RESEARCH ARTICLE

•

Regeneration and Seedling-habitat Relationships of the Marginal Population of Pitch Pine (*Pinus rigida*) After Prescribed Burning, Eastern Ontario, Canada

Miroslav Šrůtek[1]

Faculty of Biological Sciences
University of South Bohemia[2]
and
Institute of Botany
Průhonice, Czech Republic[3]

Jiří Doležal

Institute of Botany
Třeboň, Czech Republic[4]

C. Scott Findlay

Biology Department
University of Ottawa[5]

R.A. (Bud) Andress

Parks Canada[6]

•

[1] Corresponding author:
srutek@esnet.cz; +420-565433219;
Benešov 14, CZ-394 70 Kamenice n.L.,
Czech Republic

[2-6] For complete address, see list below
ABSTRACT.

ABSTRACT: Post-fire seedling establishment in relation to microsite conditions and relationships of seedlings (saplings) to older tree individuals was studied in two treatments (i.e., burned and unburned sites) in an area known as the pitch pine (*Pinus rigida*) ridge on Hill Island, St. Lawrence Islands National Park, Eastern Ontario. *Pinus rigida* is a rare tree species in Canada at the northern limit of its range. *Pinus strobus* (eastern white pine) and *Quercus alba* (white oak) are also common species of the site. The negative correlation between density of mature *P. rigida* trees and total canopy cover and hardwood density was confirmed in unburned plots on the ridge. On the other hand, *P. strobus* density was positively correlated with those parameters. The density of *P. rigida* seedlings is higher (by 48%) and *P. strobus* seedlings lower (by 82%) in burned plots than in unburned plots. Seedling recruitment was also dependent on the occurrence of seed trees of both species. The density of *P. strobus* seedlings was generally higher than that of *P. rigida* seedlings, especially in unburned plots. The long absence of fire, high seed production of *P. Strobus,* and relatively low number of *P. rigida* seed-producing trees, which have a low amount of fertile cones, are probably the main factors influencing seedling recruitment on the ridge. Discriminant analysis confirmed different seedbed requirements of both species. *Pinus strobus* seedlings occurred within both treatments, especially on deeper soil profiles with thicker litter depth, although, for seed regeneration, a mineral soil seedbed or a greatly reduced organic layer was also important. *Pinus rigida* seedling recruitment on burned and unburned plots was comparatively higher on mineral soil, thinner litter layer, and moss and lichen cushions.

Index terms: environmental variables, *Pinus rigida*, prescribed fire, regeneration, seedling recruitment

Address list:

[2] Department of Botany
Faculty of Biological Sciences
University of South Bohemia
Branišovská 35, CZ-370 05
České Budějovice

[3] Institute of Botany
Department of Geobotany
Zámek 1, CZ-252 43 Průhonice
Czech Republic

[4] Institute of Botany
Section of Plant Ecology
Dukelská 145
CZ-379 82 Třeboň
Czech Republic

[5] Biology Department
Faculty of Science
University of Ottawa
30 Marie Curie
P.O.Box 450
Ontario K1N 6N5
Canada

[6] Parks Canada
St. Lawrence Islands National Park
2 County Road #5
Mallorytown Landing
Ontario K0E 1R0
Canada

INTRODUCTION

Modern management practices in protected forest areas should follow natural processes, especially disturbance, to result in greater variation over time and space than manifested through traditional silvicultural practices (Seymour and Hunter 2000). One of the essential natural disturbances in many Canadian national parks is fire (Weber and Stocks 1998). Prescribed fires are frequently applied for restoration and active management of selected vegetation types in many North American national parks (Weber and Taylor 1992; Elliott et al. 1999; Motzkin et al. 1999; Welch et al. 2000).

Fire is a critical factor affecting the long-term dynamics of many biomes around the world (Goldammer and Jenkins 1990; Bergeron et al. 1998; Johnson and Miyanishi 2007). Many tree species, particularly in temperate and boreal forests, exhibit a flush of seedling establishment following fire and show many other types of adaptations for the regeneration of various tree parts (Lloret 1998; Welch et al. 2000; Wang 2002; Goubitz et al. 2003; Ordóñez and Retana 2004).

Plant species response to fire can be fundamentally different in different communities. In temperate and boreal areas, conifers with serotinous cones

show seedling recruitment that is largely restricted to a single point in time related to a fire event (e.g., Lamont et al. 1991). This occurs despite repeated cone crops. Although being serotinous is particularly well developed in the family *Cupresaceae* (Keeley et al. 1998), examples from other families and genera are recognized as well (Gauthier et al. 1996; Midgley and Enright 2000). Another widespread fire-induced reproductive mechanism is re-sprouting from dormant buds along the bole (Little and Somes 1964; Givnish 1981; Buchholz and Good 1982; Höllermann 1996; Šr tek et al. 2002).

Both trunk sprouting and seedling establishment in pitch pine (*Pinus rigida*) are somewhat rare in Canada, as Canadian populations occur on the northern margin of the natural distribution of the species. *Pinus rigida* prefers warmer and moister climate conditions (Greenwood et al. 2002; Day et al. 2005), which in Canada are limited to several sites along the St. Lawrence River (Vander Kloet 1973; Meilleuret et al. 1997).

Although *P. rigida* individuals have either serotinous or non-serotinous cones (not both), some seedling establishment is expected in the absence of fire. However, negligible seedling density was observed over the last several years at St. Lawrence Islands National Park and other Canadian pitch pine sites (Donnelly and McCloskey 1996; Meilleuret et al. 1997). Therefore, a prescribed burn was conducted in the spring of 1997 to promote *P. rigida* regeneration and reduce competition with other plant species on Hill Island.

The pre-burn inventory of habitat relationships and seedling (saplings) densities was conducted by Donnelly and McCloskey (1996). The purpose of this study was to characterize post-fire seedling establishment in relation to micro-site conditions and the relationships of germinants and regenerated seedlings to older tree individuals within a selected stand. Particularly, we attempted to answer the following questions: (1) Does the fire treatment affect relationships between mature trees (density and estimated cover) and pine seedling recruitment and local site conditions? (2) Are there differences in the regeneration pattern of pine seedlings between the burned and control (unburned) stands? and (3) Do the investigated biotic and abiotic factors affect the post-fire recruitment of pitch pine and white pine seedlings?

MATERIAL AND METHODS

Study site

The research was conducted on Hill Island (lat 44°21'N, long 75°59'W) in St. Lawrence Islands National Park, Eastern Ontario, Canada. Hill Island is one of the largest of 25 islands under the protection of National Parks of Canada (Anonymous 1997). The island is approximately 400 ha in size. Hill Island's forest communities are extremely varied, ranging from wet marshy lowlands to high dry rocky ridges with bedrock plant communities. One rocky ridge, referred to locally as "the pitch pine ridge," is a significant granite feature on the island. The ridge is 110 m above mean sea level, going in SW-NE direction. The ridge is covered by the largest single stand of *P. rigida* in Canada (compare to the occurrence of pitch-pine communities in the northeastern United States; Motzkin et al. 1996); it is approximately 675 m long and 150 m wide. Eastern white pine (*Pinus strobus*), white oak (*Quercus alba*), and eastern hemlock (*Tsuga canadensis*) tend to dominate the southern slopes of the ridge.

The Hill Island pitch pine ridge is afforded the highest protection level under the park's zoning system (Zone I). The climate of the area is moderated by Lake Ontario. Mean annual temperature for the Kingston Region, which is appropriate for the study site, is 6.7°C, and mean annual precipitation is 964 mm. A noticeably unsuccessful regeneration of *P. rigida* over the last couple of decades suggest predation by mammals such as white-tailed deer (*Odocoileus virginianus* Zimmerman) and porcupine (*Erethizon dorsatum*) and the absence of wildfire (Olson and Lewis 1999). Both factors appear to be contributing to *P. rigida* decline on the ridge. Acid deposition from industrial areas of the nearby U.S. states (e.g., New York, Ohio, and Pennsylvania) could also contribute to the *P. rigida* population decline in the Thousand Islands region (McClenahen and McCarthy 1990).

Sampling methods

The fire was ignited on 27 April 1997 as the prescription conditions were met (Fine Fuel Moisture Code [FFMC] of 90, relative humidity of less than 40%, wind speed less than 20 km.h^{-1}, and Rate of Spread [ROS] of 1-3 m.min^{-1}) (compare van Wagner et al. 1992). Hand torch igniting was carried out along the southwest end of the pitch pine ridge. Fire behavior was within the prescribed ROS (average 1.0 to 3.0 m.min^{-1}). Where fuel was relatively sparse, the fire crept in dried grasses and pine needles; in moss mats, the fire self-extinguished. The fire spread at higher rates in oak leaf litter (1 to 6 m.min^{-1}). Air temperature during the burn ranged from 24°C to 19°C and Relative Humidity [RH] ranged from 18 to 23%. Flame heights observed were 0.5-0.7 m, giving an intensity of 60-100 kW.m^{-1}.

The burn area was about 300 m long by about 95 m at its widest point and occupied roughly the southeastern quarter of the ridge (i.e., 1.7 ha (Saunders 1996)). Approximately the same area located in a northeast direction along the ridge was studied as unburned. Four years had elapsed since the area was burned (1997) and, at first, higher recruitment (in 2000) of *P. rigida* germinants was observed. In fact, one cohort (2001) of *P. rigida* (*P. strobus*) germinants predominated in the area. However, regenerated seedlings of 2000 were also recorded. We use the general term "seedling(s)" for both categories.

In 2001, a grid of 70 quadrat plots (5 m x 5 m) was established along 14 line transects 40 m apart, which were perpendicular to the lengthwise axis. The axis was located approximately along the ridge center of the island. The starting point of the axis was located selectively on the southwestern edge of the burned area. Five plots (10 m apart), including one central plot on the lengthwise axis, were located along each transect so that eventually 35 plots were within the burned and 35 plots within the

unburned areas. Because it is difficult to replicate a disturbance event such as fire at small spatial scale (Hurlbert 1984), the sampling design as used in this study is commonly applied for assessing the effects of prescribed fires and wildfires on forest regeneration, although the sampling plots are not true replicates (see van Mantgem et al. 2001).

To determine which plot-level attributes affect the regeneration pattern of P. rigida and P. strobus in control burned and unburned stands, we counted all seedlings within each 5-m x 5-m plot (Table 1) and measured individual seedling height, crown length, and number of branches. Percent area covered by trees (> 2 m tall), shrubs (0.8 < h < 2 m tall), herbs, graminoids, and ferns (< 0.8 m tall) and the bottom layer of bryophytes, lichens, and seedlings was recorded in each plot. Percent area covered by rock, litter, and woody debris (WD included tree branches > 1 cm in mean diameter, fallen trunks, deposited old bark, fallen cones, and exposed tree roots) was also estimated. The type of damage suffered by each seedling (drying, browsing, insect-related, dead) was recorded as well.

The number of each tree species was counted within each 5-m x 5-m plot and in an additional 5 m distance around the basic plot (i.e., within 10-m x 10-m plots). Five categories of tree were distinguished: (1) seed trees of P. rigida, (2) seed trees of P. strobus, (3) trees of P. rigida without cones, (4) trees of P. strobus without cones, and (5) hardwood trees.

To determine which factors are potentially responsible for seedling emergence within control and burned plots, we recorded the following individual parameters for each seedling found in each 5-m x 5-m plot: soil profile depth (i.e., depth to bedrock including moss, lichen, grass/sedge, and litter) measured by a calibrated steel probe, litter depth measured by ruler, litter type (needles, leaves, pulp/bark, needles+leaves, leaves+needles, needles+ blueberry (Vaccinium spp.) leaves, hare droppings, moss, leaves or needles+grass/sedge leaves, grass/sedge leaves), and soil surface features beneath each seedling (litter, moss, lichen, mineral soil, rock, grass/sedge, litter beside rock, old wood/rotten wood/bark). To test whether values of the estimated environmental variables differ between spots occupied and unoccupied by seedlings, the same parameters including profile depth, litter depth, litter type, and soil surface features were measured within each plot at

randomly selected points whose numbers equalled the number of seedlings, generating a total of 27,288 individual-level data records.

Statistical analyses

In order to explore the interrelationships between factors potentially responsible for the densities of P. rigida and P. strobus seedlings, Principal Component Analysis (PCA) was first calculated with the plot-level micro-environmental variables and seedling and tree counts. PCA was performed on the character correlation matrix (i.e., after centering and standardization as plot-level variables were measured in different units, each variable has then a zero average and unit variance). PCA was performed separately for burned and unburned plots using CANOCO for Windows (ter Braak and Šmilauer 1998; Lepš and Šmilauer 2003).

To test which plot-level micro-environmental factors significantly affect seedling density in burned and unburned plots, a generalized linear model (GLM), with Poisson error or Quasi-likelihood distribution and logarithmic link function (McCullagh and Nelder 1990; Crawley 2002), was

Table 1. The total numbers and percent proportions (in brackets) of seedlings of *Pinus rigida* and *P. strobus* in four vigour categories in experimental burned and unburned plots on Hill Island, St. Lawrence Islands National Park, eastern Ontario, Canada. Shown are also average (min-max) seedling height and crown length in cm.

Stand	unburned			burned		
P. rigida	count	height	crown	count	height	crown
no damage	210 (95)	5.6 (1.5 - 22)	4.2 (1 - 20.5)	337 (93.9)	4.7 (2.5 - 15.5)	2.9 (1 - 12)
browsed	3 (1.4)	13 (9 - 20)	8.3 (5 - 14)	7 (1.9)	5.6 (2.5 - 12)	3.9 (1 - 11)
insect	1 (0.5)	4.5	3	3 (0.8)	5.8 (3 - 8)	4.6 (2 - 7)
dead	7 (3.2)	5.7 (4 - 11)	4.1 (2 - 10)	12 (3.3)	5.4 (3 - 10)	2.5 (1 - 9)
Total	221			359		
P. strobus	count	height	crown	count	height	crown
no damage	2193 (91.5)	6 (2 - 25)	2.4 (0.5 - 18)	419 (96.5)	6 (2.5 - 21)	2.6 (1 - 12)
browsed	22 (0.9)	6.3 (3 - 14)	3.3 (0.5 - 12)	2 (0.5)	6.5 (5 - 8)	3.8 (2.5 - 5)
insect	0	-	-	0	-	-
dead	182 (7.6)	5.5 (2.5 - 10)	2.3 (1 - 7)	13 (3)	4.9 (2.5 - 6.5)	2 (1.5 - 4)
Total	2397			434		

calculated. The significance of the linear model was tested using the analysis of deviance in the S-plus package (Chambers and Hastie 1992). If the form of linear dependence was not accepted, a second-order polynomial was fitted. We conducted two types of analyses using GLM. The first tested for the significant relationship between the density of emergent seedlings and an environmental variable by including that variable alone as a predictor in a single regression. The second tested for a significant relationship between seedling density and an environmental variable having statistically controlled for factors that could potentially confound such a relationship. Akaike Information Criterion (Chambers and Hastie 1992) and the F-ratio-based test in analysis of deviance were used to decide upon acceptance or rejection of a particular predictor variable.

A stepwise discriminant function analysis (Manly 1998) was used to explore which individual-level factors are responsible for tree seedling emergence, using the attributes measured for each seedling and beside each random point (profile depth, litter depth, litter types, and soil surface features) as predictors of seedling emergence. Hence, discriminant analysis was used to investigate which variables discriminate between spots occupied and unoccupied by tree seedlings.

RESULTS

Effect of prescribed fire on local site conditions

Pinus rigida, *P. strobus* and *Quercus alba* were the most important overstory species both prior to and following the prescribed

burn. The burn reduced the densities of these species (Figure 1). Mean densities of mature *P. rigida* and *P. strobus* trees were 70% and 53%, respectively, lower in post-burn plots compared to the unburned stand. The density of mature *P. rigida* trees in unburned plots was negatively correlated with total tree canopy cover (Pearson correlation $r = -0.51$, $P = 0.003$) and hardwood tree density ($r = -0.36$, $P = 0.033$), whereas *P. strobus* tree density was positively correlated with total tree canopy cover ($r = 0.37$, $P = 0.025$, Figure 2). In the burned stand, *P. rigida* trees retained the negative correlation with total tree canopy cover ($r = -0.39$) and became even more strongly negatively correlated with hardwood tree density ($r = -0.69$) compared to the unburned stand.

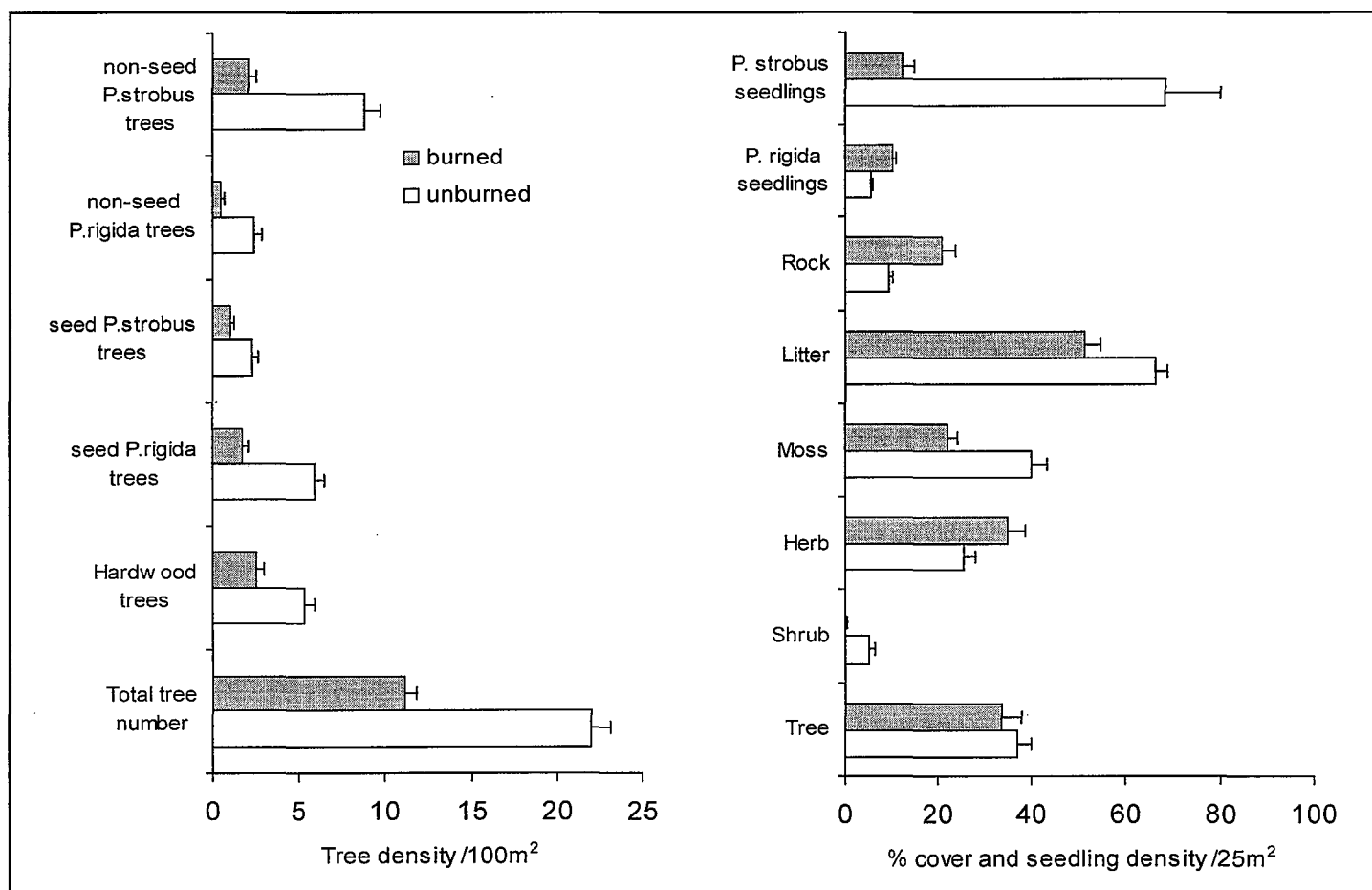The burn reduced the cover of the shrub and moss layers and increased the surface

Figure 1. Comparison of mean density (± 1 SE) of *Pinus rigida* and *P. strobus* seedlings (plots 5 x 5 m, n = 75) as well as average cover values of vegetation layers and density of mature trees (plots 10 x 10 m, n = 75) between unburned and burned stands. All tested variables differ significantly between burned and unburned stands except for percent herb and tree canopy (GLM followed by F-test).
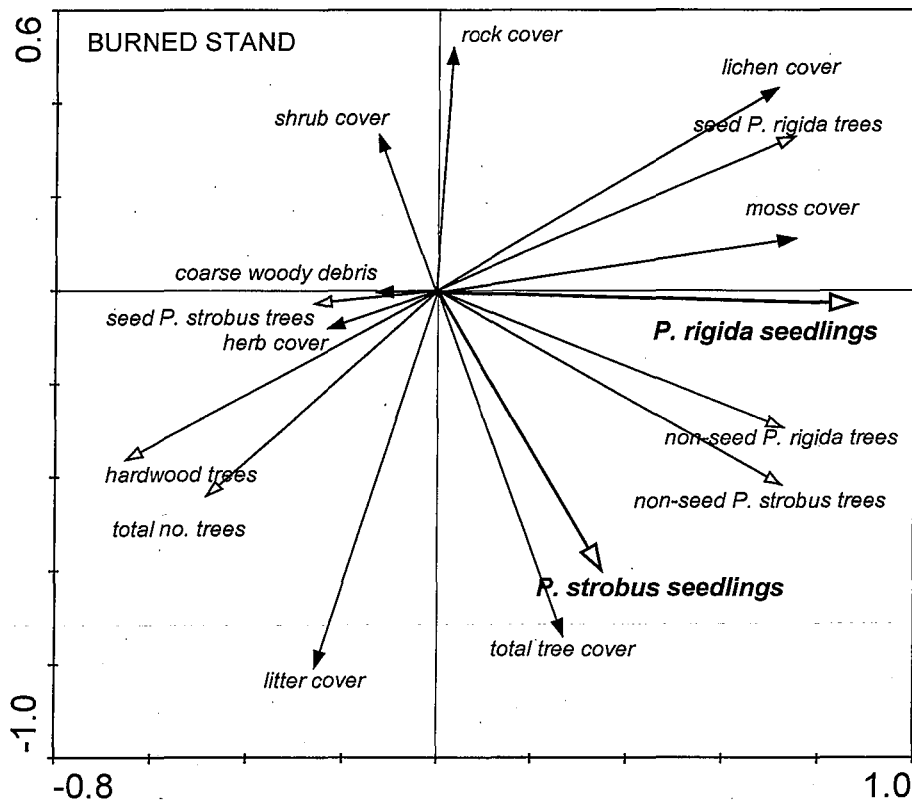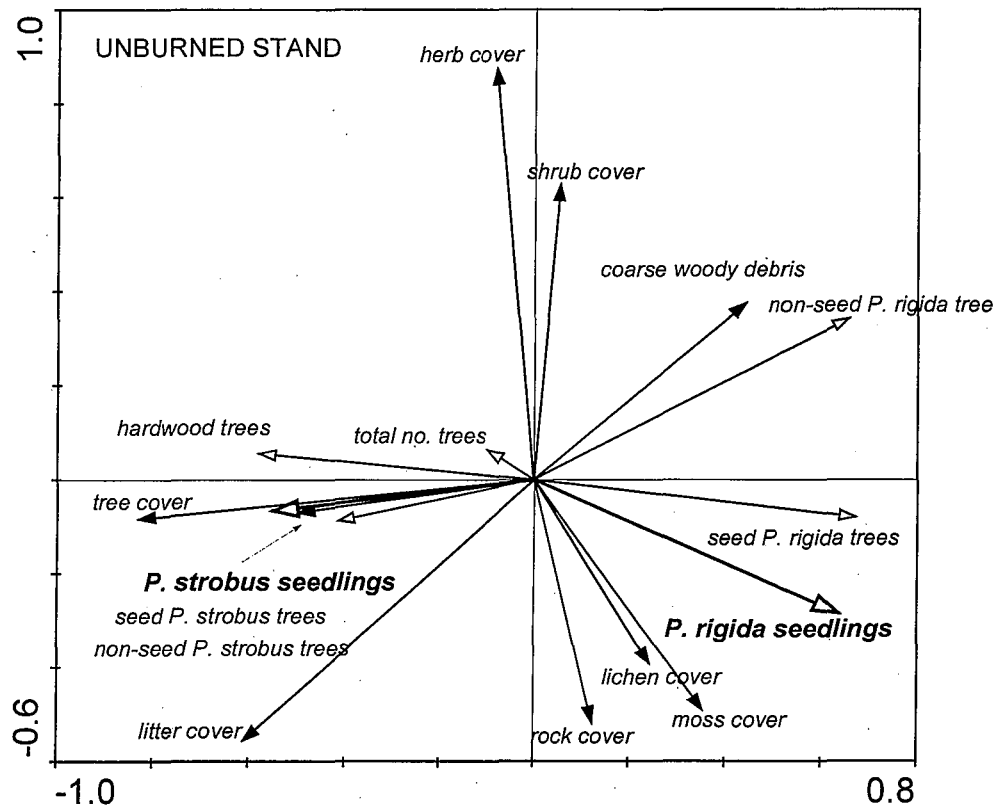
Figure 2. PCA ordination diagrams (showing first and second ordination axis) displaying the correlation pattern of the plot-level variables and seedling and tree densities in unburned and burned stands.

rock cover and percent cover of the herb layer (Figure 1). Average shrub and moss covers in the burned plots were 97% and 44%, respectively; lower compared to unburned plots. Prior to the burn, there were some correlations between the vegetation layers. The herb stratum of the forest understory in the unburned stand showed a negative correlation with moss ($r = -0.35$) and lichen cover ($r = -0.50$) and also with percent litter ($r = -0.30$) and surface rock cover ($r = -0.50$).

Litter cover was also significantly influenced by the prescribed burn. Average litter cover was 28% higher in the unburned site (Figure 1) where the litter layer was composed of pine needles and a high proportion of relatively slow decomposing oak leaves. Litter cover in unburned plots increased with total tree canopy cover ($r = 0.42$) and the number of P. strobus trees ($r = 0.34$), and decreased with increasing shrub ($r = -0.36$), herb ($r = -0.30$) and woody debris cover ($r = -0.41$). Post-burn litter cover increased with total tree canopy cover ($r = 0.51$) and hardwood tree density ($r = 0.47$).

Tree seedlings recruitment

Pinus rigida and *P. strobus* responded differently to the fire treatment. The density of *P. rigida* and *P. strobus* seedlings differed between the burned and unburned plots (Table 1 and Figure 1). The average emergence of *P. strobus* was 82% lower in the burned plots, whereas average emergence of *P. rigida* was 48% higher compared to unburned plots. In terms of absolute seedling numbers, the recruitment in both unburned and burned plots was dominated by *P. strobus*. In the unburned stand, the total number of *P. strobus* seedlings was 10.9 times higher than that of *P. Rigida*; whereas, in burned plots, *P. strobus* emergence was only 1.2 times higher than *P. rigida* emergence.

Principal component analyses and GLMs for the plot-level micro-environmental variables and *P. rigida* and *P. strobus* seedling densities indicate that the tree species may have been responding to different environmental factors (Figure 2; Table 2). In the control, unburned plots, the density of *P. rigida* seedlings was positively correlated with the density of mature *P.*

rigida seed trees ($r = 0.62$) and woody debris cover ($r = 0.41$) and negatively correlated with total tree canopy cover ($r = -0.52$), shrub cover ($r = -0.29$), and hardwood tree density ($r = -0.30$) (Figure 3). When environmental correlations were examined for the burned plots, *P. rigida* emergence showed a positive correlation with the density of mature *P. rigida* trees ($r = 0.45$) and moss cover ($r = 0.41$) and a negative correlation with the density of hardwood trees ($r = -0.28$) and *P. strobus* seed trees ($r = -0.18$). This indicates that shrubs and hardwood trees have a negative effect, and conspecific trees, mosses, and woody debris a positive effect on *P. rigida* seedling abundance. The number of *P. strobus* seedlings in pre-burn plots was positively correlated with percent total tree canopy cover ($r = 0.38$), the density of mature *P. strobus* seed trees ($r = 0.54$), and litter cover ($r = 0.41$) and negatively correlated with shrub cover ($r = -0.33$) and the number of neighboring *P. rigida* seed trees ($r = -0.27$). *Pinus strobus* seedling density in the post-burned plots was positively correlated with the total number of trees ($r = 0.54$) and moss cover ($r = 0.33$).

Table 2. The results of GLM regressions modelling the response of tree seedling density with plot-level environmental characteristics (plots 5 x 5 m). The results are the F-values associated with adding each predictor variable alone to a single regression. ▲ indicates an increase in seedling emergence with environmental variable. ▼ indicates a decrease in seedling emergence. The F-ratio statistic is followed by the estimate of the Type I error probability: [a] $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$.

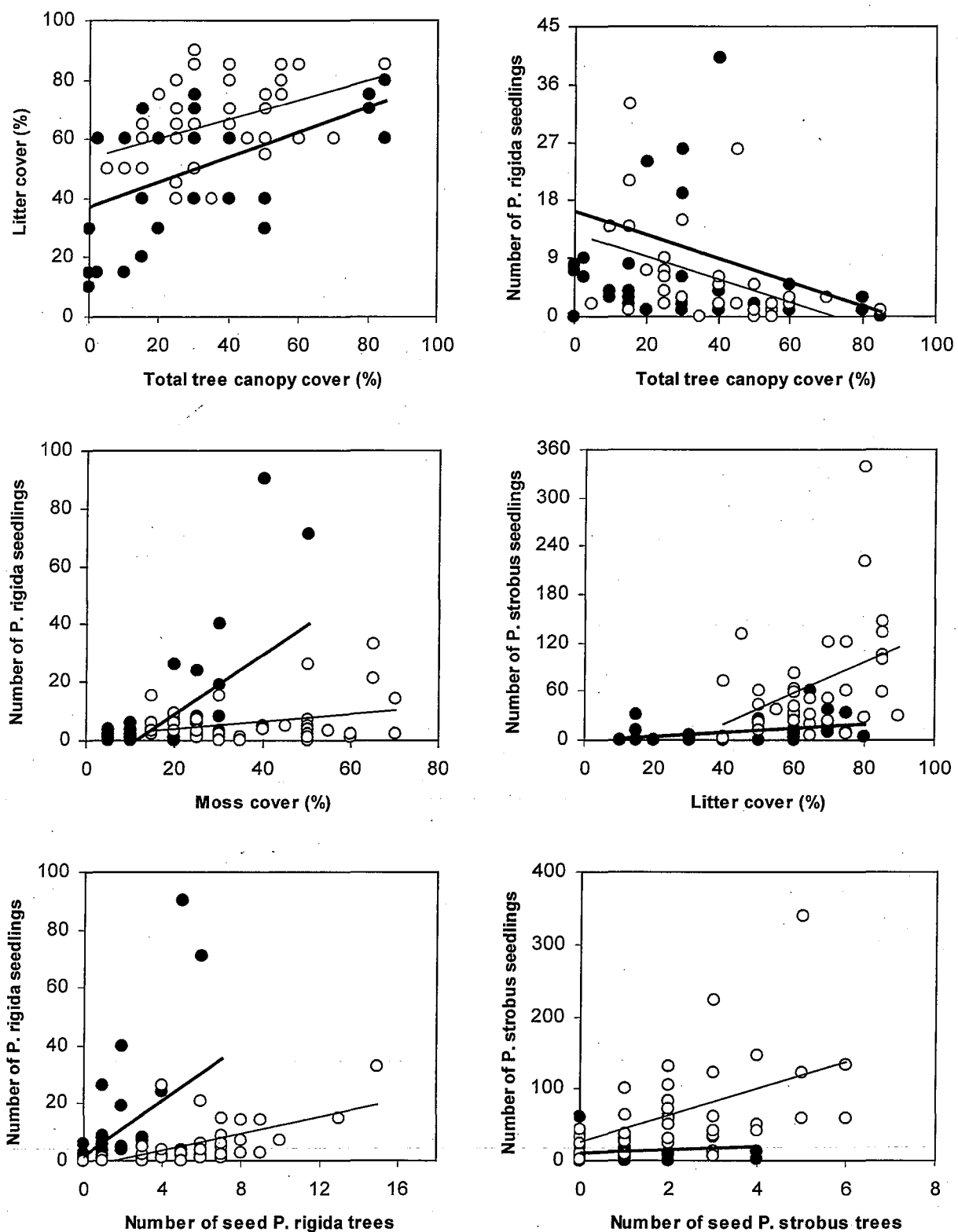|	Pinus rigida		Pinus strobus	
	unburned plots	burned plots	unburned plots	burned plots
Tree cover (%)	▼ 8.3 **	▼ 2.7 [a]	▲ 5.6 *	0.1
Shrub cover (%)	▼ 6.5 *	0.1	▼ 4.5 *	0.1
Herb cover (%)	1.2	0.5	0.2	0.1
Moss cover (%)	3.8 [a]	▲ 34.3 ***	0.1	▲ 12.7 ***
Lichen cover (%)	0.4	3.3	0.3	0.1
Litter cover (%)	1.9	1.5	▲ 7.1 *	▲ 3.1 [a]
Rock cover (%)	2.0	0.1	1.5	1.5
Branch cover (%)	▲ 4.5 *	1.1	0.2	0.1
Total tree number	0.1	0.1	2.0	▲ 7.3 **
No. seed P. rigida trees	▲ 18.1 **	▲ 13.8 ***	▼ 4.5 *	0.4
No. seed P. strobus tree	0.2	▼ 2.9 [a]	▲ 15.2 ***	0.7
No. hardwood trees	▼ 5.5 *	▼ 6.5 **	1.6	0.3

Figure 3. Relationships between the densities of *Pinus rigida* and *P. strobus* seedlings in plots 5 x 5 m and plot-level variables in unburned (open circles, thin lines) and burned (filled circles, thick lines) stands.

Adjusting for confounding variables

Our results suggest that several variables in our data set were confounded. For instance, the density of *P. strobus* seedlings in the unburned stand was positively related to total tree canopy cover and litter cover, but tree cover and litter cover were themselves positively correlated ($r = 0.41$). *Pinus rigida* seedling density in the burned plots was positively correlated with the density of *P. rigida* seed trees and moss cover, but *P. rigida* tree density and moss cover were also themselves correlated ($r = 0.41$). To assess the degree to which these inter-correlated variables could independently predict tree seedling emergence, we fitted multiple logistic regression models in which we controlled for the influence of the confounding variables (see **Material and Methods**).

Variation in *P. rigida* seedling density was most strongly associated with the density of neighboring mother trees (Figure 3). Having adjusted for the influence of con-specific trees, the previously strong positive correlation between *P. rigida* seedlings and woody debris on the forest floor in unburned plots was no longer significant. Also, after accounting for the influence of conspecific trees, the previously strong negative correlation between *P. rigida* seedlings and hardwood trees (mostly *Quercus alba*) was no longer significant. In this case, a pattern consistent with negative density dependence arose because *P. rigida* seedling density was significantly higher and hardwood tree density lower in denser patches of *P. rigida* trees. The only factors that retained significant negative correlations with *P. rigida* seedlings in unburned plots were percent total tree canopy cover and shrub cover ($P < 0.05$). When we statistically controlled for the influence of conspecific trees in the post-burn plots, *P. rigida* emergence retained a positive correlation with percent moss cover ($F = 17.1$, $P = 0.001$, Figure 3), but was no longer related to hardwood tree density and the density of mature *P. strobus* trees. *Pinus strobus* seedling emergence in unburned plots remained negatively related to percent shrub cover and *P. rigida* tree density ($P < 0.05$), after adjusting for the influence of conspecific trees, but was no longer significantly related to total tree canopy cover ($F = 2.2$, $P = 0.147$) or litter cover ($F = 2.38$, $P = 0.132$). *Pinus strobus* emergence in the burned plots was most strongly related to the total number of trees. Having adjusted for this variable, *P. strobus* seedlings were no longer correlated with percent litter cover, but retained a positive correlation to percent moss cover ($F = 5.22$, $P = 0.03$).

Stepwise discriminant analysis of tree seedling natural recruitment

Stand attributes that contributed significantly to the discriminant function and maximized the difference between the two groups are shown in Table 3. Stepwise discriminant analysis of tree seedling emergence for *P. strobus* in the unburned plots revealed that bare rock cover, thick grass (sedge) cover, and woody debris are unfavorable, whereas pine, oak, and blueberry litter, moss and lichen, and a

Table 3. The results of stepwise discriminant analysis of presence/absence of tree seedlings versus attributes measured beside each occupied and unoccupied spot (profile depth, litter depth, litter types and soil surface features). ▲ indicates a higher probability of seedling occurrence with environmental variable. ▼ indicates a lower probability of seedling occurrence with environmental variable. "na" - not analyzed. The *F*-ratio statistic is followed by the estimate of the Type I error probability: * $P < 0.05$, ** $P < 0.01$, *** $P \leq 0.001$.

	Pinus rigida		*Pinus strobus*	
	unburned plots	burned plots	unburned plots	burned plots
Litter depth	1.1	▼ 18.9 ***	0	▲ 13.5 ***
Profile depth	▲ 3.9 *	0.1	▲ 19.0 ***	3.8
Soil surface features				
Rock	▼ 7.1 **	▼ 60.6 ***	▼ 149.7 ***	▼ 17.5 ***
Mineral soil	na	0.9	na	na
Moss and lichen	▲ 29.7 ***	0.2	▲ 13.9 ***	1.8
Grass (sedge)	na	▼ 25.9 ***	▼ 29.5 ***	▼ 8.9 **
Litter types				
Needles	▲ 21.2 ***	2.6	▲ 18.0 ***	▲ 56.9 ***
Oak leaves	▲ 7.8 **	1.1	▲ 22.8 ***	▲ 41.9 ***
Moss	na	0.2	na	0.2
Blueberry leaves	0.2	1.9	▲ 19.7 ***	▼ 7.7 **
Grass leaves	na	0.1	0.14	2.1
Fallen branches	▲ 8.8 **	na	▼ 93.6 ***	na

deeper soil profile are favorable seedbeds (Figures 4 and 5). Similar results were obtained when discriminant analysis was employed for *P. strobus* in the post-burn plots where bare rock and dense grass covers and blueberry litter represented adverse seedbeds, whereas the presence of deep needle and oak litter layers represented favorable seedbed conditions. Averaged across all plots, *P. strobus* seedlings emerged on a deeper soil profile and litter layer than *P. rigida* seedlings (Figure 4). Stepwise discriminant analysis for *P. rigida* emergence in the post-burn plots revealed that deep litter, bare rock, and dense grass have a significantly negative effect on *P. rigida* seedling emergence. Similarly, in the unburned plots, bare rock cover has a negative effect, while mosses and lichens, needle and oak litter layers, and woody debris have a positive effect on seedling recruitment.

DISCUSSION

Pinus rigida is an important example of the temperate fire-dependent forest within the Canadian national parks system (Anonymous 1997). With a consistent decline in regeneration, *P. rigida* is in danger of becoming rare or extinct in both Canada and the United States (Motzkin et al. 1996). Our investigation evaluated a prescribed fire management event in what is likely
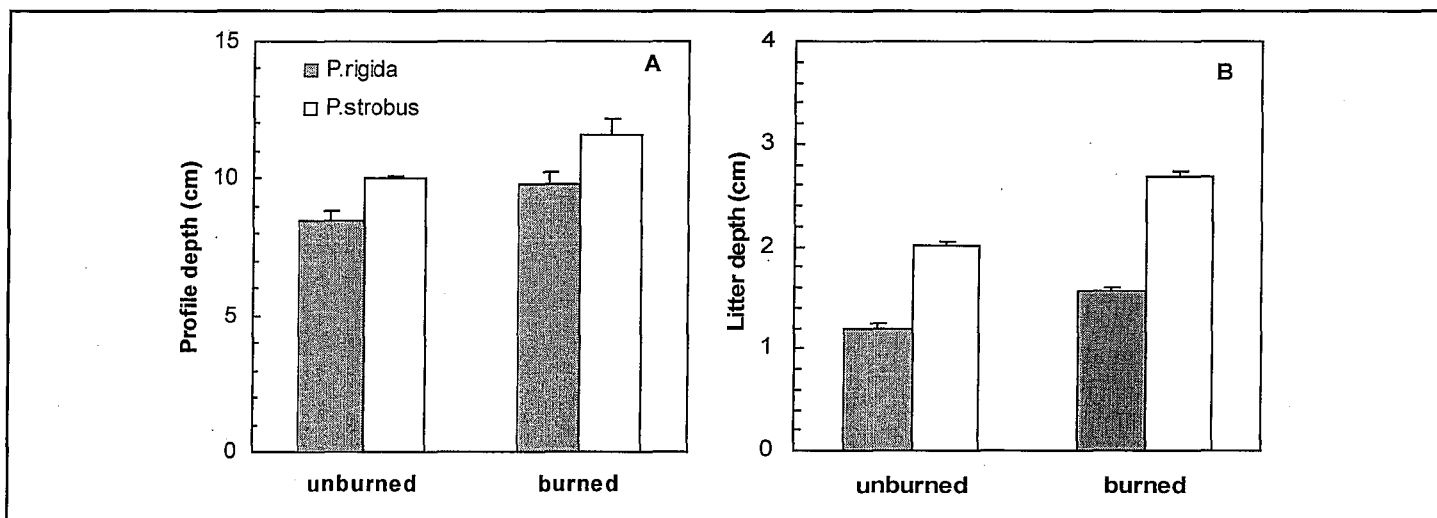

Figure 4. Comparison of average values of profile depth (A) and of litter depth (B) between *Pinus rigida* and *P. strobus* seedlings in burned and unburned plots. Each bar represents mean depth (± 1 SE).
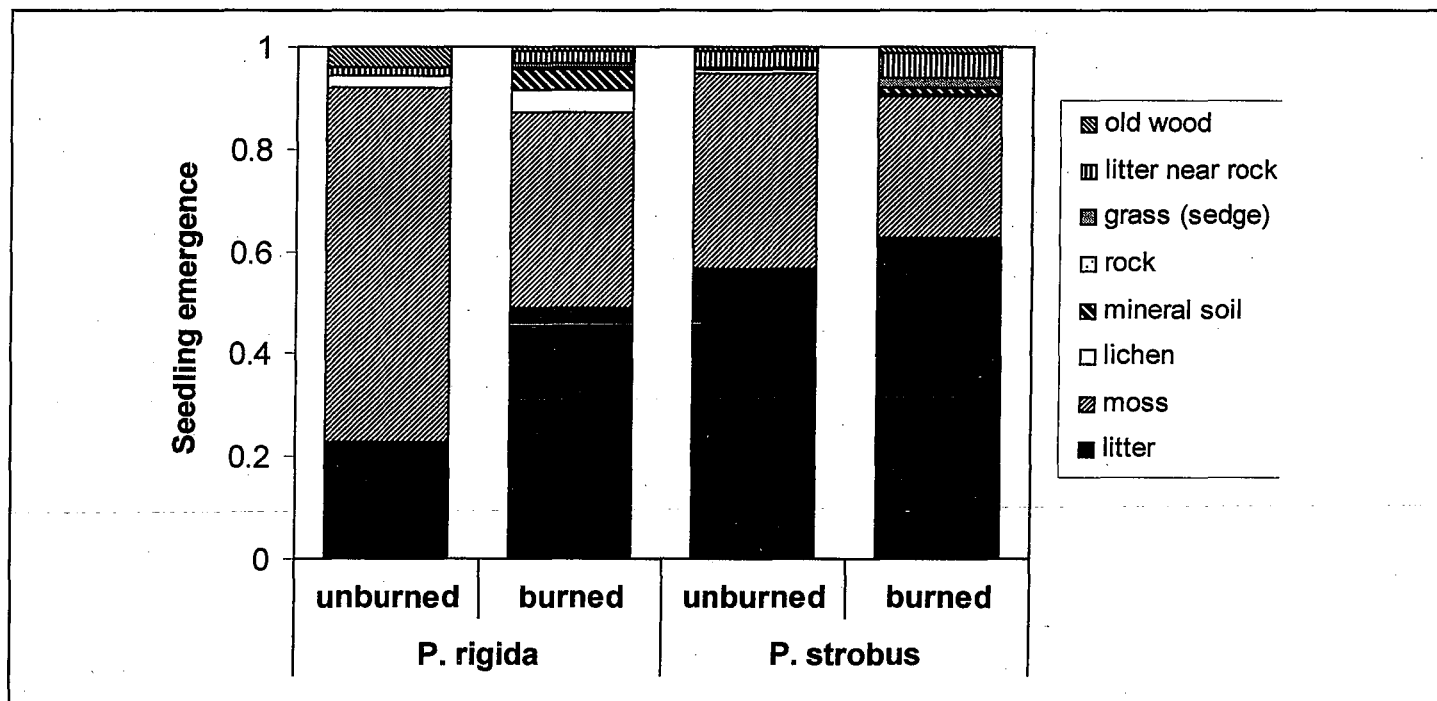

Figure 5. The proportion of *Pinus rigida* and *P. strobus* seedlings that emerged in litter, moss (or *Sphagnum*), lichen layer, mineral soil, exposed rock, grass (sedge), litter near rock and old wood (and/or rotten wood, bark) in burned and unburned plots during 2000-2001.

Canada's largest stand of *P. rigida* in St. Lawrence Islands National Park.

Prescribed fire, mature trees, seedlings and site conditions

The fire reduced the density of mature tree species on the Hill Island ridge (Figure 1). Mean density of mature *P. rigida* and *P. strobus* trees was 70% and 53% lower, respectively, in post-burn plots compared with the unburned stand. Density of mature *P. rigida* trees in unburned plots had a negative relationship with total tree canopy cover and density of hardwood trees (e.g. *Q. alba* and *Q. rubra*), whereas *P. strobus* tree density was positively related to tree cover. This shows that the less shade-tolerant *P. rigida* prefers open areas within the unburned stand. In the burned stand, *P. rigida* trees retained a negative correlation with total tree canopy cover, and became even more strongly negatively correlated with hardwood tree density compared to the unburned stand. High light and low litter are widely recognized as necessary for the regeneration of *P. rigida* and other fire-tolerant pines (Little and Garrett 1990; Waldrop and Brose 1999). There are many examples where hardwood and other fire-sensitive coniferous species (e.g., *P. strobus*; Wendel and Smith 1990) invade the overstory on sites where *P. rigida* stems are dying out in the continued absence of fire (Williams 1998; Copenheaver et al. 2000; Welch et al. 2000). For example, in fire-suppressed *P. rigida* stands in the Great Smoky Mountains National Park, Tennessee, canopy density and basal area increased with the invasion of fire-sensitive *Acer rubrum*, *P. strobus*, and *Tsuga canadensis* (Harrod et al. 1998, 2000). Substantial variation in geography, environment, and past human activities has also influenced the *P. rigida-Quercus* vegetation composition and structure across Cape Cod, Massachusetts (Motzkin et al. 2002).

Mature trees of both *P. rigida* and *P. strobus* are more resistant to surface fire than seedlings (Williams 1990) because of thicker bark (Wyant et al. 1986; Trabaud and Valina 1998; Welch et al. 2000). Moreover, *P. rigida* has a high regeneration ability by vegetative resprouting from fire-induced surface injury to stems, branches, and roots (Ledig and Little 1979). However, litter and understory burns make suitable conditions for regeneration from seeds, because seedlings of fire-tolerant species (such as *P. rigida*, *P. resinosa*, *P. pungens*, *P. halepensis* and *P. Banksiana*) are successful only on microsites that have exposed mineral soil or a thin litter layer (Engstrom and Mann 1991; Thanos et al. 1996; Williams 1998). For *P. rigida* to regenerate successfully from seeds, Ledig and Little (1979) pointed out that plentiful sunlight is a required condition together with bare mineral soil and sufficient soil moisture. Day et al. (2005) found out that warmer and moister conditions favor *P. rigida* regeneration in contrast with *P. banksiana*, which prefers a cool and dry climate.

The abundance of *P. rigida* seedlings was positively correlated with the density of *P. rigida* seed trees both on unburned and post-burned plots. A positive correlation between the basal area and density of parent trees and successful regeneration from seeds was suggested by many authors (see Greene et al. 1999 for review). Positive correlations between mature parent trees expressed by basal area and the density of seedlings and saplings were recorded within the treeline population of *P. canariensis* on Mount Teide, Canary Islands (Šrtek et al. 2002). On the other hand, the negative correlation between *P. rigida* seedling density and total tree canopy cover on Hill Island supports findings about the negative effect of low light levels under dense canopy on seed germination and seedling recruitment (Copenheaver et al. 2000; Goubitz et al. 2003).

Differences in regeneration pattern of pine seedlings

Seedling emergence in relation to fire treatment clearly follows the ecological adaptations of both pines (Little and Garrett 1990; Wendel and Smith 1990). The post-burn density of *P. rigida* seedlings was 48% higher, and *P. strobus* seedlings 82% lower, than in the unburned stand. However, the density of *P. strobus* seedlings was generally higher than for *P. rigida*

seedlings, especially in unburned plots (see Table 1). Long absence of fire, high seed production of *P. Strobus*, and the relatively low number of *P. rigida* seed-producing trees (which contain a low amount of fertile cones) are probably among the main factors affecting the low seedling recruitment on the Hill Island ridge. At the Waterboro Barrens, southern Maine, the persistence of a *P. rigida* and *Q. ilicifolia* forest has been documented to depend on frequent fire disturbances, which prevent invasion of fire intolerant species such as *P. strobus* and hardwood trees (Copenheaver et al. 2000). In our stand, the apparent negative effects of total tree canopy cover, shrub cover, and hardwood tree density on *P. rigida* seedling density correspond with findings from other areas with long-term controlled fire suppression (Motzkin et al. 1999, 2002).

A positive relationship between *P. rigida* seedling density and woody debris cover was not apparent on post-burned plots, probably due to the low amount of woody debris remaining after surface fire. In subalpine populations of *Abies lasiocarpa*, woody debris was important for initial tree regeneration on burns because it reduced soil moisture stress in summer (Little et al. 1994). Similarly, in *P. pungens*, the low amounts of leaf litter was found to enhance establishment by reducing evaporation from the soil, whereas deep leaf litter was a major barrier to seedling establishment and survival (Williams et al. 1990).

Effects of various factors on post-fire pine seedlings recruitment

Our analysis revealed different requirements of both species for the seedbed. *Pinus strobus* seedlings occurred within both treatments on deeper soil profiles with higher pine, oak, and blueberry litter (compare Wendel and Smith 1990; Williams 1990), although for seed regeneration, a mineral soil seedbed or a greatly reduced organic layer is also important (Weber and Taylor 1992). However, outcrops (bare rock cover with thin litter or, in our case, soil layer) on the one hand and thick grass (sedge) layer on the other are unfavorable microsite features for regeneration.

Pinus rigida seedling recruitment on burned and unburned plots was comparatively higher on mineral soil, lower litter layer, and moss and lichen cushions. Sedia and Ehrenfeld (2003) documented both the inhibition of seed germination by lichen tissue extracts and the inhibition of germination by thick cover of cryptogamic mats (lichens and mosses). On the other hand, they pointed out that the erect growth form of Polytrichum stems (it also occurred on the Hill Island ridge), low stem densities, or spaces between stems would allow seedlings to emerge. A moss mat can support seedling emergence to increase soil moisture (Williams et al. 1990).

Moreover, the abundance of lichens and mosses would be related to the accumulation of organic matter in and on top of the soil. In post-burned sites, the presence of an organic horizon beneath an especially rapidly growing moss mat is crucial to supply the emerged tree germinants by nutrients (particularly nitrogen) in dry outcrops and sandy soils (Ehrenfeld et al. 1997; compare DeLuca et al. 2002).

Surprisingly, needle and oak litter played a more positive than negative role for seedling recruitment, because of the very dry microsite conditions on the Hill Island ridge top. However, often conifer tree regeneration is reduced on hardwood leaf litter when compared with conifer needle or moss seedbeds (Williams et al. 1990; Greene et al. 1999; Waldrop and Brose 1999).

Obviously, a prescribed burn in spring 1997 had more positive effects on *P. strobus* than *P. rigida* seedling recruitments. The problem was that the fire's intensity was too low to open the understory, as well as the overstory, of forest stands. In general, medium-disturbance regimes would be a successful management practice for maintenance of *P. rigida* in St. Lawrence Islands National Park (compare Williams 1991; Waldrop and Brose 1999; Welch et al. 2000; Welch and Waldrop 2001).

Miroslav Šrůtek is a Research Associate at Faculty of Biological Sciences, University of South Bohemia and Institute of Botany, Academy of Sciences of the Czech Republic. He spent two years as a postdoc fellow at the Univeristy of Ottawa, Canada. His long-term studies are related to spatial pattern and dynamics of boreal and mountain temperate natural forests of the Far East and Europe. He teaches, together with J. Doležal, Forest Ecology at the University of South Bohemia.

Jiří Doležal received his PhD at Hokkaido University in Sapporo, Japan. His work focuses on plant responses to environmental and land use changes (post-fire and post-glacial succession, meadow restoration on ex-arable land) and the ecology of temperate and boreal forests in NE Asia. He teaches Forest Ecology at the University of South Bohemia, Czech Republic.

C. Scott Findlay is an Associate Professor of Biology and Director, Institute of Environment at the University of Ottawa, and a Research Associate at the Center for Cancer Therapeutics at the Ottawa Hospital Research Institute, Canada. His research interests include the effects of anthropogenic stress on ecosystem structure and function, the evolutionary dynamics of tumourigenesis and treatment relapse, the structure of cancer stem cell transcriptional networks, and metrics for evaluating scientific weight of evidence.

Bud Andress has been an employee of Parks Canada for over 36 years. He has conducted research and monitoring of various flora and fauna in the national park and the 1000 Islands region and has co-authored published papers on ospreys, common terns, and bald eagles. He spent many years monitoring the Park's rare flora, including the Park's symbol – the pitch pine (Pinus rigida).

LITERATURE CITED

Anonymous. 1997. National Parks System Plan, 3rd ed. Canadian Heritage Department, Parks Canada, Ottawa, Ont.

Bergeron, Y., O. Engermark, B. Harvey, H. Morin, and L. Sirois. 1998. Key issues in disturbance dynamics in boreal forests. Journal of Vegetation Science 9:464-468.

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

Chambers, J.M., and T.J. Hastie (eds.). 1992. Statistical Models in S. Wadsworth & Brooks/Cole Computer Science Series, Pacific Grow, Calif.

Copenheaver, C.A., A.S. White, and W.A. Patterson, III. 2000. Vegetation development in southern Maine pitch pine-scrub oak barren. Journal of the Torrey Botanical Society 127:19-32.

Crawley, M.J. 2002. Statistical Computing. Blackwell Science, Oxford, U.K.

Day, M.E., J.L. Schedlbauer, W.H. Livingston, M.S. Greenwood, A.S. White, and J.C. Brissette. 2005. Influence of seedbed, light environment, and elevated night temperature on growth and carbon allocation in pitch pine (*Pinus rigida*) and jack pine (*Pinus banksiana*) seedlings. Forest Ecology and Management 205:59-71.

DeLuca, T.H, O. Zackrisson, M.C. Nilsson, and A. Sellstedt. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419:917-920.

Donnelly, S., and S. McCloskey. 1996. Pre-burn inventory and post-burn monitoring programme of the Hill Island pitch pine (*Pinus rigida*) community. Technical Report, St. Lawrence Islands National Park, Mallorytown Landing (see address of Bud Andress, co-author), Ont.

Ehrenfeld, J.G., W.F. J. Parsons, and X. Han. 1997. Live and dead roots in forest soil horizons: contrasting effects on nitrogen dynamics. Ecology 78:348-362.

Elliott, K.J., R.L. Hendrick, A.E. Major, J.M.

Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. Forest Ecology and Management 114:199-213.

Engstrom, F.B., and D.H. Mann. 1991. Fire ecology of red pine (*Pinus resinosa*) in northern Vermont, U.S.A. Canadian Journal of Forest Research 21:882-889.

Gauthier, S., Y. Bergeron, and J.-P. Simon. 1996. Effects of fire regime on the serotiny level of jack pine. Journal of Ecology 84:539-548.

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

Goldammer, J.G., and N.J. Jenkins (eds.). 1990. Fire in Ecosystem Dynamics. Mediterranean and Northern Perspectives. Backhuys Publishers, Oegstgeest.

Goubitz, S., M.J.A. Werger, and G. Ne'eman. 2003. Germination response to fire-related factors of seeds from non-serotinous and serotinous cones. Plant Ecology 169:195-204.

Greene, D.F., J.C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29:824-839.

Greenwood, M.S., W.H. Livingston, M.E. Day, and A.S. White. 2002. Contrasting modes of survival by jack pine and pitch pine at a common range. Canadian Journal of Forest Research 32:1662-1674.

Harrod, J., M.E. Harmon, and P.S. White. 2000. Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. Journal of Vegetation Science 11:465-472.

Harrod, J., P.S. White, and M.E. Harmon. 1998. Changes in xeric forests in the western Great Smoky Mountains National Park, 1936-1995. Castanea 63:346-360.

Höllermann, P.W. 1996. Feuer als geoökodynamischer Faktor in subtropischen Winterregen-Gebieten. Das Beispiel der jüngten Wald- und Buschbrände auf den Kanarischen Inseln. Geoökodynamik 17:1-24.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Johnson, E.A., and K. Miyanishi. 2007. Plant Disturbance Ecology: the Process and the Response. Academic Press, San Diego, Calif.

Keeley, J.E., M.B. Keeley, and W.J. Bond. 1998. Stem demography and post-fire recruitment of a resprouting serotinous conifer. Journal of Vegetation Science 10:69-76.

Lamont, B.B., D.C. Le Maitre, R.M. Cowling,

and N.J. Enright. 1991. Canopy seed storage in woody plants. Botanical Review 57:277-317.

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: Ecosystems and Landscape. Academic Press, New York.

Lepš, J., and P. Šmilauer. 2003. Multivariate Analysis of Ecological Data using CANOCO. Camridge University Press, Cambridge, U.K.

Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Canadian Journal of Forest Research 24:934-944.

Little, S., and P.W. Garrett. 1990. *Pinus rigida* Mill. Pitch pine. Pp. 456-462 *in* R.M. Burns and B.H. Honkala, eds., Silvics of North America. Volume 1. Conifers. Agriculture handbook no. 654, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Little, S., and H.A. Somes. 1964. Releasing pitch pine sprouts from old stools ineffective. Journal of Forestry 62:23-26.

Lloret, F. 1998. Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. Journal of Vegetation Science 9:417-430.

Manly, B.F.J. 1998. Multivariate Statistical Methods. A Primer. 2nd ed. Chapman & Hall, London.

McClenahen, J.R., and N.H. McCarthy. 1990. An assessment of pitch pine (*Pinus rigida*) health and mortality in southern Ohio. Canadian Journal of Forest Research 20:1900-1908.

McCullagh, P., and J.A. Nelder. 1990. Generalized Linear Models, 2nd ed. Chapman & Hall, London.

Meilleur, A., J. Brisson, and A. Bouchard. 1997. Ecological analyses of the northernmost population of pitch pine (*Pinus rigida*). Canadian Journal of Forest Research 27:1342-1350.

Midgley, J.J., and N.J. Enright. 2000. Serotinous species show correlation between retention time for leaves and cones. Journal of Ecology 88:348-351.

Motzkin, G., R. Eberhardt, B. Hall., D.R. Foster, J. Harrod, and D. MacDonald. 2002. Vegetation variation across Cape Cod, Massachusetts: environmental and historical determinants. Journal of Biogeography 29:1439-1454.

Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New

England sand plain. Ecological Monographs 66:345-365.

Motzkin, G., W.A. Patterson, and D.R. Foster. 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems 2:255-273.

Olson, R., and A.M. Lewis. 1999. Porcupine ecology and damage management techniques for rural homeowners. Report B1073, University of Wyoming, College of Agriculture, Laramie.

Ordóñez, J., and J. Retana. 2004. Early reduction of post-fire recruitment of *Pinus nigra* by post-dispersal seed predation in different time-since-fire habitats. Ecography 27:449-458.

Saunders, G. 1996. Proposed burned area GPS results. Hill Island Pitch Pine Ridge. Technical Report, St. Lawrence Islands National Park, Mallorytown Landing, Ont.

Sedia, E.G., and J.G. Ehrenfeld. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos 100:447-458.

Seymour, R., and M.L. Hunter. 2000. Principles of ecological forestry. Pp. 22-61 *in* M.L. Hunter, ed., Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, U.K.

Šrůtek, M., J. Doležal, and T. Hara. 2002. Spatial structure and associations in *Pinus canariensis* population at the treeline, Pico del Teide, Tenerife, Canary Islands. Arctic, Antarctic, and Alpine Research 34:201-210.

Ter Braak, C.J.F., and P. Šmilauer. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4). Centre for Biometry, Wageningen.

Thanos, C.A., E.N. Daskalakou, and S. Nikolaidou. 1996. Early post-fire regeneration of a *Pinus halepensis* forest on Mount Párnis, Greece. Journal of Vegetation Science 7:273-280.

Trabaud, L., and J. Valina. 1998. Importance of tree size in *Pinus halepensis* fire survival. Pp. 189-196 *in* L. Trabaud, ed., Fire Management and Landscape Ecology. International Association of Wildland Fire, Fairfield, Wash.

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

van Mantgem, P., M. Schwartz, and M.B. Keifer. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Natural Areas Journal 21:266-273.

Van Wagner, Ch. E., B.J. Stocks, B.D. Lawson, M.E. Alexander, T.J. Lynham, and R.S. McAlpine. 1992. Development and structure of the Canadian Forest Fire Behaviour Prediction System. Forestry Canada Fire Danger Group. Information Report ST-X-3, Forestry Canada, Science and Sustainable Development Directorate, Ottawa, Ont.

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.

Wang, G.G. 2002. Fire severity in relation to canopy composition within burned boreal mixedwood stands. Forest Ecology and Management 163:85-92.

Weber, M.G., and B.J. Stocks. 1998. Forest fires in the boreal forests of Canada. Pp. 215-233 *in* J. M. Moreno, ed., Large Forest Fires. Backhuys Publishers, Leiden.

Weber, M.G., and S.W. Taylor. 1992. The use of prescribed fire in the management of Canada's forested lands. Forestry Chronicle 68:324-334.

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.

Welch, N.T., and T.A. Waldrop. 2001. Restoring table mountain pine (*Pinus pungens* Lamb.) communities with prescribed fire: an overview of current research. Castanea 66:42-49.

Wendel, G.W., and H.C. Smith. 1990. *Pinus strobus* L. Eastern white pine. Pp. 476-488 *in* R.M. Burns and B.H. Honkala, eds., Silvics of North America. Volume 1. Conifers. Agriculture Handbook No. 654, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Williams, Ch.E. 1990. The pines of Virginia: identification, distribution and ecology. Virginia Journal of Science 41:478-486.

Williams, Ch.E. 1991. Maintenance of the disturbance-dependent Appalachian endemic, *Pinus pungens*, under low-disturbance regimes. Natural Areas Journal 11:169-170.

Williams, Ch.E. 1998. History and status of table mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). Natural Areas Journal 18:81-90.

Williams, Ch.E., M.V. Lipscomb, W.C. Johnson, and E.T. Nilsen. 1990. Influence of leaf litter and soil moisture regime on early establishment of *Pinus pungens*. American Midland Naturalist 124:142-152.

Wyant, J.G., P.N. Omi, and R.D. Laven. 1986. Fire-induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. Forest Science 32:49-59.