.

Groeschl, D.A., J.E. Johnson, and D.W. Smith. 1993. Wildfire effects on forest floor and surface soil in a table mountain pine–pitch pine forest. International Journal of Wildland Fire 3:149-154.

Gucker, C.L. 2007. *Pinus rigida*. *In* Fire Effects Information System. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Accessed 15 Nov 2016 from <http://www.feis-crs.org/feis/>.

Haymes, K.L., and G.A. Fox. 2012. Variation among individuals in cone production in *Pinus palustris* (Pinaceae). American Journal of Botany 99:640-645.

Hille, M., and J. den Ouden. 2004. Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire and soil scarification. European Journal of Forest Research 123:213-218.

Hobbs, R.J., and D.A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93-110.

Jonsson, L.M., J. Dighton, J. Lussenhop, and R.T. Koide. 2006. The effect of mixing ground leaf litters to soil on the development of pitch pine ectomycorrhizal and soil arthropod communities in natural soil microcosm systems. Soil Biology & Biochemistry 38:134-144.

Ledig, F.T., and J.H. Fryer. 1972. Pocket of variability in *Pinus rigida*. Evolution 26:259-266.

Ledig, F.T., and S. Little. 1979. Pitch pine (*Pinus rigida* Mill.): Ecology, physiology and genetics. Pp. 347–371 *in* R.T.T. Forman, ed., Pine Barrens: Ecosystem and Landscapes. Academic Press, New York, NY.

Ledig, F.T., P.E. Smouse, and J.L. Hom. 2015. Postglacial migration and adaptation for dispersal in pitch pine (Pinaceae). American Journal of Botany 102:2074-2091.

Lee, H., W. Bakowsky, J. Riley, J. Bowles, M. Puddister, P. Uhlig, and S. McMurray. 1998. Ecological Land Classification for Southern Ontario: First Approximation and its Application. Ontario Ministry of Natural Resources, Southcentral Science Section, Science Development and Transfer Branch, North Bay, ON.

Little, S. 1953. Prescribed burning as a tool of forest management in the northeastern states. Journal of Forestry 51:496-500.

Little, S., and E.B. Moore. 1952. Mechanical preparation of seedbeds for converting oak-pine stands to pine. Journal of Forestry 50:840-844.

Little, S., and H.A. Somes. 1956. Buds enable pitch and shortleaf pines to recover from injury. USDA Forest Service, Northeast Forest Experimental Station. Station paper No. 81. Available from <https://www.nrs.fs.fed.us/pubs/sp/sp_ne081.pdf>.

Lynch, M.B. 2008. Pitch Pine Assessment in St. Lawrence Islands National Park: 2008 Report. Available from Thousand Islands National Park, 2 County Rd. 5, Mallorytown, ON, K0E 1R0.

Ne'eman, G., S. Goubitz, and R. Nathan. 2004. Reproductive traits of *Pinus halepensis* in the light of fire – A critical review. Plant Ecology 171:69-79.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58:123-138.

Parker, K.R., and J.A. Wiens. 2005. Assessing recovery following environmental accidents: Environmental variation, ecological assumptions, and strategies. Ecological Applications 15:2037-2051.

Parker, W.C., D.G. Pitt, and A.E. Morneault. 2009. Influence of woody and herbaceous competition on microclimate and growth of eastern white pine (*Pinus strobus* L.) seedlings planted in a central Ontario clearcut. Forest Ecology and Management 258:2013-2025.

Peters, G., and A. Sala. 2008. Reproductive output of ponderosa pine in response to thinning and prescribed burning in western Montana. Canadian Journal of Forest Research 38:844-850.

Rogeau, M.P. 2007. Preliminary Fire Regime Study: St. Lawrence Islands National Park of Canada. Available from Thousand Islands National Park, 2 County Rd. 5, Mallorytown, ON, K0E 1R0.

Simons, A.M. 2014. Playing smart vs. playing safe: The joint expression of phenotypic plasticity and potential bet hedging across and within thermal environments. Journal of Evolutionary Biology 27:1047-1056.

SLINP 1993. Pitch pine population study and management plan. Prepared by Ecologistics for St. Lawrence Islands National Park. Available from Thousand Islands National Park, 2 County Rd. 5, Mallorytown, ON, K0E 1R0.

Smith, E.P., D.R. Orvos, and J. Cairns. 1993. Impact assessment using the before-after-control-impact (BACI) model – Concerns and comments. Canadian Journal of Fisheries and Aquatic Sciences 50:627-637.

Srutek, M., J. Dolezal, C.S. Findlay, and R.A. Andress. 2008. Regeneration and seedling-habitat relationships of the marginal population of pitch pine (*Pinus rigida*) after prescribed burning, eastern Ontario, Canada. Natural Areas Journal 28:155-167.

Taylor, S.W., R.G. Pike, and M.E. Alexander. 1997. Field Guide to the Canadian Forest Fire Behavior Prediction (FBP) System. Canadian Forest Service Pacific Forestry Centre and B.C. Ministry of Forests Research Branch, Victoria, BC.

Vander Kloet, S.P. 1973. The biological status of pitch pine, *Pinus rigida* in Ontario and adjacent New York. Canadian Field Naturalist 87:249-253.

Vander Kloet, S.P. 1981. Status of *Pinus rigida* in Canada (with special reference to St. Lawrence Islands National Park). Available from Thousand Islands National Park, 2 County Rd. 5, Mallorytown, ON, K0E 1R0.

Van Sleeuwen, M. 2006. Natural Fire Regimes in Ontario. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, Toronto, ON. Available from <https://www.ontarioparks.com/pdf/fire/fire_research_2006.pdf>.

Wagner, I., and A.M. Simons. 2009. Divergence among arctic and alpine populations of the annual, *Koenigia islandica*: Morphology, life history and phenology. Ecography 32:114-122.

Waldrop, T.A., and P.H. Brose. 1999. A comparison of fire intensity levels for stand replacement of table mountain pine (*Pinus pungens* Lamb.). Forest Ecology and Management 113:155-166.

Welch, N.T., T.A. Waldrop, and E.R. Buckner. 2000. Response of southern Appalachian table mountain pine (*Pinus pungens*) and pitch pine (*P. rigida*) stands to prescribed burning. Forest Ecology and Management 136:185-197.

Westveld, M., R.I. Ashman, H.I. Baldwin, R.P. Holdsworth, R.S. Johnson, J.H. Lambert, H.J. Lutz, L. Swain, and M. Standish. 1956. Natural forest vegetation zones of New England. Journal of Forestry 54:332-338.

Windisch, A.G. 1999. Fire ecology of the New Jersey pine plains and vicinity. Doctoral diss., Rutgers, The State University of New Jersey, New Brunswick.

Witzke, C. 1996. Pitch pine (*Pinus rigida* Miller) genetics, reproductions and silvicultural management. A literature review and annotated bibliography. Eastern Ontario Model Forest. Information Report No. 20. Available upon request from the Eastern Ontario Model Forest, 10 Campus Drive, Unit #3, Kemptville, ON, K0G1J0. <modelforest@eomf.on.ca>.