Dynamics and morphology of giant circular patterns of low tree density in black spruce stands in northern Quebec

Jean-François Giroux, Yves Bergeron, and Jean J. Veillette

Abstract: Giant circular patterns of low tree density in black spruce (*Picea mariana*) stands were investigated in the Abitibi region of Quebec. We used dendrochronological techniques to test the hypotheses that ring patterns of low tree density are caused either by radial changes in spruce mortality or productivity. Seven circles were sampled. We found no gradient in the age of spruce along circle radii suggesting that rings of low tree density do not expand radially, that is, they are not spatially dynamic entities. The results indicate, however, that spruce trees were less dense and productive within the rings due to excessive moisture in the soil. Measurements of surface elevation, thickness of the organic layer and elevation of the mineral substrate across the circles revealed that a depression in the mineral soil beneath the rings traps the surface water and this area of poor drainage seems to prevent the establishment of black spruce within the rings. The origin of the ring-shaped depressions was attributed to geological or geomorphological causes.

Key words: black spruce, *Picea mariana*, mortality, productivity, rings, geomorphology**.**

Résumé : Des formations circulaires géantes caractérisées par une densité arborescente faible ont été étudiées dans des peuplements d'épinettes noires (*Picea mariana*) de l'Abitibi au Québec. Les hypothèses liées à un processus de mortalité radiale ou à une baisse de productivité dans l'anneau ont été documentées dans sept cercles à l'aide de techniques dendrochronologiques. L'absence d'un gradient d'âge des épinettes ne supporte pas une expansion radiale des anneaux. Par contre, les résultats indiquent que la productivité et la densité des épinettes sont plus faibles dans l'anneau à cause de l'humidité excessive du sol à cet endroit. Des relevés topographiques de la surface du sol, de l'épaisseur de la couche organique et de l'altitude du substrat minéral ont démontré l'existence d'une dépression dans le sol minéral sous l'anneau. Cette dépression, dans un environnement comme celui-ci où la nappe phréatique est près de la surface, piège les eaux de surface et maintient l'humidité excessive du sol prévenant ainsi l'établissement de l'épinette noire. Les anneaux sont donc statiques et l'origine de la dépression annulaire relève de causes géologiques ou géomorphologiques.

Mots clés : épinette noire, *Picea mariana*, mortalité, productivité, anneau, géomorphologie.

Introduction

While mapping surficial geology in the Abitibi region of Quebec, the Geological Survey of Canada discovered more than 800 whitish rings, on aerial photographs, in black spruce forests (Veillette and Giroux 1999). While most of these rings are located between 49°N and 50°N, a few have been observed south of 48°N and some others around 51°N. For example, similar rings have been observed in the interior of the Gaspé Peninsula by one of us (J.J.V.), near Gaspé, Quebec (S. Fortin, personal communication, 1998), and on Anticosti Island (Dubois 1993). More than 2000 rings have been mapped in the boreal forests of northern Ontario by Veillette and Giroux (1999). While the rings are found almost exclusively in stands of black spruce (*Picea mariana*), they may also occur in balsam fir (*Abies balsamea*) and tamarack (*Larix laricina*) stands. The rings are generally almost perfectly circular (in this paper, the term "circle" designates the combination of the rings themselves and the area inside them, while "ring" designates the whitish, ring-shaped bands alone). The average diameter of circles in the Abitibi region is 310 m (n = 641) but the width of the ring rarely exceeds 30 m (Veillette and Smith 1992). The circles may occur isolated or in clusters, with 2 or more in contact. Their whitish tone on black and white aerial photographs is due to the opening in the forest cover (Fig. 1), which allows the ground vegetation to be seen from the air, and thus produces a higher albedo within the ring than in the surrounding forest cover.

Several mechanisms have been proposed to explain the origin of these rings. Some suggest the rings are caused by the contours of nearly circular thermokarst lakes, man-made shapes, the outline of buried kimberlite pipes, periglacial landforms, circular features caused by gas pockets trapped in the soil, clusters of craters from showers of meteorites, and

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J. Giroux and Y. Bergeron.[1] Groupe de recherche en écologie forestière interuniversitaire, Département des Sciences biologiques, Université du Québec à Montréal, P.O. Box 8888, Centre-Ville Station, Montréal, QC H3C 3P8, Canada.
J.J. Veillette. Natural Resources Canada, Earth Sciences Sector, Geological Survey of Canada, 601 Booth Street, Ottawa, ON K1A 0E8, Canada.

[1] Corresponding author (e-mail: bergeron.yves@uqam.ca).

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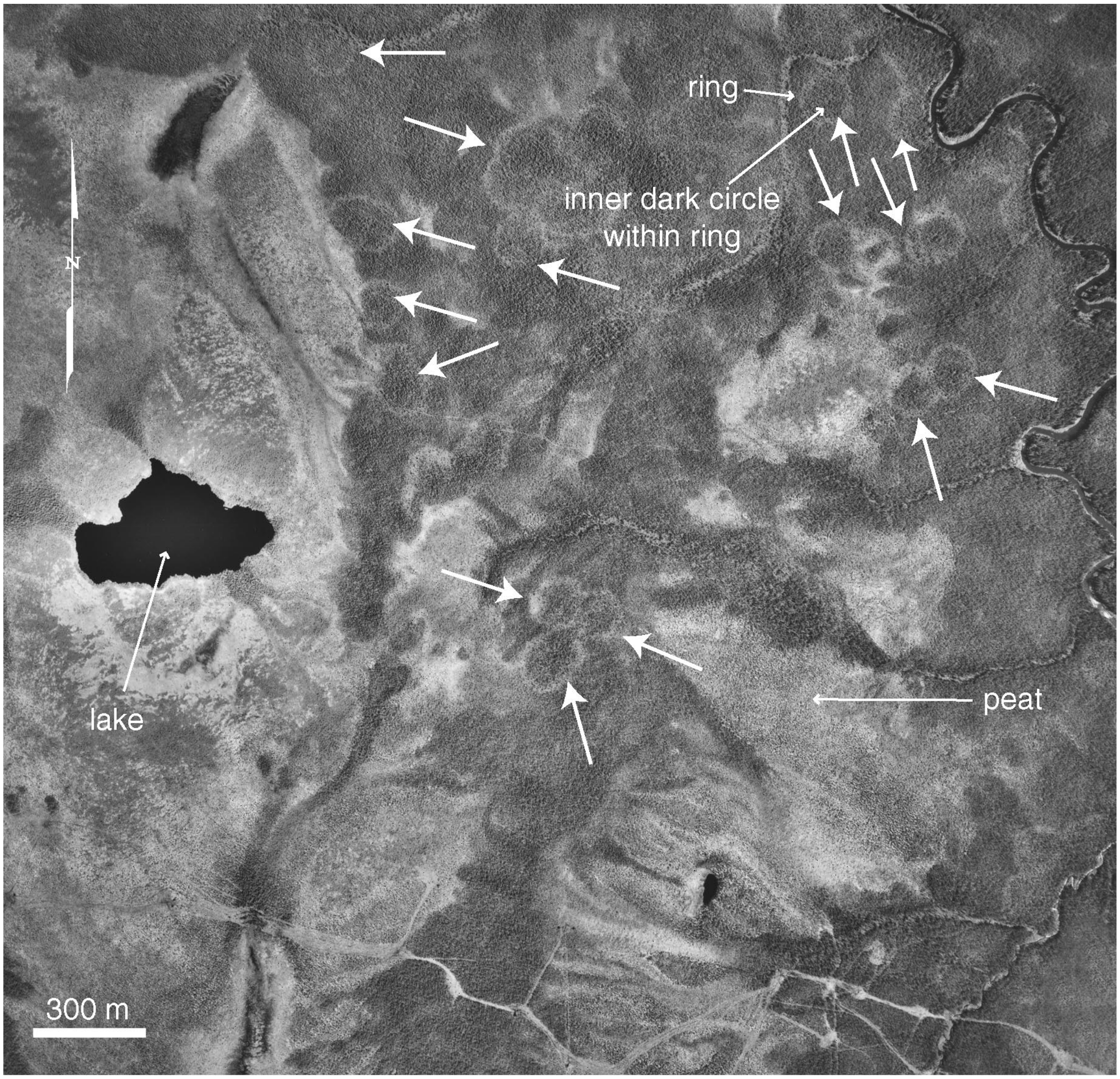
Fig. 1. Aerial photograph showing several whitish rings in northwestern Abitibi, Quebec.



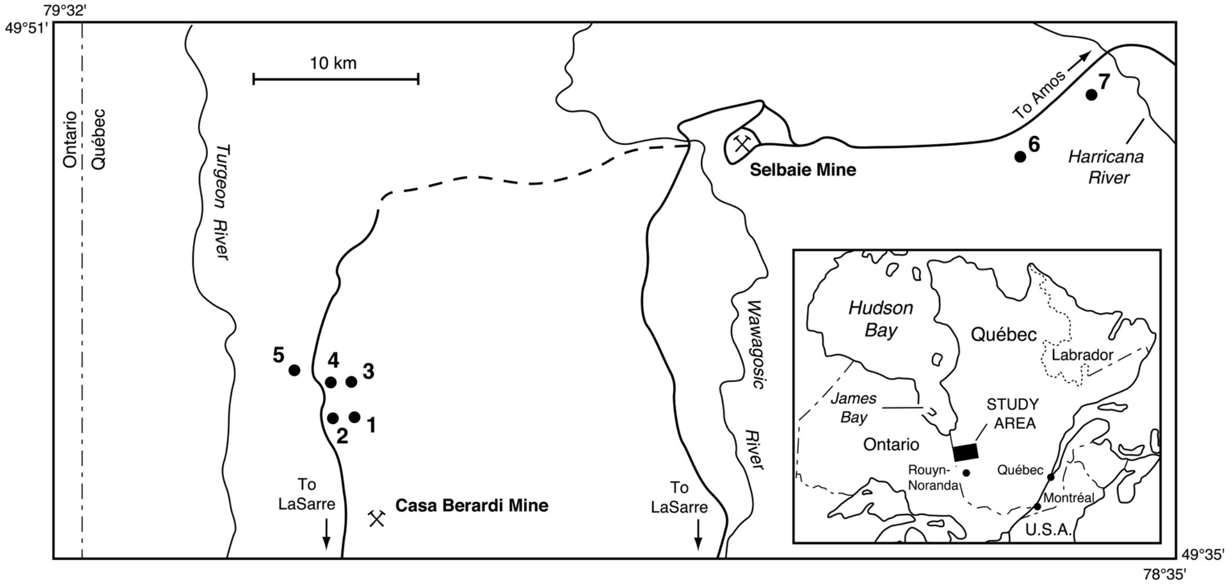
even landing sites of extraterrestrial spacecraft (Mollard 1980; Veillette and Giroux 1999). The hypothesis that has received the most attention to date rests on the assumption that the rings result from mortality caused by a fungus with a radial growth pattern (Mollard 1980; Veillette and Smith 1992; Dubois 1993), but no studies have produced supporting evidence.

If the low density of trees inside the rings is caused by significant spruce mortality resulting from fungal infection at these locations, mortality should start at a central point and radiate outward forming the small whitish circles that are visible on aerial photographs. As mortality progresses outward, trees should start to regenerate from the center of the circle and also progress outward (Mollard 1980). Trees should, therefore, be older at the center of the circle and progressively younger as one approaches the ring. Because segments of rings occur along streams, which suggest that the growth of the rings is arrested by water bodies, Veillette and Smith (1992) favored a biological origin of the rings but they could find no supporting evidence other than the rings/streams relationship. Based on the work of Veillette and Smith (1992), Dubois (1994), proposed a mycological origin for the rings.

Several organisms including spruce budworm (*Choristoneura fumiferana*) (MacLean 1980), pinewood nematode (*Bursaphelenchus xylophilus*) (Futai and Sutherland 1989), dwarf mistletoe (*Arceuthobium pusillum*) (Baker and French 1991), and several species of fungus (Whitney 1995), can cause significant mortality of black spruce. Of these organisms, only dwarf mistletoe and fungi propagate radially (Baker and French 1991; Wargo and Shaw 1985). However, if dwarf mistletoe was present in the rings, it would have been easily observed since it grows on tree branches and can be seen with the naked eye. Moreover, dwarf mistletoe is rarely observed in the Abitibi region (Marie-Victorin 1964). This explains why Mollard (1980) proposed that fungi are the most likely organisms to cause the formation of the rings.

If the rings result from non-biological processes, the ring-shaped bands may represent areas where spruce had experi-

Fig. 2. Location of the seven rings (numbered 1 to 7) sampled during this study.



enced great difficulty in growing due to some underlying, circular geological formations or geochemical processes affecting soil characteristics and tree growth (Veillette and Giroux 1999). Contrary to the biological scenario, however, rings formed in association with geological or geomorphological processes would be static.

One objective of this study was to examine vegetation within, and in the vicinity of, seven selected circles using dendrochronological and other techniques to determine whether structure and composition of the vegetation were static or changing radially. A lack of evidence for radial changes in vegetation led to further investigations into abiotic causes of ring formation. Consequently, we tested the hypothesis that differences in surficial deposits or drainage conditions were responsible for the lower productivity and the lower density of black spruce within the rings.

Methods

Study area

Figure 2 shows the location of the seven rings studied. Black spruce stands in these areas are relatively unproductive and have little commercial value. The mineral substrate underlying the circles consists of pebbly clay resulting from the reworking of glacial Lake Ojibway clays by late glacial surges (Veillette 1989). The mineral substrate is generally covered with a layer of well-decomposed organic matter (10–30 cm thick) that is topped by mosses and peat accumulated to depths exceeding 30 cm in many places.

Rings selected for detailed analysis

Seven rings were sampled over the summers of 1996 and 1997. Rings were selected close to roads to facilitate access. Two different areas were chosen to provide a representative sample of the region. Five rings were sampled east of the Turgeon River, close to the Casa Bérardi mine, and two others west of the Harricana River, near the Selbaie mine road (Fig. 2). Ring diameter ranged from 125 to 200 m.

Sampling procedure

Starting from the center of each circle, four radii were laid out, at the ground surface, in the direction of the four cardinal points and extended 50 m beyond the outside edge of the ring. Five 10 × 10 m quadrats were established along each radius: one at the center of the circle (common to all four radii), one halfway between the center of the circle and the center of the ring, one inside the circle at 10 m from the inside edge of the ring, one at the center of the ring, and one 20 m outside the ring. A total of 17 quadrats were thus defined for each circle. To obtain data on the mineral substrate and ground cover (plants under 1 m high), sampling points were spaced at 10-m intervals along each of the four radius. For determination of water and carbonate content and grain-size only one radius per ring was sampled.

Vegetation

In each 10 × 10 m quadrat, the breast height diameter (dbh) of all living and dead trees over one meter in height was measured and the trees were assigned to diameter classes (<1 cm, 1–5 cm, 5–10 cm, 10–15 cm, and so on). Core samples were taken at the base (15 cm from the ground) of the three living trees with a dbh > 5 cm that were located closest to the center of each quadrat. From these data, tree basal area was calculated for each species in each quadrat, for both living and dead trees. Relative mortality was calculated by dividing the basal area of dead trees by the total basal area (basal area of living trees + basal area of dead trees). Percent cover of each vascular and non-vascular understory plant species, with a maximum height of less than 1 meter, was estimated in a 1 × 1 m quadrat located at 10-m intervals along each of the four radii.

Productivity

The number of years taken to reach a certain height and the total basal area in the 10 × 10 m quadrats were used as indicators of productivity. The two largest living spruce trees in each 10 × 10 m quadrat were cut down. After the height of each tree was measured, three cross-sections were taken: at the base, at a height of 1.3 m, and at a height of 2.3 m. The basal section was used to determine the tree's final age, and the two other sections were used to determine how many years the tree continued to grow after it reached these heights. By subtraction, we calculated the number of years the tree took to reach a height of 1.3 m, and the number of years to grow from this height to 2.3 m.

Table 1. Variables assessed and results of simple and multiple regression analyses.

y	x_1	x_2	x_3	equation	R^2	p
{ln [basal area of dead spruce (cm^2)]}^{2}	Distance from ring (m)	—	—	$y = 0.0386\ x_1 + 40.8110$	0.0056	0.4311
Sand (%)	Distance from ring (m)	—	—	$y = –0.1609\ x_1 + 35.3142$	0.0543	0.2421
Silt (%)	Distance from ring (m)	—	—	$y = 0.1431\ x_1 + 60.2071$	0.0591	0.2218
Clay (%)	Distance from ring (m)	—	—	$y = 0.0178\ x_1 + 4.4807$	0.0198	0.4841
Carbonate (%)	Distance from ring (m)	—	—	$y = 0.0186\ x_1 + 4.3128$	0.0052	0.7009
ln [basal area of living trees (cm^2)] (circles 4, 5, 6, and 7)	ln (distance from ring (m))	—	—	$y = 0.3127\ x_1 + 6.3817$	0.2484	<0.0001
ln [basal area of living trees (cm^2)] (circles 1, 2, and 3)	ln (distance from ring (m))	—	—	$y = 0.2324\ x_1 + 6.1983$	0.1182	0.0135
ln [time needed to grow from the base to a height of 1.3 m (years)] (circles 1, 2, 3, 4, and 5)	Relative elevation of mineral substrate (m)	—	—	$y = 0.0201\ x_1 + 3.5829$	0.0025	0.5014
ln [time needed to grow from the base to a height of 1.3 m (years)] (circle 6)	Relative elevation of mineral substrate (m)	—	—	$y = –0.1224\ x_1 + 4.1661$	0.0799	0.1171
ln [time needed to grow from the base to a height of 1.3 m (years)] (circle 7)	Relative elevation of mineral substrate (m)	—	—	$y = 0.0252\ x_1 +3.2143$	0.0077	0.6573
ln [spruce height (m)] (circles 1, 3, and 6)	ln [age (years)]	ln [relative elevation of mineral substrate (m) + 0.1]	—	$y = 0.1907\ x_1 + 0.089\ x_2 + 1.0616$	0.3344	<0.0001
ln [spruce height (m)] (circles 2, 4, and 5)	ln [age (years)]	ln [relative elevation of mineral substrate (m) + 0.1]	ln [distance from ring (m)]	$y = 1.1068\ x_1 + 4.0368\ x_2 + 1.426 x_3 – 3.4648$	0.4393	<0.0001
ln [spruce height(m)] (circle 7)	ln [age (years)]	—	—	$y = 7.69\ x_1 – 35.81$	0.8776	<0.0001

Fig. 3. Age variation of black spruce expressed as a function of the distance from the ring.

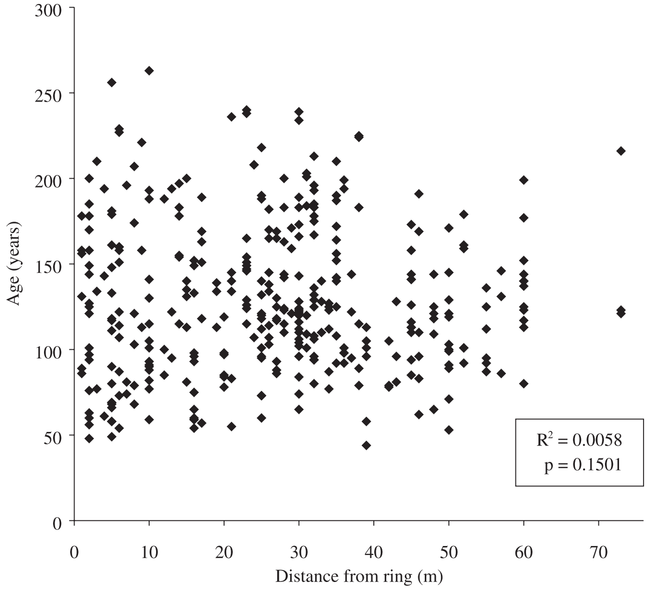
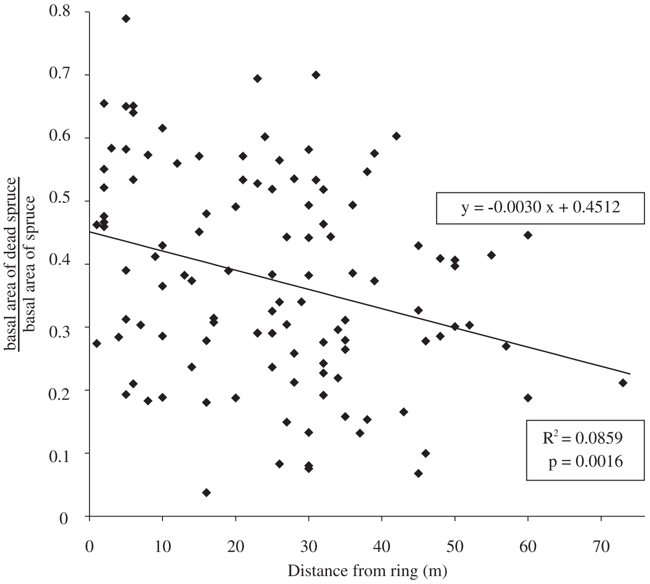


Fig. 4. Relative mortality of black spruce expressed as a function of the distance from the ring.



Topography within the circles and analysis of mineral substrate

At 10-m intervals along each circle radius, the elevation of the mineral substrate, relative to the center of the circle, was determined using a theodolite. An elevation of 0 m was assigned to the lowest point in each circle. At each 10-m interval, we also recorded the thickness of the organic layer overlying the mineral substrate, which was measured from samples taken with a soil auger. The relative elevation of the mineral substrate was then determined by subtracting the thickness of the organic layer from the elevation of the soil surface. A sample of approximately 250 mL was taken from the surface of the mineral substrate to determine grain-size and water and carbonate contents. In the laboratory, carbonate content was measured using the Chittik apparatus (Dreimanis 1962) and grain-size was determined with a Galai 2010 densimetric apparatus.

Statistical analyses

For each studied variable, we first used a covariance analysis to test if there were relationships between the variables and distance from the rings or relative elevation of the mineral substrate among the seven circles. Circles with similar relationships were grouped together for the rest of the analyses.

Simple regression analyses were performed to determine whether tree age or mortality varied as a function of distance from the ring. Because productivity may be related to distance from the ring, or to the relative elevation of the mineral substrate, multiple regressions including these two variables were also performed for the basal area of the living trees, time needed to grow from one point to another, tree height, and the percent cover of the most abundant species. Since the height and age of spruce are closely related, age was used as a covariable in the analysis of height. Where a multiple regression showed that only one variable had a significant influence, or when it showed significant multi-collinearity among independent variables, the non-significant variables were removed from the model and a simple regression was performed.

A simple regression was performed for each variable associated with the substrate as a function of distance from the ring to determine if these variables showed any patterns in the ring.

Various data transformations (shown in Table 1 and in the formulas for the regression curves) were performed before applying the regression analyses. For the regression between elevation of the mineral substrate and the distance from the ring, elevation data were ranked because the residuals were not normally distributed. However, to provide a clearer picture of the relationships, raw data were plotted on our graphs. All of the statistical analyses were performed using SAS 6.12 software (SAS Institute Inc. 1992).

Results

Age and mortality

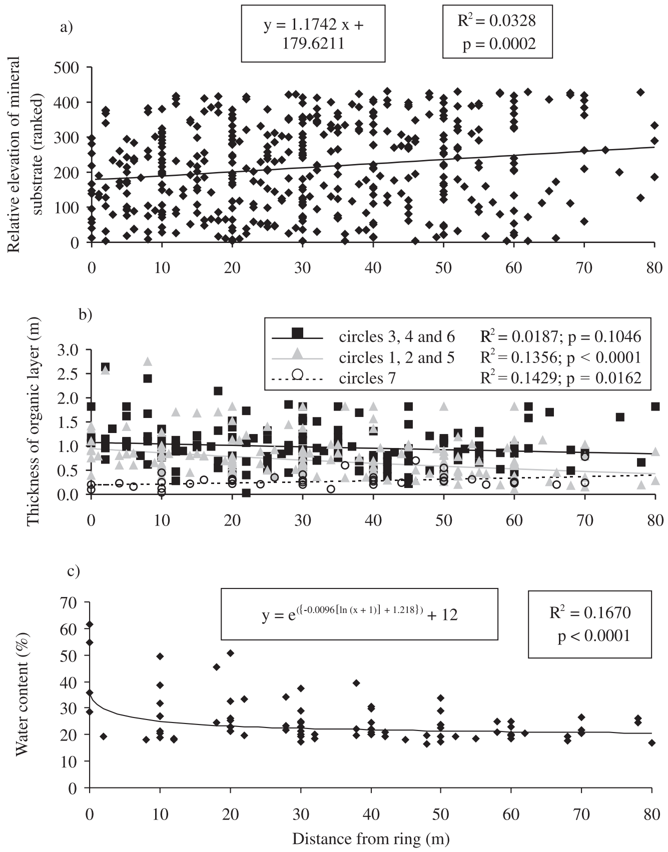
Neither the age nor basal area of dead black spruce varied significantly with distance from the ring (Fig. 3; Table 1). However, relative mortality of black spruce increased significantly with decreasing distance from the ring (Fig. 4). This indicates that a higher proportion of the total basal area of spruce is comprised of dead trees in the ring.

Productivity

Variation in the substrate characteristics associated with the rings may affect productivity. Elevation of the mineral substrate rose significantly with distance outward and inward from the ring (Fig. 5*a*), that is, it is lower in the ring. Thickness of the organic layer and the water content of the mineral layer increased towards the ring (Figs. 5*b* and 5*c*). Grain-size and carbonate content analyses, however, did not reveal any significant variation with distance from the ring (Table 1). As distance to the rings and mineral substrate elevation may have independent effects on productivity, both were incorporated into the regression model for the analysis of productivity-related variables, thus giving rise to multiple regressions.

Distance from the ring was the only significant variable included in the regression model explaining variation in the basal area of living trees (Table 1). The increase in basal area with distance from the ring confirms what can be seen in the aerial photographs, that is, the tree cover is more open

Fig. 5. Variation of three substrate-related variables. (*a*) Relative elevation of mineral substrate, (*b*) thickness of organic layer, and (*c*) water content of mineral substrate, expressed as a function of the distance from the ring.



within and in the immediate vicinity of the ring compared with beyond the ring or at the center of the circle.

Tree height growth to 1.3 m did not show significant relationships with distance or elevation (Table 1). However, the time needed to grow from 1.3 m to 2.3 m was significantly shorter as we move from lower to higher elevation for four of the seven circles (Fig. 6).

Because total tree height is a function of age, this variable was included a priori into the multiple regression models (Table 1). In all circles but one, elevation was the main explanatory factor of total tree height. Distance from the rings was only included in the regression models for one group of circles (Table 1). This suggests that trees of equivalent age will be shorter when the elevation of the mineral substrate is low and when they are close to the ring.

Topography of the circles

To clearly depict the topography of the circles and relate it to the basal area of the spruce within the ring, profiles of the mineral substrate were produced for selected contrasted circles and radii. For radii where the basal area of live black spruce in a quadrat was less than 25% of the average basal area for all of the quadrats in the circle, the elevation of the mineral substrate was higher on either side of the ring. Along the south radius of circle five (Fig. 7*a*) for example, the surface of the mineral substrate dropped by about 3 m over a horizontal distance of approximately 40 m, from inside the circle toward the ring (slope = 7.5%), and by over 4 m from outside the circle toward the ring (slope = 8%) over a distance of 50 m. Along the west radius of circle seven (Fig. 7*b*), the depression in the mineral substrate was less pronounced but still apparent; as one approaches the ring from either inside or outside the circle, elevation of the mineral substrate decreased by more than 1 m over a horizontal distance of approximately 20 m (slope = 5%). However, when a radius cuts across the ring in an area where tree density was high (more specifically, where the basal area of live black spruce in the quadrat located within the ring was greater than the average basal area for all of the quadrats in the circle), the surface of the mineral substrate did not rise away from the ring; on the contrary, it is higher within the ring than at the center of the circle. The absence of a depression beneath some segments of rings (what has been previously explained as gaps in ring development) explains why elevation rather than distance from the rings is closely related to productivity variables.

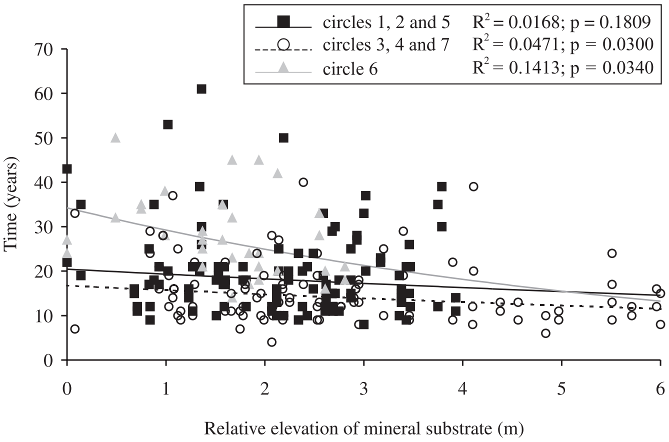
Discussion

Ring evolution

Our results confirm that the whitish zones (the ring) observed on black and white aerial photographs are linked to high relative mortality of spruce and lower total basal area. Our working hypothesis was that these rings represented zones of previously normal tree cover that were decimated by a pathogenic organism causing significant tree mortality. According to the scenario of radial expansion of mortality, productivity should be relatively uniform throughout the circle with massive mortality within the ring. The basal area of dead spruce should, therefore, be higher within the ring. However, total mortality is not higher there and thus, the rings studied show no evidence of massive mortality caused by a pathogen.

The relatively uniform age of spruce across the diameters of the rings provides further evidence that radial changes in vegetation structure or composition have no biological origin. Rings may expand at a slow rate but the chance that this can be detected by examining tree ages is extremely remote given the known rates of growth for various fungi that cause tree mortality. For example, the radial expansion of the species *Fomes annosus* in pine forests ranges from 0.4 to 1.4 m per year (Rishbeth 1951; Miller and Kelman 1966; Sinclair 1964 in Slaughter and Parmeter 1995; Hodges 1974 in Slaughter and Parmeter 1995). Also in pine forests, *Heterobasidion annosum* has achieved rates of radial expansion in its distribution from 0.217 to 0.67 m per year (Goheen and Goheen 1989 in Slaughter and Parmeter 1995; Monroy and Parmeter 1989 in Slaughter and Parmeter 1995; Slaughter and Parmeter 1995). *Armillaria* spp. have exhibited radial growth of 0.2 to 1.3 m per year in various types of forests (Rishbeth 1968; Kable 1974; Shaw and Roth 1976; Smith et al. 1992). A ring expanding at the slowest of these observed rates (0.2 m per year) would cover a distance of 50 m over the average lifetime of a spruce (about 250 years according to the present study). This means that the average age of the trees would be very low within the ring but increase from the ring toward the center of the circle for a distance of 50 m

Fig. 6. Variations of black spruce time needed to grow from 1.3 to 2.3 m in height, expressed as a function of the relative elevation of the mineral substrate.



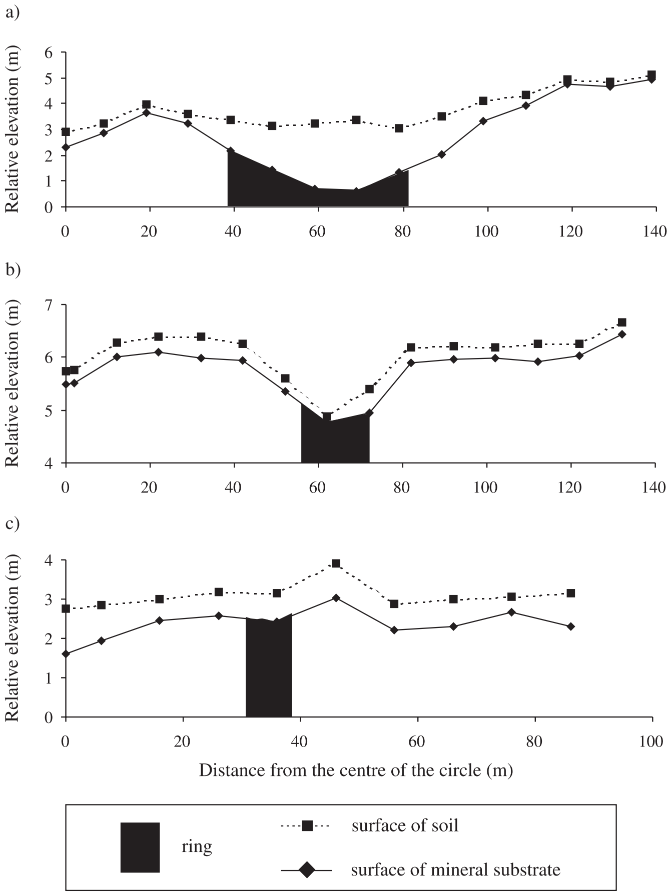
and then stabilize. Since this distance is much greater than the distance between the quadrats sampled, an increase in tree age with distance from the ring would certainly have been observed if the rings examined had in fact evolved this way. These results support earlier observations using a series of aerial photographs taken 26 years apart which failed to detect any measurable expansion for two rings tangent to a cut line (Veillette and Smith 1992). Consequently, the hypothesis of ongoing mortality due to fungal attack is unlikely.

Veillette and Smith (1992) have also suggested that the rings may have grown somewhat in the past but are now static. Pathogenic fungi are, in fact, known to go through a growth phase followed by a stabilization phase (Nandris et al. 1988; Slaughter and Parmeter 1995). However, this latter phase is caused by reduced activity of the fungus. If the rings were occupied by a fungus in its stabilization phase, then a certain rise in productivity should be observed in the ring because, even if the fungi do not degenerate during this phase, they lose their capacity to kill trees (Nandris et al. 1988). However, our results indicate no such recovery in productivity, which should be demonstrated by a substantial presence of young trees within the ring.

Productivity

An alternate hypothesis explaining the presence of rings is that low productivity of black spruce in the rings produces more open stands. Observed decreases in total basal area and height growth, together with higher relative mortality in the rings, support this hypothesis. The productivity of black spruce depends on many environmental factors, including sunlight, temperature, precipitation, and soil nutrients and moisture (Lamhamedi and Bernier 1994). However, since light is not a limiting factor within the ring and climate is the same over the whole circle, soil-related factors are more likely to explain the decrease in productivity. Numerous studies have shown that in poorly drained environments, like those in our study area, the soil factor having the strongest influence on black spruce productivity is the quality of drainage (Lieffers and Rothwell 1987; Dang and Lieffers 1989; Lieffers and Macdonald 1990; Macdonald and Lieffers 1990; Mugasha et al. 1993; Wang and Macdonald 1993). These studies have shown that poor drainage reduces nutrient absorption, photosynthesis, and hence productivity of black spruce. Consequently, the relationship we observed between tree productivity and the elevation of the mineral substrate could be explained as follows: where the water table is very close to or at the surface, which is the case for most rings we sampled, the elevation of the mineral substrate is low and the soil is saturated (Freeze and Cherry 1979). Thus, excessive soil moisture associated with low elevations of the mineral substrate is the dominant factor that interferes with the growth of the spruce within the rings.

Fig. 7. Elevation profiles along three radii: (*a*) south radius of circle No. 5; (*b*) west radius of circle No. 7; (*c*) south radius of circle No. 6.



The distribution of other plant species (Giroux 1999) also reflects the greater soil moisture within the rings. *Larix laricina*, *Alnus rugosa*, *Smilacina trifolia*, *Chamaedaphne* *calyculata,* and *Kalmia polifolia* are more abundant in the rings and are characteristic plants of wet and boggy areas (Montague and Givnish 1996; Conlin and Lieffers 1993; Nielsen 1999). In contrast, species that grow better on well-drained soils become less abundant closer to the rings and where the relative elevation of the mineral substrate decreases. This is the case for *Pleurozium schreberi* and *Dicranum polysetum,* which are characteristic of forested areas and dry bogs (Nicholson and Gignac 1995; Gignac 1992).

Topography of the circles

The elevation profiles of the mineral substrate along certain radii clearly show that the presence of a ring (an area where there are very few trees) corresponds to depressions in the mineral substrate. In a poorly drained environment, with an impervious clay substrate, such as is the case in our study area, this depression traps water that impairs the growth of black spruce and explains the presence of the rings. Water content of the mineral substrate in the rings was clearly higher than inside and outside the rings. The organic layer was also thicker because decomposition of organic material is lower under conditions of high soil moisture (Moorhead and Reynolds 1993). In contrast, when the area where a radius intersects a ring covered with trees (or more precisely the logical extension of the ring since a segment of ring covered with trees is not a ring per se), it coincides with the absence of a depression in the mineral substrate. In some cases the area of intersection corresponds with a rise in elevation of the mineral substrate.

The data collected from all radii were used in the regression of relative elevation of the mineral substrate against distance from the ring. The R^2 and the slope of the resulting equation were low, probably because data from some transects without depression in the ring were included in the analysis. These results, and close examination of the aerial photographs, indicate that many rings are discontinuous. Some rings show gaps where the black spruce is dense (dark tone on aerial photographs). These coincide with a higher elevation of the mineral substrate such as shown for the south portion of ring 6, which is higher than the center of the circle (Fig. 7).

Conclusion

Our data on the mortality and productivity of black spruce as well as relationships between the topography of the surface of the rings and circles and that of the mineral substrate, suggest that the location of the rings coincides with areas of excessive soil moisture that severely limit the productivity of black spruce. We found no evidence to support the hypothesis that the rings are the result of fungal activity. The excessive soil moisture was caused by ring-shaped depressions that trap moisture and favor peat development. The origin of the depressions, however, cannot be explained by any known geomorphological process, and they do not correspond to any known landforms. New data on the distribution of similar rings in Eastern Canada revealed a strong correlation between the distribution of rings and the presence of a calcareous substrate (Veillette and Giroux 1999). These data, along with the results of the present study, led Veillette and Giroux to conclude that the most likely processes explaining the circular depressions in the mineral substrate were caused by mechanisms driven from below the surface rather than geomorphological agents acting at the ground surface. This hypothesis has formed the basis of recent research, undertaken jointly by the Geological Survey of Canada and the Ontario Geological Survey, showing that the circular depressions beneath rings are the result of carbonate depletion within the rings (Hamilton et al. 1999). Electrochemical processes taking place at depth in the unconsolidated deposits seem to explain ring formation according to a geophysical/geochemical model developed by Hamilton (1998). The Ontario Geological Survey, in cooperation with mineral exploration companies, is continuing research on the formation of the rings and their potential link with mineralized sources.

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References

Baker, F.A., and French, D.W. 1991. Radial enlargement of mortality centers caused by *Arceuthobium pusillum* Peck in black spruce stands. Forest Sci. **37**: 364–367.

Conlin, T.S.S., and Lieffers, V.J. 1993. Anaerobic and aerobic CO_2 efflux rates from boreal forest conifer roots at low temperatures. Can. J. For. Res. **23**: 767–771.

Dang, Q.L., and Lieffers, V.J. 1989. Assessment of patterns of response of tree ring growth of black spruce following peatland drainage. Can. J. For. Res. **19**: 924–929.

Dreimanis, A. 1962. Quantitative gasometric determination of calcite and dolomite by using Chittick apparatus. J. Sediment. Petrol. **32**: 520–529.

Dubois, J.M.M. 1993. Les ronds mystérieux de l'île d'Anticosti. Revue Dialogue Scientifique, **1**: 19–21.

Dubois, J.-M. 1994. Mycological origin of rings in the coniferous forest of Anticosti Island in the Gulf of Saint Lawrence, Canada. Photo-Interpretation 1993–3, Juillet-Août, Éditions Eska, 27, rue Dunois, 75013, Paris. pp. 209–210 (text also available in French and Spanish).

Freeze, R.A., and Cherry, J.A. 1979. Groundwater. Prentice-Hall, Inc., Englewoods Cliffs, N.J.

Futai, K., and Sutherland, J.R. 1989. Pathogenicity and attraction to host extracts of Canadian pinewood nematodes: studies with

Scots pine, western larch, and black spruce seedlings. Can. J. For. Res. **19**: 1256–1261.

Gignac, L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. Bryol. **95**: 406–418.

Giroux, J.-F. 1999. Dynamique, morphologie et végétation de sept anneaux géants blanchâtres formés par des peuplements d'épinettes noires du nord de l'Abitibi. Mémoire de maîtrise en biologie, Université du Québec à Montréal. p. 48.

Hamilton, S. M. 1998. Electrochemical mass-transport in overburden: a new model to account for the formation of selective leach geochemical anomalies in glacial terrain. J. Geochem. Explor. **63**:155–172.

Hamilton, S.M., Veillette, J.J., and Komararechka, R. 1999. A geological model to account for the formation and surprising circularity of forest rings of the James Bay basin. Poster presented at the 1999 Prospectors and Developers Association of Canada annual meeting, March 16, 1999. Toronto, Ont.

Kable, P.F. 1974. Spread of *Armillariella* sp. in a peach orchard. Trans. Brit. Mycol. Soc. **62**: 89–98.

Lamhamedi, M.S., and Bernier, P.Y. 1994. Ecophysiology and field performance of black spruce (*Picea mariana*): a review. Ann. Sci. For. **51**: 529–551.

Lieffers, V.J., and Rothwell, R.L. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Can. J. Bot. **65**: 817–821.

Lieffers, V.J., and MacDonald, S.E. 1990. Growth and foliar nutrient status of black spruce and tamarack in relation to depth of water table in some peatlands in Alberta. Can. J. For. Res. **20**: 805–809.

MacDonald, S.E., and Lieffers, V.J. 1990. Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. Can. J. For. Res. **20**: 995–1000.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. **56**: 213–221.

Marie-Victorin. 1964. Flore laurentienne, 2^{e} édition. Les Presses de l'Université de Montréal, Montréal, Que.

Miller, T., and Kelman, A. 1966. Growth of *Fomes annosus* in roots of suppressed and dominant loblolly pines. Forest Sci. **12**: 225–233.

Mollard, J. 1980. Landforms and surface materials of Canada: a stereoscopic atlas and glossary, 6^{e} édition, Regina, Sask.

Montague, T.G., and Givnish, T.J. 1996. Distribution of black spruce versus eastern larch along peatland gradients: relationship to relative stature, growth rate, and shade tolerance. Can. J. Bot. **74**: 1514–1532.

Moorhead, D.L., and Reynolds, J.F. 1993. Effects of climate change on decomposition in arctic tussock tundra: a modeling synthesis. Arct. Alp. Res. **25**: 403–412.

Mugasha, A.G., Pluth, D.J., and Hillman, G.R. 1993. Foliar responses of tamarack and black spruce to drainage and fertilization of a minerotrophic peatland. Can. J. For. Res. **23**: 166–180.

Nandris, D., Nicole, M., and Geiger, J.P. 1988. Root-rot diseases of the rubber tree in the Ivory Coast. 1. Severity, dynamics, and characterization of epidemics. Can. J. For. Res. **18**: 1248–1254.

Nicholson, B.J., and Gignac, L.D. 1995. Ecotope dimensions of peatland bryophyte indicator species along gradients in the Mackenzie River basin, Canada. Bryol. **98**: 437–451.

Nielsen, E. 1999. Effects of inundation on tamarack (*Larix laricina*): Implications for use of trees in monitoring lake-level rise. Geological Survey of Canada, Ottawa, Ont. Open file 3470. p. 403–411.

Rishbeth, J. 1951. Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. III. Natural and experimental infection of pines, and some factors affecting severity of the disease. Ann. Bot. **15**: 137–145.

Rishbeth, J. 1968. The growth rate of *Armillaria mellea*. Trans. Brit. Mycol. Soc. **51**: 575–586.

SAS Institute Inc. 1992. SAS user's guide: Stastistics. SAS Institute Inc. Cary, N.C.

Shaw, C.G. III, and Roth, L.F. 1976. Persistence and distribution of a clone of *Armillaria mellea* in a ponderosa pine forest. Phytopathol. **66**: 1210–1213.

Slaughter, G.W., and Parmeter, J.R. 1995. Enlargement of tree-mortality centers surrounding pine stumps infected by *Heterobasidion annosum* in northeastern California. Can. J. For. Res. **25**: 244–252.

Smith, M., Bruhn, J.N., and Anderson, J.B. 1992. The fungus *Armillaria bulbosa* is among the largest and older living organisms. Nature, **356**: 428–431.

Veillette, J.J. 1989. Ice movements, till sheets, and glacial transport in Abitibi-Timiskaming, Québec and Ontario. *In* Drift prospecting. *Edited by* R.N.W. DiLabio and W.B. Coker. Geological Survey of Canada, Ottawa, Ont. Paper 89–20. pp. 139–154.

Veillette, J.J., and Giroux, J.F. 1999. The enigmatic rings of the James Bay Lowland; a probable geological origin. Geological Survey of Canada, Ottawa, Ont. Open file 3708. p. 39.

Veillette, J.J., and Smith, M. 1992. Les grands anneaux du nord de l'Abitibi, un nouvel outil de datation relative? Bulletin de l'AQQUA, **18**: 76.

Wang, Z.M., and MacDonald, S.E. 1993. Peatland and upland black spruce populations in Alberta: morphology and ecophysiology. Can. J. For. Res. **23**: 33–40.

Wargo, P.M., and Shaw, C.G. III. 1985. Armillaria root rot: the puzzle is being solved. Plant Dis. **69**: 826–832.

Whitney, R.D. 1995. Root-rotting fungi in white spruce, black spruce, and balsam fir in northern Ontario. Can. J. For. Res. **25**: 1209–1230.