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Research article

Factors responsible for the co-occurrence of forested and unforested rock outcrops in the boreal forest

Hugo Asselin*, Annie Belleau and Yves Bergeron
*NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda (Québec), Canada, J9X 5E4; *Author for correspondence (e-mail: hugo.asselin@uqat.ca)*

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Abstract

Rock outcrops in the boreal forest of Québec can show either of two different states: a forested state with >25% tree cover, and an unforested state (<25% tree cover). We tested three different hypotheses that might explain the co-occurrence of forested and unforested rock outcrops: (1) differences in bedrock geology, with unforested outcrops associated to bedrock types inimical to tree growth; (2) unforested outcrops as recently disturbed sites undergoing secondary succession towards a forested state; (3) unforested outcrops as an alternative stable state to forested outcrops, induced by post-fire regeneration failure. Digitized forest inventory maps were used along with bedrock geology maps and time-since-fire maps to compare forested and unforested outcrops for bedrock geology type and date of the last fire. Field surveys were conducted on 28 outcrops (14 forested, 14 unforested) to gather information regarding tree species composition and site characteristics (thickness of the organic matter layer, percent cover of lichens, mosses and ericaceous shrubs). None of the three hypotheses explain the co-occurrence of forested and unforested rock outcrops in the boreal forest of Québec. Both outcrop types occur on the same bedrock geology types. Unforested outcrops are not recently disturbed sites in early-successional states, as no clear distinction could be made in tree species composition and date of the last fire between the two outcrop types. Forested and unforested outcrops are not alternative stable states, as unforested outcrops are unstable and cannot maintain themselves through time in the prolonged absence of fire. Hence, unforested rock outcrops could be viewed as degraded, diverging post-fire types maintained by the late Holocene disturbance regime, characterized by high fire frequencies.

Introduction

According to the classical concept of succession (Clements 1916, 1936), forest stands return to early successional stages following a disturbance (e.g., fire). Given time, the stands then succeed through a sequence of different, predictable states, towards the climax (Clements 1916, 1936). However, a growing body of literature reports on alternative successional pathways that can lead to local-scale peculiarities (Cattelino et al. 1979; Payette 1992; Whithlock 1993; Hobbs 1994; Fastie 1995; Frelich and Reich 1998; Lynch 1998; Paine et al. 1998; Sedia and Ehrenfeld 2003; Chapin et al. 2004; Jasinski and Payette 2005).

On rock outcrops of the boreal forest of Québec, the climax forest is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) and eastern white cedar (*Thuja occidentalis* L.) (Bergeron and Dubuc 1989). However, many rock outcrops show an alternative to the forested state characterized by < 25% tree cover. The reasons for a reduced tree cover on these outcrops are unknown. Three different hypotheses can be put forward to explain the co-occurrence of forested and unforested rock outcrops: (1) Bedrock geology type has been suggested as a possible factor explaining differences in vegetation patterns between sites (Strahler 1978; Wiser et al. 1996; Kruckeberg 2002); (2) Unforested outcrops could represent recently disturbed sites undergoing secondary succession, eventually leading to a forested climax (Skutch 1929; Oosting and Anderson 1939; Gaudreau 1979); (3) Forested and unforested rock outcrops could also be viewed as alternative stable states, with unforested outcrops resulting from post-fire regeneration failure.

This study uses cartographic and field data to investigate which of the three aforementioned hypotheses best explains the co-occurrence of forested and unforested rock outcrops in the boreal forest.

Methods

Study area

The study area is located in the Abitibi region of western Québec (Figure 1) and overlaps two bioclimatic domains. The northern part belongs to the black spruce – feather moss bioclimatic domain, and the southern part to the balsam fir (*Abies balsamea* (L.) Mill.) – paper birch (*Betula papyrifera* Marsh.) bioclimatic domain (Grondin 1996; Saucier et al. 1998; Bergeron et al. 2004b). The bedrock geology is composed of granitoid (50%), volcanic (40%), and sedimentary (10%) rocks formed ca. 2.7 billion years ago (Hocq and Verpaelst 1994). After the Wisconsin glaciation, glacial lakes Barlow and Ojibway covered the region until their abrupt discharge through Hudson Bay ca. 7900 years ago (Vincent and Hardy 1977; Veillette 1994). Clay deposits are found below ca. 300 m, the level attained by lake Barlow-Ojibway prior to its discharge (Veillette 1994). Higher elevations acted as islands during the glacial lakes episode and are now either covered by water-reworked glacial deposits or left bare as rock outcrops (Bergeron et al. 1982; Clayden and Bouchard 1983). Rock outcrops are more frequent in the southern zone, sometimes referred to as the Abitibi Highlands (Asselin 1995). From south to north across the study area, mean annual temperature varies from 1.7 to 0 °C, and mean annual precipitation from 880 to 975 mm (Environment Canada 2005).

Data collection

Two different types of data were used in this study. First, digitized forest inventory maps, bedrock

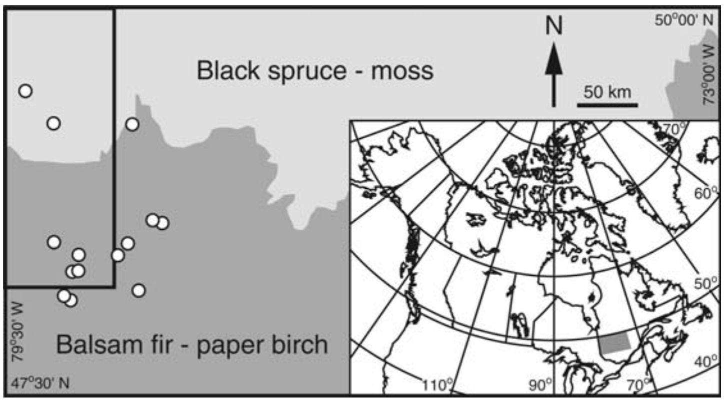

Figure 1. Location of the study area. The rectangle represents the total area covered by the maps used in the cartographic study (between 48°15′ and 50°00′ N and between 78°30′ and 79°30′ W) and the 14 dots correspond to the sites where field data were gathered (two outcrops at each site, one forested and one unforested). The black spruce – moss and balsam fir – paper birch bioclimatic domains are shown as shaded areas.

geology maps, and time-since-fire maps were analyzed using a geographic information system to determine if bedrock geology type and date of the last fire play a role in outcrop openness. Second, field data from 28 outcrops were used to verify for differences in species composition and site characteristics between forested and unforested outcrops.

Map data

Using digitized forest inventory maps (Figure 1) and a geographic information system (ArcView 3.2; ESRI Inc., New York, USA), all polygons with elevation higher than the mean (350 m a.s.l. in the southern portion of the study area and 300 m a.s.l. in the northern portion) and with no soil deposit or only a thin soil layer (<25 cm) were designated as rock outcrops ($N = 1532$). Polygons for which the forest inventory maps indicated disturbance by logging or insect outbreaks ($N = 698$) were not used in the analyses. From the remaining polygons, those with the dry, bare land attribute and $<25\%$ tree cover were considered as unforested outcrops ($N = 289$). The other polygons ($>25\%$ tree cover) were considered as forested outcrops ($N = 545$).

The superposition of bedrock geology maps to the forest inventory maps allowed a bedrock geology type to be assigned to each selected polygon. For simplification, the original number of bedrock geology types (27) was reduced by grouping into functional groups (Table 1). Bedrock geology types were first grouped according to formation process (igneous, sedimentary or metamorphic). Different igneous types were then separated according to cooling process (extrusive or intrusive) and to acidity (reflecting composition in silica (acid or felsic) and ferro-magnesium (basic or mafic)). Because metamorphic and ultramafic rocks are rare in the region, they were grouped in the 'other' category.

Table 1. Grouping of the different bedrock geology types.

Formation modality	Cooling process	Acidity	Group
Igneous	Extrusive	Felsic	Rhyolite
		Intermediate	Andesite
		Mafic	Basalt
		Ultramafic	*Other*
	Intrusive	Felsic	Granite
		Intermediate	Diorite
		Mafic	Gabbro
		Ultramafic	*Other*
Sedimentary			Sedimentary
Metamorphic			Other

The date of the last fire was determined for each polygon (forested and unforested) using archival data from the Fire Protection Service of Québec for post-1945 fires and a dendroecological reconstruction (Bergeron et al. 2004b) for pre-1945 fires. Dates were assigned to one of six 50-year classes (1701–1750; 1751–1800; 1801–1850; 1851–1900; 1901–1950; 1951–2000). The spatial resolution of the fire reconstruction was lower for the pre-1945 and thus small fires might have been missed, as well as small patches of unburnt territory inside large fires. The data was used nonetheless, as the margin of error was assumed to be the same for both forested and unforested rock outcrops.

To decipher the possible influence of bedrock geology type on outcrop forest cover, the frequency distribution of bedrock geology types was compared for forested and unforested outcrops using a chi-square test (Zar 1996). A chi-square test was also used to compare the frequency distribution of dates of the last fire for forested and unforested outcrops in order to determine whether unforested outcrops burned more recently than forested outcrops. The 1701–1750 class was underrepresented and thus excluded from the analysis.

Field data

Field inventories were conducted in the summer of 2002 on 28 rock outcrops, i.e. 14 pairs of forested and unforested outcrops (Figure 1), selected on the bases of accessibility and absence of logging or insect disturbance. All visited outcrops were small (13 ± 10 ha) and had an elongated shape. For each outcrop, tree species were inventoried at every 20 m along a 200 m transect using the point-centred quadrant method (Mueller-Dombois and Ellenberg 1974). At each sampling point, the nearest tree with a DBH (diameter at breast height) >7 cm was selected in each of the four quadrants, and the species, DBH, height and distance from the point were noted. Regeneration was also inventoried by noting the nearest individual with a height <1 m in each quadrant of each sampling point. The percent cover of lichens, mosses and ericaceous shrubs was visually estimated inside a 4 m^2 quadrat centred on each sampling point. The thickness of the organic matter layer was measured in the centre and at each corner of the 4 m^2 quadrat to calculate an average value.

A correspondence analysis (CA) was used to investigate the relationship between tree species composition and outcrop forest cover using CANOCO 4.5 (ter Braak and Šmilauer 2002). The 28 sites were ordered according to the relative frequency of tree (DHB >7 cm) and regeneration (height <1 m) species. If unforested outcrops are recently disturbed sites undergoing secondary succession, they should be more closely associated to early-successional species.

The thickness of the organic matter layer, as well as the percent cover of lichens, mosses and ericaceous shrubs were used as environmental (site) variables in a stepwise discriminant function analysis (DFA) using SPSS 11.0 1 (SPSS, 2001) to determine the role played by site factors in outcrop openness. For both types of outcrops to be alternative stable states, they should show no difference in site characteristics (Connell and Sousa 1983; Hobbs 1994; Jasinski and Asselin 2004), or, if they do, the differences should postdate the establishment of the stands (Sousa and Connell 1985). Furthermore, forested and unforested outcrops will only be considered alternative stable states if they both are persistent (i.e., pass through one or more turnovers) (Connell and Sousa 1983; Jasinski and Asselin 2004).

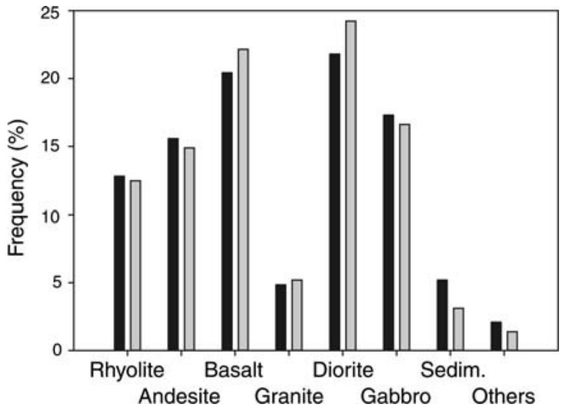

Figure 2. Frequency distribution of bedrock geology types for forested (black bars, $N = 545$) and unforested (grey bars, $N = 289$) outcrops.

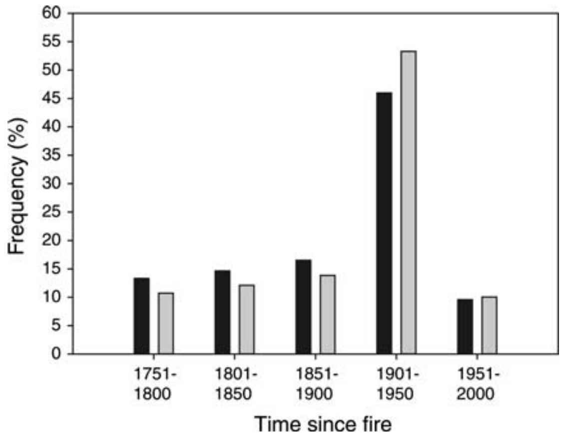

Figure 3. Frequency distribution of time-since-fire data for forested (black bars, $N = 533$) and unforested (grey bars, $N = 289$) outcrops.

Results

Map data

According to the last forest inventory data (Québec Ministry of Natural Resources 1994), the study area presents 1532 outcrops. From the 834 outcrops retained for analysis (outcrops for which there was no apparent logging or insect disturbance), 35% (289/834) were characterized as unforested (i.e., with $<25\%$ forest cover). No difference was found between forested and unforested outcrops for bedrock geology type (chi-square, $p > 0.75$; Figure 2) and date of the last fire (chi-square, $p > 0.25$; Figure 3).

Field data

A correspondence analysis (CA) using the relative frequency of tree species for the 28 sampled outcrops did not show any clear segregation pattern between forested and unforested outcrops (Figure 4a). The variance of tree species data explained by the first two CA axes was 33.6 and 25.1%, respectively (total = 58.7%). Trembling aspen (*Populus tremuloides* Michx.), red maple (*Acer rubrum* L.), and white spruce (*Picea glauca* (Moench) Voss.) appeared more closely associated to forested outcrops. Black spruce, red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.) seemed to be more closely associated to unforested outcrops. The other species were indifferently associated to forested or unforested outcrops: paper birch, eastern larch (*Larix laricina* (Du Roi) Koch.), eastern white cedar, jack pine (*Pinus banksiana* Lamb.), and balsam fir.

The CA for regeneration composition did not show any marked difference between forested and unforested outcrops (Figure 4b). The first two CA axes explained 26.6 and 25.5% of the variance, respectively (total = 52.1%). The CA nevertheless showed that some light-demanding species were more closely associated with unforested outcrops (paper birch, jack pine, red pine), while shade-tolerant species were associated with forested outcrops (white spruce, balsam fir, eastern white cedar).

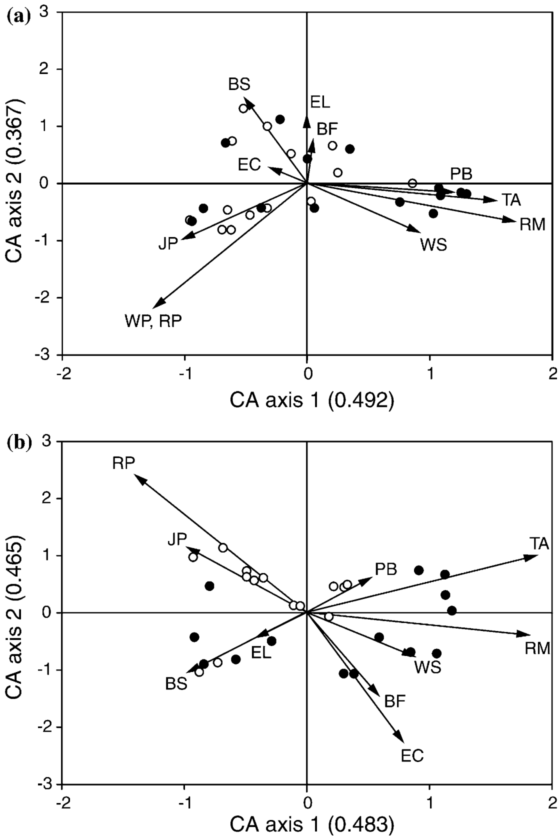

Figure 4. Scatterplots of first and second axes of the correspondence analysis for trees (DBH > 7 cm) (a) and for regeneration (height < 1 m) (b), with eigenvalues in brackets. Total inertia is 1.463 for trees and 1.820 for regeneration. Black dots = forested outcrops, white dots = unforested outcrops. BF = balsam fir; BS = black spruce; EC = eastern white cedar; EL = eastern larch; JP = jack pine; PB = paper birch; RM = red maple; RP = red pine; TA = trembling aspen; WP = white pine; WS = white spruce.

However, trembling aspen (a light-demanding species) was more closely associated with forested outcrops and red maple (a shade-tolerant species) was more closely associated with unforested outcrops. Other species (black spruce, eastern larch) were indifferently associated to forested or unforested outcrops.

A stepwise discriminant function analysis (DFA) was performed to determine which of the environmental variables best discriminated between forested and unforested outcrops. The standardized canonical discriminant function coefficients are shown in Table 2. The only variables retained were thickness of the organic matter layer and percent lichen cover. The thickness of the organic matter layer was strongly, positively correlated to the discriminant function and forested outcrops had a thicker organic matter layer. By contrast, lichen cover was negatively correlated to the discriminant function and unforested outcrops had more lichen. Percent cover of mosses and ericaceous shrubs were not selected by the stepwise procedure.

Discussion

Although bedrock geology type has previously been shown to affect species composition on rock outcrops (Strahler 1978; Wiser et al. 1996; Kruckeberg 2002), results of a chi-square test comparing forested and unforested outcrops did not show any difference for bedrock geology type ($p > 0.75$; Figure 2), thus this factor is excluded as a potential explanation for the occurrence of unforested rock outcrops in the boreal forest. This does not mean that bedrock geology type has no influence on species composition, but the effects are probably more pronounced for lower vegetation strata. Hence, the reason for co-occurrence of forested and unforested rock outcrops should be sought elsewhere.

Changes in vegetation composition during the Holocene can be linked to changes in disturbance regimes (Green 1982; Bergeron 1998). Therefore, understanding fire legacy could help explain the presence or absence of a forest cover on rock outcrops. Fire is the main disturbance agent affecting boreal forest stands (Rowe and Scotter 1973; Heinselman 1981; Payette 1992). Fire has already been identified as the triggering

Table 2. Results of the dicriminant function analysis (DFA) performed on forested vs. unforested outcrops.

	Standardized coefficient
Organic matter thickness	0.961
Lichen cover	−0.565
Moss cover	Not selected
Ericaceous shrubs cover	Not selected

Standardized canonical discriminant function coefficients are given for a standard DFA and for a stepwise DFA.

mechanism of landscape opening in the forest-tundra of Québec (Payette and Gagnon 1985; Arseneault and Payette 1992), where deforestation took place over the last 3000 years (Gajewski et al. 1993; Asselin and Payette 2005) due to post-fire regeneration failure under a cool climate (Sirois and Payette 1991). A similar explanation has been provided for the origin, ca. 2500 years ago, of park-forest vegetation in Wyoming (Lynch 1998), where pine-spruce-fir forests were replaced by *Artemisia*-dominated, treeless parks following post-fire regeneration failure due to a cool climate. Whitlock (1993) attributed the origin of park forests in Yellowstone National Park over the last 2000 years to climatic conditions, increased fire frequency, and bark beetle infestations. Fire also played a key role in the origin of the southernmost spruce-lichen woodlands in Québec. Regeneration failure following compound disturbances (i.e., a spruce budworm outbreak closely followed by a fire) caused the transformation of spruce-moss forests into spruce-lichen woodlands between 1440 and 580 years ago (Payette et al. 2000; Jasinski and Payette 2005).

Fire-induced deforestation was already suggested as a potential explanation for the occurrence of unforested rock outcrops (Skutch 1929; Oosting and Anderson 1939; Gaudreau 1979). However, these authors expected that, given time, deforested outcrops would undergo succession towards a closed-crown, forested state. This study presents two lines of evidence suggesting this might not be the case. First, a chi-square test revealed no difference between the frequency distribution of date of the last fire for forested and unforested outcrops ($p > 0.25$; Figure 3). Second, if unforested outcrops were in early successional stages, their vegetation composition should be dominated by early-successional species. However, CA results do not show a clear distinction between forested and unforested outcrops in regards to species composition of mature trees and regeneration (Figure 4). Moreover, trembling aspen – a species usually associated with early-successional stages – was more closely associated with forested outcrops, and red maple – a shade-tolerant species – was more closely associated with unforested outcrops (Figure 4). Other species (most notably black spruce and eastern larch) were indifferently associated to forested or unforested outcrops, maybe reflecting a broad range of tolerance.

Increased fire frequency in the late Holocene (roughly the last 3000 years) that led to landscape opening in other regions (Whitlock 1993; Lynch 1998; Asselin and Payette 2005; Jasinski and Payette 2005) also occurred in the boreal forest of Québec where fire intervals were 2–3 times longer in the mid-Holocene (7500–2500 years ago) than during the last 2500 years (Bergeron et al. 1998; Carcaillet et al. 2001). This increased the likeliness that severe or successive fire events would eliminate the organic matter layer from rock outcrops and thus cause the initiation of primary succession, which can take up to 5–10 times longer than secondary succession (Barbour et al. 1987). Although primary succession on rock outcrops has been extensively studied (Whitehouse 1933; Oosting and Anderson 1937, 1939; McVaugh 1943; Keever et al. 1951; Winterringer and Vestal 1956; Burbanck and Platt 1964; Shure and Ragsdale 1977; Phillips 1981; Burbanck and Phillips 1983; Uno and Collins 1987), very few accounts are available as to how much time is necessary to return to a forested state. Burbanck and Platt (1964) obtained a radiocarbon date of 670 years BP (before present) for an outcrop of the Piedmont Plateau of Georgia. Similarly, the study of an andesitic chronosequence by Lilienfein et al. (2003) showed that the development of a closed forest took about 600 years on a volcanic mudflow in California. Studying primary succession on fluvial terraces, Mann and Plug (1999) found that it took ca. 1000 years before a forest cover developed on the sites. In southern Québec, Muller and Richard (2001) found that the 'periglacial desert' phase lasted ca. 1000–1500 years after deglaciation. Thus, the limited evidence available points towards a timeframe of ca. 1000 years for primary succession to proceed on rock outcrops. A palaeoecological study of an unforested rock outcrop in the Abitibi region showed that openness resulted from increased fire frequency starting 1465 years ago (Larocque et al. 2003). It thus seems that mechanisms must have taken place that prevented this outcrop (and possibly others) to develop a closed canopy and to remain in its unforested state.

Differences between forested and unforested outcrops for organic matter thickness and lichen cover (as revealed by the DFA; Table 2) could explain why unforested outcrops tend to remain open longer than expected. The most important factors for successful tree colonization are distance from seed-bearing individuals (Asselin et al. 2001) and availability of safe sites for germination (Simard et al. 2003). Distance from seed-bearing trees is not an issue for rock outcrops, as the surrounding forest acts as a permanent seed bank guaranteeing constant seed supply. Unforested rock outcrops are associated with thinner organic matter layers (Table 2), thus increasing the likeliness of occurrence of patches of bare rock. The microclimate associated with bare rock surfaces (hot and dry) is detrimental to tree seed germination, which requires cooler and wetter microsites provided by organic matter accumulation (Burbanck and Platt 1964; Shure and Ragsdale 1977; Phillips 1981, 1982; Burbanck and Phillips 1983; Uno and Collins 1987; Houle and Phillips 1989). Higher frequency of summer droughts in the late Holocene (Carcaillet et al. 2001) renders the thin organic matter layer of unforested outcrops more susceptible to erosion (McVaugh 1943; Winterringer and Vestal 1956; Shure and Ragsdale 1977; Clayden and Bouchard 1983), reducing the likelihood of accumulations thick enough to allow tree seed germination. Apart from the detrimental effects of bare rock surfaces, physical and chemical effects of lichens (which are associated with unforested outcrops; Table 2) have been shown to prevent seed germination (Brown and Mikola 1974; Kershaw 1977; Houle and Filion 2003; Sedia and Ehrenfeld 2003). Although germination is possible in cracks between lichen patches or on exposed mineral soil (Cowles 1982; Sirois 1993), it is unlikely that it might lead to canopy closure under a regime of frequent forest fires.

Percent cover of mosses and ericaceous shrubs were not selected by the stepwise DFA. Moss cover is more closely associated with forested outcrops and yielded the same (although reverse) information as lichen cover. It was thus rejected by the stepwise procedure. The absence of a difference between forested and unforested outcrops with regards to percent cover of ericaceous shrubs minimizes the potential effects of allelopathy on tree seed germination and establishment (Mallik 2003).

Are forested and unforested rock outcrops alternative stable states?

Two aspects are fundamental in the definition of alternative stable states. First, both states should occur under the same environmental conditions (Connell and Sousa 1983; Hobbs 1994; Jasinski and Asselin 2004). Once an alternative stable state establishes on a particular site, the new species assemblage will undoubtedly affect environmental conditions. This is accounted for by the theory of alternative stable states, but the change must come from the new assemblage, and not from the disturbance that caused the shift to a new state or by climate change (Sousa and Connell 1985). The second essential component of the definition of alternative stable states is that they must maintain themselves through time, i.e., they must be persistent (Connell and Sousa 1983; Jasinski and Asselin 2004).

Unforested rock outcrops of the boreal forest cannot be interpreted as an alternative stable state to the forested outcrops because neither of the two fundamental conditions are met. There is evidence of recent fire occurrence on some forested rock outcrops (Figure 3). Thus, unless all the organic matter is removed, an outcrop deforested by fire will undergo secondary succession towards a forested climax state. If, on the other hand, the organic matter layer is totally removed by a rapid succession of fires or by an exceptionally severe fire, then the outcrop will undergo primary succession. There is no alternative. Although unforested rock outcrops are maintained as such by recurrent fire events that prevent canopy closure (Clayden and Bouchard 1983), successional species replacements occur in the lower vegetation strata (lichens, mosses, Cyperaceae, Poaceae and lowlying shrubs; H. Asselin personal observation). Thus, unforested outcrops are unstable, i.e., their state cannot be maintained through time in the prolonged absence of fire.

Conclusion

No evidence could be found to support the three hypotheses explored in the present paper regarding the co-occurrence of forested and unforested rock outcrops in the boreal forest: (1) There was no difference in bedrock geology type between forested and unforested outcrops; (2) Unforested outcrops are not recently disturbed sites undergoing secondary postfire succession; and (3) Forested and unforested outcrops do not fit the definition of alternative stable states. Alternatively, boreal unforested rock outcrops could be considered as degraded, diverging post-fire types (*sensu* Payette 1992). Although this hypothesis bears some resemblance with the second of the three aforementioned hypotheses (fire plays a central role), it involves a different timescale. A diverging (unforested) post-fire type is created when the organic matter covering a rock outcrop is completely eliminated by successive fires or by a single, high severity fire. The disturbance does not have to be recent (as in hypothesis 2) and could have happened anytime during the late Holocene (the last 3000 years), a period characterized by high fire frequencies. The primary succession that follows complete removal of organic matter takes much longer to complete than the usual post-fire secondary succession and return to the forested type is precluded by the high fire frequencies typical of the late Holocene. However, fire frequencies have been decreasing in eastern boreal forests since the end of the Little Ice Age (Bergeron and Archambault 1993; Bergeron et al. 2001) and the trend is predicted to continue – although modestly – during the 21st century (Bergeron et al. 2004a). Conditions might thus eventually allow unforested rock outcrops to proceed towards a forested state.

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