Paludification dynamics in the boreal forest of the James Bay Lowlands: effect of time since fire and topography

Martin Simard, Pierre Y. Bernier, Yves Bergeron, David Paré, and Lakhdar Guérine

Abstract: In many northern forest ecosystems, soil organic matter accumulation can lead to paludification and forest productivity losses. Paludification rate is primarily influenced by topography and time elapsed since fire, two factors whose influence is often confounded and whose discrimination would help forest management. This study, which was conducted in the black spruce (*Picea mariana* (Mill.) BSP) boreal forest of northwestern Quebec (Canada), aimed to (1) quantify the effect of slope and time since fire on paludification rates, (2) determine whether soil organic layer depth could be estimated by surface variables that can potentially be remotely sensed, and (3) relate the degree of paludification to tree productivity. In this study, soil organic layer depth was used as an estimator of the degree of paludification. Slope and postfire age strongly affected paludification dynamics. Young stands growing on steep slopes had thinner organic layers and lower organic matter accumulation rates compared with young stands growing on flat sites. Black spruce basal area and *Sphagnum* cover were strong predictors of organic layer depth, potentially allowing mapping of paludification degree across the landscape. Tree productivity was negatively related to organic layer depth (R^2 = 0.57). The equations developed here can be used to quantify forest productivity decline in stands that are undergoing paludification, as well as potential productivity recovery given appropriate site preparation techniques.

Résumé : Dans plusieurs écosystèmes forestiers nordiques, l'accumulation de matière organique peut mener à la paludification des sols et entraîner des pertes de productivité forestière. Le taux de paludification est principalement influencé par la topographie et le temps écoulé depuis le dernier feu, deux facteurs dont l'influence est souvent confondue et dont la séparation aiderait à l'aménagement forestier. Cette étude réalisée dans la pessière noire (*Picea mariana* (Mill.) BSP) du nord-ouest du Québec (Canada) avait comme objectifs : (1) de quantifier l'effet de la pente et du temps depuis le dernier feu sur le taux de paludification, (2) de déterminer si l'épaisseur de la couche organique pouvait être estimée à partir de deux variables de surface quantifiables au moyen de la télédétection, et (3) d'établir la relation entre le degré de paludification et la productivité des arbres. Dans cette étude, l'épaisseur de la couche organique du sol a été utilisée pour estimer le degré de paludification. La pente et l'âge des peuplements après feu influencent fortement la dynamique de paludification. La couche organique était plus mince et avait un taux d'accumulation plus faible dans les jeunes peuplements établis sur des pentes fortes que dans les peuplements d'âge similaire établis sur terrain plat. La surface terrière en épinette noire et le recouvrement de sphaignes avaient un fort pouvoir de prédiction de l'épaisseur de la couche organique, ce qui pourrait permettre de cartographier le degré de paludification à l'échelle du paysage. Enfin, la productivité des arbres était négativement reliée à l'épaisseur de la couche organique (R^2 = 0,57). Les équations développées dans ce travail peuvent être utilisées pour quantifier le déclin de productivité forestière dans les peuplements sujets à la paludification, ainsi que le potentiel de récupération de productivité à la suite d'une préparation de terrain appropriée.

Introduction

Forest productivity varies naturally over time and space, and understanding this variability is essential for managing forests in a manner that balances timber production and maintenance of ecological integrity. In boreal ecosystems, the spatial variability of forest productivity is largely driven by fine-scale topography through its control on soil drainage

Received 25 February 2008. Accepted 24 November 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 25 February 2009.

M. Simard[1,2] and L. Guérine. NSERC–UQAT–UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 4E5, Canada, and Centre d'études sur la forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-ville, Montréal, QC H3C 3P8, Canada; Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du PEPS, P.O. Box 10380, stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.
P.Y. Bernier and D. Paré. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du PEPS, P.O. Box 10380, stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.
Y. Bergeron. NSERC–UQAT–UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 4E5, Canada, and Centre d'études sur la forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-ville, Montréal, QC H3C 3P8, Canada.

[1]Corresponding author (e-mail: simard@wisc.edu).
[2]Present address: University of Wisconsin, Department of Zoology, Birge Hall, 430 Lincoln Drive, Madison, WI 53706, USA.

(Wang et al. 2003; Bond-Lamberty et al. 2004) and by heterogeneity in disturbance interval and severity (Kimmins 1996). For example, soil burn severity controls postfire recruitment and growth (Lecomte et al. 2006*b*; Greene et al. 2007). Forest productivity has also been shown to decline with age in the absence of large-scale disturbances, and the underlying causal factors of this decline are still debated (Ryan et al. 2004). In northern ecosystems, one probable cause of productivity decline with time is the accumulation of a thick organic layer that cools the soil and reduces nutrient cycling (Van Cleve et al. 1983*a*; Prescott et al. 2000). As a result, soil preparation techniques that disturb soil organic layers to enhance forest productivity are used in many parts of the world (Paavilainen and Päivänen 1995; Lavoie et al. 2005). Prediction of global change and forest management effects in these ecosystems can only be done through a good understanding of how forest productivity varies in time and space (Bond-Lamberty et al. 2004; Grant 2004).

In northwestern Quebec (Canada), on the clay plains of the James Bay Lowlands, boreal forest soils accumulate thick organic layers over time through a phenomenon called paludification (Heinselman 1963; Payette and Rochefort 2001). Paludification is characterized by a gradual colonization of forested sites by *Sphagnum* moss species (Van Cleve et al. 1983*a*; Fenton et al. 2005). After stand establishment following a fire, the gradual accumulation of organic matter lowers soil temperature and creates a perched water table close to the soil surface (Fenton et al. 2006; Simard et al. 2007). Bryophyte and shrub diversity is reduced (Lecomte et al. 2005; Fenton and Bergeron 2006), and as stands open up (Harper et al. 2005; Lecomte et al. 2006*a*), tree productivity declines (Van Cleve et al. 1983*b*; Lecomte et al. 2006*b*). In the extended absence of fire, paludification can reduce forest productivity by up to 50%–80% compared with postfire values (Simard et al. 2007). Forest succession between fire events can therefore be an important driver of paludification, independently of site topography or drainage. Topography also has a determinant effect on paludification rates and productivity (Lavoie et al. 2007). Since it is water retention that ultimately enables the growth of *Sphagnum* and the accumulation of organic matter, sites with greater slopes, and hence more lateral drainage, should show a lower degree of paludification than flatter sites. Generally, paludification is always caused by the same proximate mechanism, i.e., high water table, but is ultimately driven by two different factors (topography and succession) that can independently modulate the rate and magnitude of the paludification process. However, as both drivers operate simultaneously on forest stands, their respective effects are difficult to tease apart.

Fire is an important process that may return paludified sites to their high productivity status by consuming accumulated soil organic layers (Kimmins 1996). Like fire, forest management can modify the successional trajectory of forests and, when used appropriately, could possibly set back the paludification process and restore the productivity of paludified sites (Lavoie et al. 2005). Planning treatments on sites undergoing paludification requires an a priori estimate of their potential for recovery of forest productivity. To do this, we need a method that can be used to quantify the relative importance of succession and topography on paludification, and to evaluate the potential recovery of site productivity at the site and landscape levels.

The goals of this study were therefore (1) to develop empirical models that would allow quantification of both the current state of paludification and the potential degree of paludification following disturbance of the organic layer, (2) to determine whether the degree of paludification could be mapped in forest stands across the James Bay Lowlands, and (3) to relate the degree of paludification to tree productivity. In this study, soil organic layer depth was used as an estimator of the degree of paludification. We hypothesized that initial (postfire) rates of soil organic matter accumulation would decrease with increasing slope and that soil organic layer thickness of sites with different slopes would converge in the long run in the absence of disturbances.

Methods

Study area

The study area (49°00′–50°30′N, 78°30′–79°30′W) is located in the boreal zone of western Quebec, (Canada). This part of the Precambrian Shield is covered with glaciolacustrine clays that have been reworked by glacial surges, resulting in a relatively compact deposit composed of clay and gravel that is called the Cochrane Till (Veillette 1994). The mostly flat region (mean altitude = 250 m a.s.l.) shows three major soil types, Luvisols, Gleysols, and Organic soils (Soil Classification Working Group 1998), which reflect the variable thickness of the organic layer (about 10 to >200 cm). The dominant forest types are black spruce (*Picea mariana* (Mill.) BSP) – feathermoss and black spruce – *Sphagnum*, with an understory dominated by ericaceous shrubs (*Rhododendron groenlandicum*, *Kalmia angustifolia*, *Vaccinium* spp). Jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) also occur in pure or mixed stands, and secondary tree species include balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), and tamarack (*Larix laricina* (DuRoi) K. Koch) (Gauthier et al. 2000). The region's mean annual temperature is –0.7 °C (mean temperatures of January and July are –20.0 °C and 16.1 °C, respectively), and annual precipitation is 905 mm, 35% of which falls during the growing season (Matagami weather station (49°46′N, 77°49′W), Environment Canada 2006). Forest harvesting has taken place since the 1970s on the most productive sites.

Site selection

Our intent was to perform field sampling across a broad range of slopes and postfire stand ages. We first selected stands of different postfire ages using a stand initiation map (map of time elapsed since the last stand-replacing fire) developed earlier for the study area (Bergeron et al. 2004) and refined with radiocarbon dating (Lecomte et al. 2006*b*). Postfire stand age was determined from fire-scar dating, tree-ring dating (stump height) of synchronously established cohorts of early-successional tree species (live or dead dominant trees), and radiocarbon dating of soil charcoals (for older fires, when the postfire cohort was missing). Each stand had to be dominated by black spruce, show no sign of anthropogenic disturbance, and be within 2 km of a road. We then systematically distributed sampling plots within

Table 1. Distribution of plots by slope class, stand, and postfire stand age.

Postfire stand age (years)	No. stands sampled	Slope class (%)															Total no. of plots
		0	1	2	3	4	5	6	7	8	9	10	11	12	14	16	
90	2	4	15	22	10	9	6		2	1			1		1	1	72
99	2		9	19	7	1	1										37
173	2	1	15	17	6		1										40
179	2	1	9	18	8	3		1	1			1		1	1		44
229	1		6	9	1		1										17
329	1			4	4	2											10
369	1			1	4	2	1										8
714	1	1	9	14	6	1					1						32
	Total no. of plots	7	63	104	46	18	10	1	3	1	1	1	1	1	2	1	260

each stand on a 100 m grid using a geographic information system with the objective of capturing within-stand topographic variability. In total, we sampled 281 plots (our experimental unit) ranging in slope from 0% to 16%, hierarchically nested in 12 stands ranging in postfire age from 90 to 714 years (Table 1).

Field measurements and sample processing

During the summer of 2004, the sampling plots were located in the field using a GPS unit. From the center of each plot, slope was measured in the four cardinal directions over a 15 m measurement base using a clinometer mounted on a tripod. Tree basal area was measured in three prism points (factor 2, metric): one in the plot center and two more at 15 m on the east and west sides of the plot center. Ground cover (presence, 5%, 10%, 20%, etc.) of major bryophyte taxa (*Sphagnum* spp., feathermosses, lichens) and deadwood was estimated in four 1 m^2 quadrats located 10 m from the plot center in the four cardinal directions. Total depth of soil organic layer was also measured in the four quadrats using a soil auger.

Statistical analyses

Preanalysis of the data revealed a few anomalies with organic layer depth measurements, corresponding to plots where estimation of soil organic layer thickness had been constrained either by frozen ground or by the length of the soil auger in cases of very deep layers. These plots were deleted from the data set. After these modifications, our final data set contained 260 of the original 281 plots (Table 1).

To address our first study objective, we performed a regression analysis to quantify the effect of postfire stand age and topography on the accumulation rate of the organic layer. The effect of postfire stand age (A) and slope (S) and their interaction on soil organic layer depth (D) was tested using a mixed model with stand as a random effect (PROC MIXED, SAS Institute Inc. 2003). The explanatory variable S was defined as the steepest of the four slopes measured at each plot.

To address our second study objective, we related soil organic layer depth (D) to variables that could possibly be detected and mapped through multispectral satellite imagery: plot basal area (G; mean of three prism points) and percent cover of *Sphagnum* mosses (C_{SPH}; mean of four quadrats). The analysis also included the interaction of these two variables, and stand as a random effect. Basal area and *Sphagnum* cover have been shown to vary considerably with the degree of paludification (Fenton et al. 2005, Lecomte et al. 2005), and as surface properties, they can potentially be estimated via remote sensing (Bubier et al. 1997; Hyyppä et al. 2000). The variables A, D, and C_{SPH} were log transformed (base 10 for A and D; $\log(n + 1)$ for C_{SPH}, which had null values) to meet the assumptions of homogeneity and normality of the residuals. For both regressions, model selection was based on the lowest corrected Akaike information criterion value (Burnham and Anderson 2002).

Paludification–productivity relationship

To quantify the relationship between the degree of paludification and tree productivity, we reanalyzed site index and soil organic layer thickness data previously published in Simard et al. (2007). The data were sampled in 22 black spruce stands ranging in postfire age from 52 to 2355 years, all located in the study area. In each stand, we selected three black spruce trees of the dominant cohort and, when present, three additional trees of both the second and third height cohort. We selected the second and third cohorts based on the vertical distribution of trees in the canopy and on the diameter at breast height structure of the stands. The cohorts had to be separated by a vertical distance of at least 5 m, and to avoid sampling suppressed trees, all sampled trees (n = 147) had to be growing in full light and be free of any connection with a living genet.

During the summers of 1999 to 2001, two measurements of soil organic layer depth were taken in opposite directions at 10 cm from the base of each tree. Stem analyses were performed on each selected tree by sampling cross sections at 0 m, 0.4 m, 1 m, and every 1 m thereafter. Cross sections were finely sanded and cross-dated under 40× magnification. For each tree, we calculated site index as the height growth during 50 years of free (i.e., unsuppressed) growth, using stem height increment patterns to define major inflexions in the age–height growth curve indicating growth release (Curtis 1964).

For the current work, we related site index to mean organic layer depth at the tree level using reduced major axis regression on log-transformed variables (Sokal and Rohlf 1995). Only trees belonging to the youngest cohort were kept for the analysis (total n = 64 trees) because site index of young trees is more representative of current growing conditions (current organic layer depth measured in the field) than is site index of older trees. Even then, site index in this data set is slightly overestimated in relation to organic layer depth, because it integrates growing conditions of the past 50 years during which the organic layer was thinner.

Results

Paludification dynamics: effect of postfire stand age and slope

Variability in soil organic layer depth across the 260 plots was best explained by both postfire stand age and slope (Table 2). Rates of organic matter accumulation were highest on flatter sites and diminished with increasing slope (Fig. 1). Soil organic layer depth (D, cm) can be predicted with the following equation:

$$[1]\qquad \log(D) = 0.3728\ \log(A) - 0.02089S + 0.8510$$

where S (%) is the maximum of four plot-level slope measurements, and A (years) is postfire stand age.

Predicting organic layer depth

Plot basal area ranged from 10 to 60 m^2/ha, with an average within-plot standard deviation of 4.6 m^2/ha (mean coefficient of variation = 19%). Basal area and *Sphagnum* moss cover together were the best predictors of organic layer depth (Table 3), with deep organic soils associated with low basal area and high *Sphagnum* cover. The depth of the organic layer, our estimator of paludification status, can thus be expressed as a linear combination of *Sphagnum* cover (C_{SPH}, %) and basal area (G, m^2/ha) with the following equation:

$$[2]\qquad \log(D) = 0.09740\ \log(C_{SPH} + 1) - 0.00473G + 1.6336$$

Paludification and site productivity

Site index was negatively related to soil organic layer depth, which explained 57% of the variance in site index (Fig. 2). The shape of the relationship suggests that the greatest decline in site index occurs when the first 20 to 40 cm of organic soil accumulate: the regression predicts a 50% drop in site index, from 14 to 7 m, with an increase in organic layer depth from 15 to 30 cm.

Discussion

We have defined two models through which we can estimate soil organic layer depth, used as a proxy for the degree of paludification, and its increase over time in the absence of fire. The dynamic portrait provided by eq. 1 makes possible the estimation of soil organic layer depth as a function of slope and postfire stand age and thus the determination of a postfire stand's possible trajectory from its initial conditions to its various degrees of paludification (Fig. 1). This statistical model supports our hypothesis of slower organic matter accumulation on steeper slopes but does not support the hypothesis that all stands, irrespective of slope, converge to a high degree of paludification. The work nevertheless shows that organic layer accumulation is not confined to flat sites and that successional dynamics in the boreal forest of northwestern Quebec drive all black spruce dominated stands towards greater degrees of paludification.

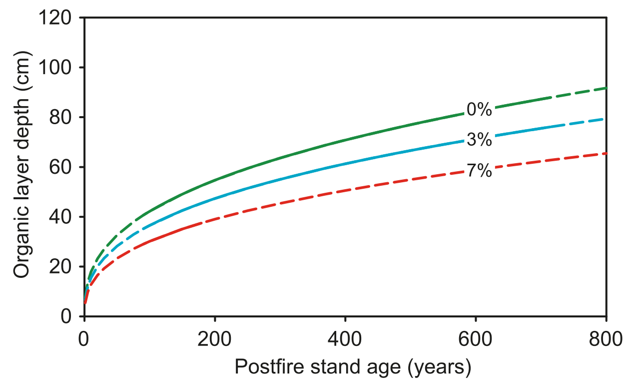
Table 2. Results of the mixed linear model relating soil organic layer depth to postfire stand age (A) and slope (S).

Covariance parameters					
	Ratio	Estimate	SE	Z	P
Stand	1.3268	0.02263	0.01057	2.14	0.0161
Fixed effects					
	ddf*	Estimate	SE	F	P
log(A)	9.89	0.3728	0.1663	5.03	0.0491
S	252	–0.02089	0.004279	23.84	<0.0001
log(A) × S	—	—	—	—	ns

Note: n = 260; SE, standard error; ddf, denominator degrees of freedom; ns, nonsignificant.

*Numerator degrees of freedom are all equal to 1.

Fig. 1. Change in soil organic layer depth with postfire stand age in stands of different slopes (identified above each regression line). Broken lines indicate range of extrapolation.



Equation 2 enables us to quantitatively define the current degree of paludification of a site (i.e., its organic layer depth) based on *Sphagnum* cover and tree basal area. Previous research has shown that the depth of organic layer consumption varies enormously among fires and within a fire (Lecomte et al. 2005, 2006*a*), and including such initial conditions in our analysis would significantly improve the predictive capacity of eq. 1. However, burn severity is not easily obtained in the field, nor is it available spatially. Similarly, the identification of *Sphagnum* species could increase prediction of organic layer depth in the field because different species are associated with different soil moisture levels (Fenton and Bergeron 2006), but again this information cannot be obtained spatially for large areas (10^3–10^4 km^2). By contrast, use of two easily observable variables in eq. 2 offers two advantages. The first is by providing a quick method of evaluating the on-site degree of paludification through easily measurable variables. The second is that, if these two variables can be related to multispectral signatures from satellite imagery, it may then be possible to map the current paludification status of black spruce stands across the James Bay Lowlands.

Figure 1 shows that in this area of low permeability surface deposits and low slopes postfire stand age drives the paludification process, while topography modulates both the degree of initial postfire paludification as well as rates of the

Table 3. Results of the mixed linear model relating soil organic layer depth to basal area (*G*) and *Sphagnum* percent cover (C_{SPH}).

Covariance parameters					
	Ratio	Estimate	SE	*Z*	*P*
Stand	1.1764	0.01624	0.007378	2.20	0.0139
Fixed effects					
	ddf*	Estimate	SE	*F*	*P*
G	254	–0.00473	0.000975	23.58	<0.0001
log(C_{SPH}+1)	254	0.09740	0.01475	43.64	<0.0001
$G \times$ log(C_{SPH}+1)	—	—	—	—	ns

Note: n = 260; SE, standard error; ddf, denominator degrees of freedom; ns, nonsignificant.

*Numerator degrees of freedom are all equal to 1.

Fig. 2. Relationship between soil organic layer depth and site index (n = 64; R^2 = 0.57; F = 81.0; P < 0.0001). Shaded area represents 95% confidence limits of the predicted mean.

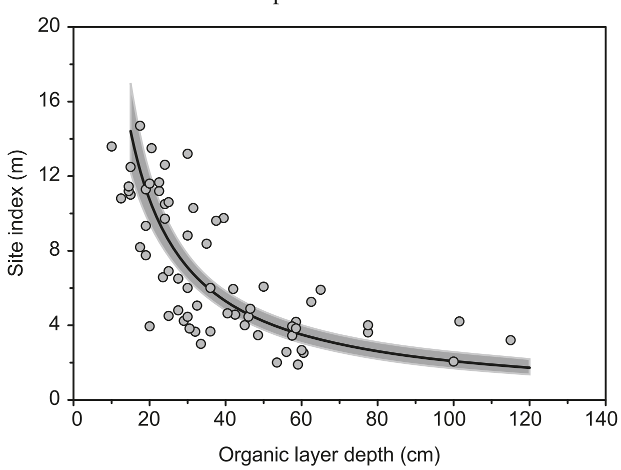
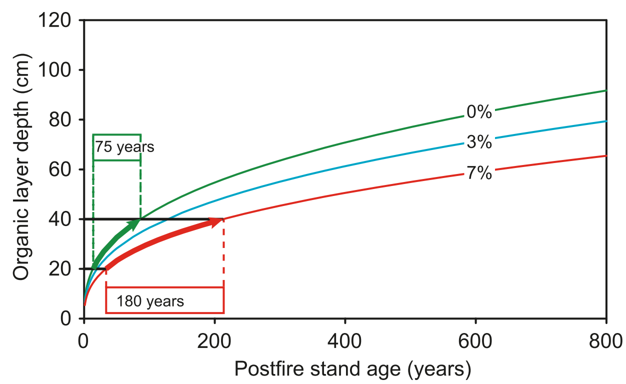


Fig. 3. Example of treatment effect duration (horizontal bars) on a 0% slope site and a 7% slope site. The hypothetical treatment reduces soil organic layer depth to 20 cm, and treatment effect is assumed to end when the subsequent accumulation of organic matter pushes this depth back to 40 cm. Regression lines are the same as in Fig. 1.



paludification process (Table 2, Fig. 1). Young stands growing on flat sites have thick organic layers (about 33 cm at 50 years) and higher initial rates of organic layer accumulation compared with young stands growing on even modestly sloping sites (3% to 7%, which have, respectively, 28 and 23 cm of organic soil at 50 years). This apparently small difference in organic layer depth translates into large differences in productivity because of the nonlinear relationship between soil organic layer depth and site index (Fig. 2). Because black spruce roots are confined to the top 20–30 cm of the soil, the sharp drop in tree productivity associated with the accumulation of the first 20–40 cm of organic matter corresponds to the transition from a state where tree roots are located in the nutrient-rich mineral soil to a state where most roots are located in the organic layer, where nutrient availability is low (Simard et al. 2007).

Predicting potential productivity gains

The difference between the current organic layer depth of an older stand and its initial (at 50–100 years) organic layer depth represents the potential recovery of a site if the effect of succession is reversed through fire or forest management. With the assumption that a reduction of the organic layer would translate to increased forest productivity (Fig. 2), the model suggests that for stands sharing a similar current soil organic layer depth (e.g., current status = 40 cm), stands growing on steeper slopes have a greater recovery potential (e.g., organic layer depth at 50 years on 7% slopes = 23 cm) than stands growing on flat terrain (e.g., organic layer depth at 50 years on 0% slopes = 33 cm). The model also suggests that a soil organic layer depth reduced to 20 cm following fire or scarification would take 180 years to return to a depth of 40 cm for the 7% slope site, but only 75 years for the flat site (Fig. 3). A very small difference in slope, in the order of 3% to 7%, can therefore make a large difference in the maintenance of productivity following treatment.

Forest management through emulation of natural disturbance dynamics is receiving increasing attention in both academia and industry (Attiwill 1994; Perera et al. 2004). The two contrasting trajectories on flat versus sloping sites outlined above provide a basis for managing soil organic layer and forest productivity in the black spruce forests of the Clay Belt of Quebec and Ontario, where forest succession and smoldering fires act antagonistically to move forest stands up or down the productivity gradient. Management strategies for the maintenance or improvement of forest productivity in this area should focus on sloping sites. The lower recovery potential and shorter duration of treatment effects on flat sites provide few ecological or economic motives to manage soils on these sites. The equations developed in this study can be used to estimate potential productivity gains in currently unproductive stands, assuming that the removal or disturbance of the organic layer emulates the effect of fire on the degree of paludification. To quantify the recovery potential of a particular stand, all that is needed is to calculate the difference between its current degree of paludification (soil organic layer depth measured in the field or estimated with *Sphagnum* cover and basal area using eq. 2) and the potential degree of paludification of a young stand (e.g., 50–100 years) on the same slope (using eq. 1). The calculated reduction in organic layer depth can then be expressed in terms of increased potential productivity using the site index – organic layer depth relationship (Fig. 2). Potential productivity gains are greater on steeper slopes and lower on flat sites (Fig. 3).

One important assumption in the methodology to quantify potential recovery following human intervention is that we can indeed emulate site-level effects of natural fires on forest productivity. Disking and trenching are site preparation methodologies with well-documented beneficial effects on soil microenvironment and seedling establishment and growth (Sutton 1993; Lavoie et al. 2005). However, it is not clear at this point how the effectiveness of these methods varies with increased depth of soil organic layer. Prescribed burns may also be used to restore productivity, but more work is required to determine how to best use them for restoring productivity on sites undergoing paludification.

Conclusion

Fire frequency in our study area has decreased over the last centuries (Bergeron et al. 2004) and could potentially continue to decrease in the future (Flannigan et al. 1998, but see Flannigan et al. 2005). Such a trend may gradually bring more forested areas in the region toward a greater degree of paludification and lower productivity. In addition, current forest management practices in the area are designed to minimize soil disturbance, in effect promoting growth of *Sphagnum* moss. Protection of soils through careful logging practices maintains sites on a path leading towards a low-productivity paludified status. Maintenance of forest productivity on these sites may require severe disturbance of organic layers, similar to the effects of high-severity fires (Lavoie et al. 2005). The methodology developed here could be useful in selecting sites where soil management techniques could be applied for maintaining or increasing forest productivity.

Acknowledgements

We thank P. Leblanc and T. Jones for field assistance and M. Bernier-Cardou (Canadian Forest Service) and C. Ané (University of Wisconsin - Madison) for statistical advice. This study was funded by Canada Economic Development, Regional Strategic Initiative - Abitibi-Témiscamingue (RSI-Abitibi) and the ministère des Ressources naturelles et de la Faune du Québec (Volet 1). Additional funding was provided through a postdoctoral fellowship to L. Guérine by the NSERC–UQAT–UQAM Industrial Chair in Sustainable Forest Management. We gratefully acknowledge the support of our industrial partner Tembec.

References

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. **63**: 247–300. doi:10.1016/0378-1127(94)90114-7.

Bergeron, Y., Gauthier, S., Flannigan, M.D., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology, **85**: 1916–1932. doi:10.1890/02-0716.

Bond-Lamberty, B., Wang, C., and Gower, S.T. 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Change Biol. **10**: 473–487. doi:10.1111/j.1529-8817.2003.0742.x.

Bubier, J.L., Rock, B.N., and Crill, P.M. 1997. Spectral reflectance measurements of boreal wetland and forest mosses. J. Geophys. Res. **102**: 29 483 – 29 494. doi:10.1029/97JD02316.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Curtis, R.O. 1964. A stem-analysis approach to site-index curves. For. Sci. **10**: 241–256.

Environment Canada. 2006. Canadian Climate Normals 1971–2000. [Online.] Available from www.climate.weatheroffice.ec.gc.ca [accessed 11 March 2006].

Fenton, N., and Bergeron, Y. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. J. Veg. Sci. **17**: 65–76. doi:10.1658/1100-9233(2006)017[0065:FSIABB]2.0.CO;2.

Fenton, N., Lecomte, N., Légaré, S., and Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For. Ecol. Manage. **213**: 151–159. doi:10.1016/j.foreco.2005.03.017.

Fenton, N., Légaré, S., Bergeron, Y., and Paré, D. 2006. Soil oxygen within boreal forests across an age gradient. Can. J. Soil Sci. **86**: 1–9.

Flannigan, M.D., Bergeron, Y., Engelmark, O., and Wotton, B.M. 1998. Future wildfire in circumboreal forests in relation to global warming. J. Veg. Sci. **9**: 469–476. doi:10.2307/3237261.

Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., and Stocks, B.J. 2005. Future area burned in Canada. Clim. Change, **72**: 1–16. doi:10.1007/s10584-005-5935-y.

Gauthier, S., De Grandpré, L., and Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. **11**: 781–790. doi:10.2307/3236548.

Grant, R.F. 2004. Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. Tree Physiol. **24**: 1–18. PMID:14652210.

Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noel, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., and Swift, L. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can. J. For. Res. **37**: 1012–1023. doi:10.1139/X06-245.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., and De Grandpré, L. 2005. Structural development following fire in black spruce boreal forest. For. Ecol. Manage. **206**: 293–306. doi:10.1016/j.foreco.2004.11.008.

Heinselman, M.L. 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz region, Minnesota. Ecol. Monogr. **33**: 327–374. doi:10.2307/1950750.

Hyyppä, J., Hyyppä, H., Inkinen, M., Engdahl, M., Linko, S., and Zhu, Y.-H. 2000. Accuracy comparison of various remote sensing data sources in the retrieval of forest stand attributes. For. Ecol. Manage. **128**: 109–120. doi:10.1016/S0378-1127(99)00278-9.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Am. J. **60**: 1643–1654.

Lavoie, M., Paré, D., Fenton, N., Groot, A., and Taylor, K. 2005. Paludification and management of forested peatlands in Canada: a literature review. Environ. Rev. **13**: 21–50. doi:10.1139/a05-006.

Lavoie, M., Harper, K.A., Paré, D., and Bergeron, Y. 2007. Spatial pattern in the organic layer and tree growth: a case study from regenerating *Picea mariana* stands prone to paludification. J. Veg. Sci. **18**: 213–222. doi:10.1658/1100-9233(2007)18[213:SPITOL]2.0.CO;2.

Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H., and Richard, P.J.H. 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. J. Veg. Sci. **16**: 665–674. doi:10.1658/1100-9233(2005)016[0665:EOFSAI]2.0.CO;2.

Lecomte, N., Simard, M., and Bergeron, Y. 2006*a*. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience, **13**: 152–163. doi:10.2980/i1195-6860-13-2-152.1.

Lecomte, N., Simard, M., Fenton, N., and Bergeron, Y. 2006*b*. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems (N. Y., Print), **9**: 1215–1230. doi:10.1007/s10021-004-0168-x.

Paavilainen, E., and Päivänen, J. (*Editors*). 1995. Peatland forestry: ecology and principles. Springer-Verlag, Berlin.

Payette, S., and Rochefort, L. (*Editors*). 2001. Écologie des tourbières du Québec–Labrador. Les Presses de l'Université Laval, Québec, Que.

Perera, A.H., Buse, L.J., and Weber, M.G. (*Editors*). 2004. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York.

Prescott, C.E., Maynard, D.G., and Laiho, R. 2000. Humus in northern forests: friend or foe? For. Ecol. Manage. **133**: 23–36. doi:10.1016/S0378-1127(99)00295-9.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., and Senock, R.S. 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. **74**: 393–414. doi:10.1890/03-4037.

SAS Institute Inc. 2003. SAS/STAT Statistical Software, v. 9.1. SAS Publishing, Cary, N.C.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**: 1619–1637. doi:10.1890/06-1795.1. PMID:17913128.

Soil Classification Working Group. 1998. The Canadian System of Soil Classification. 3rd ed. Agriculture and Agri-Food Canada, Ottawa, Ont.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. Freeman, New York.

Sutton, R.F. 1993. Mounding site preparation: a review of European and North American experience. New For. **7**: 151–192.

Van Cleve, K., Dyrness, C.T., Viereck, L.A., Fox, J., Chapin, F.S., III, and Oechel, W.C. 1983*a*. Taiga ecosystems in interior Alaska. Bioscience, **33**: 39–44. doi:10.2307/1309243.

Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983*b*. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. **13**: 747–766. doi:10.1139/x83-105.

Veillette, J.J. 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Quat. Sci. Rev. **13**: 945–971. doi:10.1016/0277-3791(94)90010-8.

Wang, C., Bond-Lamberty, B., and Gower, S.T. 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob. Change Biol. **9**: 1066–1079. doi:10.1046/j.1365-2486.2003.00645.x.