

ARTICLE

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Exploring forest productivity at an early age after fire: a case study at the northern limit of commercial forests in Quebec¹

Rik Van Bogaert, Sylvie Gauthier, Frédéric Raulier, Jean-Pierre Saucier, Dominique Boucher, André Robitaille, and Yves Bergeron

> Abstract: Interest in northern forests is increasing worldwide for both timber production and climate change mitigation. Studies exploring forest productivity at an early age after fire and its determining factors are greatly needed. We studied forest productivity, defined as the combined quality of stocking and growth, of 116 10- to 30-year-old postfire sites. The sites were spread over a 90 000 km² area north of the Quebec commercial forestry limit and were dominated by Picea mariana (Mill.) B.S.P. and Pinus banksiana Lamb. Seventy-two percent of our sites were classified as unproductive, mainly because of poor growth. Because growth was mostly determined by climatic factors, afforestation alone may not be sufficient to increase stand productivity in our study area. In addition, our results suggest that P. banksiana on dry sites may be less resilient to fire than previously thought, presumably because of poor site quality and climate. Overall, this is one of the first studies to explore productivity issues at an early age in natural northern forests, and the analysis scheme that defines forest productivity as the result of growth and stocking could provide a useful tool to identify similar issues elsewhere.

> Key words: northern natural forests, young stands, productivity, stocking, growth, wildfire, jack pine, black spruce, boreal forest.

Résumé : Avec l'intérêt croissant à travers le monde envers les forêts du nord tant pour la production de fibre que pour l'atténuation des changements climatiques, des travaux explorant la productivité forestière peu après le feu et les facteurs qui la déterminent sont requis. Nous avons étudié la productivité des forêts, définie en termes de qualité du coefficient de distribution (stocking) et de la croissance, dans 116 sites de 10-30 années après feu distribués dans une zone de 90 000 km² au nord de la limite d'attribution des forêts commerciales du Québec et dominé par Picea mariana (Mill.) B.S.P. et Pinus banksiana Lamb. Soixante-douze pour cent des sites ont été classés comme improductifs, principalement en raison de la faible croissance. Puisque la croissance est fortement liée à des facteurs climatiques, le boisement seul ne serait pas suffisant pour augmenter la productivité des peuplements dans notre zone d'étude. En outre, nos résultats montrent que P. banksiana sur des sites secs pourrait être moins résilient au feu qu'on ne le pensait, probablement à cause de mauvaises conditions de sites et du climat. Finalement, notre étude est l'une des premières à explorer les enjeux de productivité en bas âge dans les forêts naturelles du nord. Le schéma d'analyse proposé, en définissant la productivité des peuplements sur la base de la croissance et du coefficient de distribution, pourrait fournir un outil intéressant pour évaluer des problèmes similaires de manière précoce dans d'autres systèmes.

Mots-clés : forêts naturelles nordiques, peuplements jeunes, productivité, stocking, croissance, feux, pin gris, épinette noire, forêt boréale.

Introduction

In our current world, growing economic needs often meet ecological challenges. One such challenge is to cover increasing demands for wood without causing large-scale deforestation that may lead to further accelerating climate change (Intergovernmental Panel on Climate Change (IPCC) 2007; Kurz et al. 2013). The vast and largely unexplored natural resource of northern forests could bring economic benefits through timber production and ecological (climatic) benefits, if forest management could succeed in increasing northern forest productivity (in terms of both tree growth and tree density by planting), as these forest areas could store higher amounts of carbon (Lindner and Karjalainen 2007; Kurbanov et al. 2007; Lemprière et al. 2013). Worldwide, policy makers and communities have been discussing the possibility of afforestation of northern open woodlands or the possibility of extending forest management at northern latitudes (Gunnarsson 1999; Juday et al. 2005; Kurbanov et al. 2007; Nordic Council 2010; Lemprière et al. 2013). However, previous studies have pointed out that several factors (e.g., climate, fire recurrence, herbivory, soil constraints, and pollution) related to forest productivity may limit the potential for such expansion of forest management activities (Vlassova 2002; Eysteinsson 2009; Van Bogaert et al. 2011; Mansuy et al. 2013; Gauthier et al. 2014).

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R. Van Bogaert, S. Gauthier, and D. Boucher. Natural Resources Canada, Canadian Forest Service, 1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.

F. Raulier. Département des sciences du bois et de la forêt, Faculté de foresterie, de géographie et de géomatique, 2405, rue de la Terrasse, Pavillon Abitibi-Price, bureau 2145-B, Université Laval, Québec, QC G1V 0A6, Canada.

I.-P. Saucier and A. Robitaille. Ministère des Forêts, de la Faune et des Parcs du Ouébec. Direction de la recherche forestière, 2700 rue Einstein, Ouébec, OC G1P 3W8, Canada

Y. Bergeron. Chaire industrielle CRSNG UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Temiscamingue, 445 boul de l'université Rouyn Noranda, QC J9X 5E4, Canada.

Corresponding author: Rik Van Bogaert (e-mail: rikvanbogaert@gmail.com).

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Issues of forest productivity are fundamentally linked to the limitations in the availability of radiation, temperature, and water (Landsberg and Sands 2011). For instance, forest productivity decreases with latitude and altitude as climate deteriorates (Körner and Paulsen 2004; Kindermann et al. 2008) and black spruce (*Picea mariana* (Mill.) B.S.P.) forests gradually transform from a closed-crown forest type in the south into a lichen open woodland type towards the north (Callaghan et al. 2002; Beaudoin et al. 2014). In addition to climatic factors, fire, being the primary disturbance factor in most of the northern circumboreal forest (Johnson 1996), is an important factor driving regional differences in forest productivity (Mack et al. 2008; Gauthier et al. 2014). Further, at more local scales, forest productivity is often limited by site conditions (McMurtrie et al. 1990; Tanner et al. 1998).

Basically, in the absence of repeated disturbances, forest productivity is related to the capacity of a site to produce biomass in a certain amount of time (Ryan et al. 1997; Skovsgaard and Vanclay 2008) and can be considered as the result of two critical factors: (i) tree density (or stocking) and (ii) individual tree growth. Forest managers use this concept to control stand density to obtain the required tree sizes at the moment of harvest (Assmann 1970; Drew and Flewelling 1979): for an equivalent timber volume production, a low tree density is related to a higher mean tree volume, whereas a low mean tree volume is related to a higher tree density. This concept remains approximately valid while stand density remains above a certain critical value related to the tree size (full stocking, Drew and Flewelling 1979), minimally above crown closure (full site occupancy, Krajicek et al. 1961). Moreover, in terms of stand yield and (or) stem size, some thresholds are required to consider a stand as being productive enough to be incorporated into the timber production area. Such thresholds are not absolute and are related to the profitability of harvesting operations and to the capacities of the wood-processing facilities (e.g., Duerr et al. 1956).

Studies on the productivity of young postfire natural forests (first ca. <30 years since the last fire) are rare. A better understanding of factors determining forest productivity at an early stage is required, particularly at higher latitudes, as trees need a significantly longer time period to reach a minimum size to be considered as saplings (tree height > 100 or 130 cm). Studies by Mallik (2003) and Ruel et al. (2004) and a summarizing paper by Rheault (2013) have shown that, at higher latitudes in eastern Canada (>48°N), naturally regenerating black spruce take, on average, 25 years to reach the sapling stage of 100 cm. Omitting this time period likely has important consequences for expected harvest volumes (Sims et al. 1990; Mailly and Gaudreault 2005): forest productivity is usually rated with site index (SI) curves that are based on measurements taken at a stem height of 100 or 130 cm. Therefore, if a SI curve suggests a total period of ca. 50 years to reach a given dominant height equivalent to the SI, it actually corresponds to a period longer than 75 years. Studying initial productivity of naturally regenerating sites may thus be a key to successful forest management at northern latitudes.

In search of the climatic, edaphic, and site history related factors that could possibly explain a forest area's productivity, we will use the productivity square illustrated in Fig. 1. Because this study focuses on young stands, tree density is replaced by stocking as it is likely a better indication of regeneration success and future stand productivity (Feng et al. 2006). Following our definition of productivity, we can logically distinguish four productivity classes: "productive" in which both stocking and growth exceed a predefined threshold, "unproductive because of bad stocking", "unproductive because of bad growth", and "very unproductive because of both bad stocking and growth" (Fig. 1). This simple concept could facilitate the identification of productive natural forest areas and especially contribute to finding the causes of nonproductive areas. For instance, if most unproductive areas are having growth problems in addition to stocking deficiencies, pro**Fig. 1.** Productivity square concept. Productivity was defined as a product of stocking and growth. Therefore, we can distinguish four productivity classes, one productive class (P = productive, both stocking and growth are good) and three unproductive classes: BS = bad stocking, but good growth; BG = bad growth, but good stocking; and BB = bad stocking and bad growth.



ductivity may still be insufficient even following major afforestation efforts, whereas areas with good growth but poor stocking are likely to benefit from plantation. Moreover, understanding which factors are involved in growth or stocking limitation will further enhance our ability to take appropriate management actions.

In Quebec, the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) recently initiated a major project to better quantify some criteria and thresholds that had been used to delimit the northern timber allocation limit that was set in 2002. This study makes up part of this project and will explore how to define productivity thresholds for young natural postfire sites situated just north of this boundary. Specifically, this study aims to (*i*) classify postfire sites into productivity classes using the productivity square to identify site productivity issues and (*ii*) identify the factors (climatic, edaphic, and site history related) that determine a site's classification in the productivity square. By doing this, we will also contribute to closing the gap in research on productivity of commercial and young stands.

Material and methods

Study area

The study area was located in the boreal forest area of Quebec, just north of the current (2002) northern timber allocation limit. The area stretched from 50.9°N to 53.0°N and from 72.5°W to 78.0°W, comprising ca. 90 000 km², roughly the size of Portugal or Maine (USA) (Fig. 2). More specifically, the area corresponds to the northwestern part of the black spruce feather moss domain, an area — despite its highly variable forest density — defined as a closed-crown forest type compared with the open woodland lichen type domain to the north.

The climate is subarctic, and mean annual temperature for the normal period 1971–2000 ranges from -1.0 °C in the south to -4.0 °C in the northeast (BioSIM 9; Régnière and Saint-Amant 2008). Similarly, the number of growing degree days > 5 °C (hereafter DD) ranges from ca. 1200 in the south to ca. 700 in the northeast. However, the DD range for our study sites was smaller, ranging from ca. 1140 to ca. 890 (BioSIM 9). Following a west–east altitudinal gradient of ca. 100 m above sea level (a.s.l.) near James Bay in the west and ca. 550 m a.s.l. in the east, annual precipitation increases from ca. 700 to ca. 950 mm in the same direction (BioSIM 9; Régnière and Saint-Amant 2008). Organic soils prevail in the western part (76°W–78°W), whereas deep till deposits are

Fig. 2. The study area in northwestern meridional Quebec. The rectangle with broken line marks the 90 000 km² large area with 116 plots situated between 50.9°N and 53°N, north of the current boundary of commercial forestry. The darker lines to the right in the inset represent a dense network of 600 m a.s.l. isolines, indicating that the area east of Lake Mistassini is generally higher in elevation and often exceeds 600 m a.s.l. Note that the scale bars only serve as a reference as scale varies within both maps as a result of projection characteristics.



common in the more eastern part. Permafrost is rare, presumably covering <1% of the area (Natural Resources Canada 2009). The study area is currently characterized by one of the shortest fire cycles observed in eastern North America and varies predominantly between 44 and 94 years (calculated from 1972–2009 data; fig. 5 in Gauthier et al. 2015).

Even though black spruce is the dominant tree species in Quebec's boreal forest, jack pine (*Pinus banksiana* Lamb.) is commonly found in the central to western parts, particularly northwest of Lake Mistassini where the tree species is dominant or co-dominant in >46% of the stands (MRN 2014, appendix 6, map 46). In our study sites, jack pine was observed in 69 of the 116 sites (59.5%) after fire.

Sampling

In Quebec, the MFFP developed a northern forest inventory program that was carried out from 2005 to 2009. The program started with detailed forest mapping in 2005, followed by intensive data collecting via sample plots between 2006 and 2009. Despite limited road access, a total of 116 sites were selected over an area of 90 000 km² according to two criteria: (*i*) a fire had occurred 10 to 30 years before the time of sampling, i.e., a time period that should be sufficiently long for the completion of the establishment of all seedlings, and (*ii*) each a priori defined surface deposit-drainage class should be well represented in the sampling.

The sampling period of 2006–2009 implies that forest fires dated back to the period 1976–99 (however, 1996 was the most recent fire among all sites). For each site, a plot of 400 m² was established to characterize the forest and the site (Berger et al. 2008). Both stocking and growth data were recorded in 10 microplots (see below for details).

Response and predictor variables

To answer our research questions, we identified three main response variables: stocking, growth, and productivity. Stocking was preferred to tree density because for early-stage stands, it may be a better indicator of future stand productivity (Feng et al. 2006). To identify the presumed driving factors of these response variables, we also collected information on eight climatic, eight edaphic, and six site history related factors, hereafter called predictors (Table 1). The climatic predictors were latitude, mean summer temperature, mean summer precipitation, altitude, DD, aspect, drought code, and drought code relative to the superficial deposit type. Edaphic predictors were proportion of sand, silt, and clay in the mineral soil, drainage, slope, residual organic layer depth, mineral soil layer thickness, and stoniness. Site history related predictors were species dominance before fire, prefire stocking, stand age at the time of the last fire, time since fire, fire cycle length, and fire severity (Table 1). For details on how these variables were measured, see Appendix A.

Stocking

To determine stocking, a 40 m long transect line with 10 microplots along its length was established at each site. Each microplot had a radius of 1.69 m and a surface area of 9 m², a surface area considered large enough to record both pre- and post-fire stocking (Bella 1976; Bella and DeFranceschi 1978). Prefire stocking was estimated to explore its potential effect on postfire stocking. Therefore, the proportion of microplots with one or more individuals established before the last fire (i.e., dead or surviving trees) was determined. Similarly, a site's postfire stocking was defined as the proportion of microplots that contained one or more tree recruits >15 cm tall (Berger et al. 2008). To allow for a more accurate identification of postfire productivity issues, both total stocking (i.e., stocking irrespective of tree species) and species-specific stocking were determined for each site. However, as species-specific stocking of a site may be low because of factors not related to site productivity and fire impact, but rather because of local tree species competition or an already long-term low pres-

| Predictor | Definition | Data type | How obtained? | Data or analysis characteristics | Retained |
|-----------------------------|---|---------------------------|---|--|--|
| Climatic 1. LATIT | Latitude (in decimal degrees) | Numeric (continuous) | In situ | Collinear ($r_s = 0.91$) with growing degree days (DD) and SUM_TEMP ($r_s = 0.82$); however, sometimes found to be the only significant predictor in the model | Only in analyses where AIC _c justified its inclusion (see text) |
| 2. SUM_TEMP | Mean summer (June to August) temperature for the normal period 1970–2000 for each site | Numeric (continuous) | BioSIM (interpolation) | Collinear (r_s = 0.96) with growing degree days (DD) and LATIT (r_s = 0.82); in addition, tested in all analyses less significant than DD or LATIT | No |
| 3. SUM_PREC | Mean summer (June to August) precipitation for the normal period 1970–2000 for each site | Numeric (continuous) | BioSIM (interpolation) | Collinear with ALTTT ($r_s = 0.82$); ALTTT was preferred as predictor because it was determined in situ rather than modelled; also, ALTTT tested in all analyses more significant than SUM_PREC | No |
| 4. ALTIT | Altitude (m above sea level) | Numeric (continuous) | In situ | Collinear with SUM_PREC ($r_{\rm s} = 0.91$) | Yes |
| 5. DD | Absolute number of growing degree days (≥5 °C) during the growing season that is defined as the number of days between two periods of three consecutive days with a negative minimum daily temperature | Numeric (counts) | BioSIM (interpolation) | Collinear ($r_s = 0.91$) with latitude and SUM_TEMP ($r_s = 0.96$) but usually most significant predictor | Yes |
| 6. ASPECT | Three classes: north, flat, and south | Numeric (ordinal, counts) | In situ | Was not collinear with any of the other predictors | Yes |
| 7. DC | Canadian drought code: a numerical rating of water holding capacity and drying time for fuels at a soil depth of 10–20 cm implying a 52-day time lag (de Groot 1987) | Numeric (continuous) | BioSIM (interpolation) | Showed no relationship with any of the response variables and was no suppressor variable | No |
| 8. DC_soil_type | DC corrected for soil deposit type, i.e., DC value +1 SD if dry deposit and –1 SD if wet deposit (dry and wet defined according to Mansuy et al. 2011) | Numeric (continuous) | BioSIM (interpolation) and self-defined correction factor | Showed no relationship with any of the response variables and was no suppressor variable | No |
| E daphic 9. SAND | Proportion of sand in mineral soil sample | Numeric (%) | Sampled in situ (determined a posteriori in the lab) | Collinear with SILT and CLAY (r _s = 0.99); SAND was generally a more significant predictor than SILT or CLAY | Yes |
| 10. SILT | Proportion of silt in mineral soil sample | Numeric (%) | Sampled in situ (determined a posteriori in the lab) | Collinear with SAND and CLAY ($r_s = 0.99$) | No |
| 11. CLAY | Proportion of clay in mineral soil sample | Numeric (%) | Sampled in situ (determined a posteriori in the lab) | Collinear with SILT and SAND ($r_{\rm s}$ = 0.99) | No |

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| Table 1 (| concluded). |
|-----------|-------------|
|-----------|-------------|

| Predictor | Definition | Data type | How obtained? | Data or analysis characteristics | Retained |
|------------------------------------|--|--|--|--|-----------------------------------|
| 12. DRAIN | Drainage: determined in situ and classified as dry, mesic, or wet using standard criteria described in Berger et al. (2008) | Numeric (ordinal, counts) | In situ | Collinear with rOL ($r_s = 0.81$) but was consistently found to be a better model predictor | Yes |
| 13. SLOPE | Average incline for the site | Numeric (%) | In situ | Outliers (log-transformed) | Yes |
| 14. rOL | Residual soil organic layer depth (measured up to 99 cm; values ≥100 cm were rounded to 99 cm) | Numeric (continuous) | In situ | Collinear with DRAIN ($r_{\rm s}$ = 0.81) | No |
| 15. ML | Mineral soil layer thickness (1 mm accuracy; values ≥1 m were rounded to 999 mm) | Numeric (continuous) | In situ | Showed no relationship with any of the response variables and was no suppressor variable | No |
| 16. STONINESS | Estimated volume % of the soil sample extracted up to a depth of 70 cm with a precision of 10%. A stone was considered a rocky element with a minimal diameter of 2 mm (Berger et al. 2008) | Numeric (%) | Sampled in situ (determined a posteriori in the lab | Showed no relationship with any of the response variables and was no suppressor variable | No |
| Site history 17. PRE_DOM | Prefire species dominance: >50% of tree individuals in microplots | Categorical (0, black spruce; 1, jack pine) | In situ | Showed only obvious relationships with response variables that were species- specific such as "jack pine stocking" | No |
| 18. PRE_STK | Prefire stocking, computed species specifically and overall | Numeric (%) | In situ | Showed only a relationship with the response variables "total stocking" and "black spruce growth" | Yes, but only for two analyses |
| 19. STAND_AGE | Age of dominant (oldest) tree population before fire | Numeric (counts) | Dendrochronological analysis on in situ samples | Showed only a relationship with the response variable "black spruce growth"; outliers (log-transformed) | Yes, but only for one analysis |
| 20. TSF | Time since fire (in years) | Numeric (counts) | Cartographic analysis | Besides the relationship found between black spruce stocking and TSF, showed no relationship with any of the response variables and was no suppressor variable | No |
| 21. FIRE_CYCLE | The time that it takes for a study area to have burned completely (Gauthier et al. 2014) | Numeric (counts) | Cartographic analysis (Gauthier et al. 2015) | Showed no relationship with any of the response variables and was no suppressor variable | No |
| 22. FIRE_SEV | Crown fire severity: low (site has surviving trees) and high (no survivors) | Categorical (0, low; 1, high) | In situ | Showed only a relationship with the response variable "growth all" | Yes, but only for one analysis |

Note: Predictors are listed in three groups: climatic, edaphic, and site history related variables. All predictors were tested for collinearity and redundancy as some showed no relationship with any of the response variables and were therefore excluded from all analyses (cf. two rightmost columns). The abbreviation *r*_s stands for Spearman rank correlation.

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Table 2. Inclusion criteria and number of sites retained for the nine analyses.

| Condition | Black spruce $(n = 70)^a$ | Jack pine (n = 55) | Total (n = 116) |
|--|---------------------------|-----------------------|--------------------|
| Stocking ^b | | | |
| TSF > 20 years | 33 | NA | 38 |
| TSF \leq 20 years and postfire stocking (>15 cm) \geq 60% | 15 | NA | 33 |
| $17 \le \text{TSF} \le 20$ years and postfire stocking (>15 cm) < 60% | 4 | NA | 4 |
| TSF ≤ 20 years and only pine recorded as pre- or post-fire (>15 cm) stocking | NA | NA | 10 |
| Total | 52 | 55 | 85 |
| Growth ^c | | | |
| Stocking > 0 | (70–2) 68 | (55–5) 50 | (116–3) 113 |
| Productivity | | | |
| Criteria for stocking and growth are met | 52 | 50 | 85 |
| Sites that belonged to BS class (excluded) | 1 | 0 | 3 |
| Total | 51 | 50 | 82 |

Note: The total number of sites included in the final analyses is indicated in bold. For further details on the site inclusion criteria, refer to Appendix B. NA, not available.

^{*a*}The number of sites in parentheses represents the total number of black spruce dominated and jack pine dominated sites and total number of sites. As nine prefire sites were co-dominated, i.e., had an equal proportion of microplots dominated by either black spruce or jack pine, and were therefore considered both jack pine and black spruce sites, the total sum of spruce and pine sites does not add up to 116.

^bAs postfire stocking of young (≤ 20 years) black spruce sites could not be determined with certainty because <15 cm seedlings were not counted in the field, the table clarifies how we maximized the number of sites for stocking quality (good or bad) analyses.

Because growth quality could only be determined for sites for which postfire stocking was not zero, the number of sites in the actual analysis is generally lower than the total number of sites.

ence of the tree species in the specific area, species-specific postfire stocking was analyzed by including only those sites for which the species' prefire stocking was equal or higher compared with that of its competitor. Sites with a dominant or co-dominant prefire stocking of black spruce were called "black spruce sites," and similarly, sites for which prefire stocking of jack pine was equally high or higher than that of black spruce were called "jack pine sites". This stratification of sites according to prefire species dominance was also used for species-specific analyses of growth and productivity (see below). In total, we distinguished 68 black spruce sites and 55 jack pine sites (Table 2 and Appendix B).

For all types of stocking response (total, black spruce, and jack pine), we applied a 60% threshold to distinguish between bad (<60%) and good (\geq 60%) stocking. Previous studies have identified that a minimum of 600 to 700 stems-ha⁻¹ of commercial-sized stems (50–70 dm³) are needed for a site to return to a closed-canopy stand (Newton 1998; Sharma and Zhang 2007). Using 9 m² microplots and assuming one stem per microplot, a minimal tree density of 666 stems-ha⁻¹ corresponds best to a 60% stocking threshold, whereas a 50% or 70% threshold corresponds to 555 or 777 stems-ha⁻¹, respectively.

Because <15 cm seedlings were not recorded, postfire stocking may be dependent on the time since fire at the time of sampling. For black spruce, known for its slow initial growth (Zasada et al. 1987), we found a significant relationship between postfire stocking and time since fire (TSF) ($R^2 = 0.134$, P < 0.001; Appendix B). However, the correlation was no longer observed if we excluded all sites with a TSF \leq 20 years. Therefore, black spruce stocking sites were included in the analysis based on our ability to correctly classify them as bad or good (for more details, see Table 2 and Appendix B). This implied that young sites (TSF \leq 20 years) with bad (<60%) stocking were generally excluded from the analysis because it was unclear if low stocking was a result of poor regeneration or the fact that black spruce seedlings had not yet reached a height of 15 cm. As a result, postfire stocking estimates for this tree species could present a TSF effect (younger sites could have better stocking than older sites) that should be interpreted with caution. In contrast, for jack pine, known for its rapid juvenile growth, most seedlings, even those growing on poor soils, had already exceeded the height of 15 cm 10 to 30 years after fire. In fact, no relationship between TSF and postfire jack pine stocking was observed.

Growth

Defining a site's growth potential

In accordance with standard sampling procedures in Quebec, for each microplot, the different size classes that were observed among the postfire recruits were recorded (Berger et al. 2008). In total, six size classes were defined: two for seedlings (heights of 15–60 cm and >60 cm) and four for saplings (DBH classes with intervals of 2.0 cm starting with 1.0–2.9 cm). No tree-sized (DBH \geq 9.0 cm) size classes were defined because no postfire recruits of this size were observed. In addition to listing the different size classes observed in each microplot, the height of the tallest seed-ling was recorded with an accuracy of 1 cm.

To express the growth potential of a site as a single value, we computed the median of the largest size class observed in each microplot. If two size classes had an equal number of microplots (occurred in <10% of the sites), then the median size class for the site was considered the smallest size class. This rounding to the smallest size assured that 50% of the microplots had a recruit equally big or bigger than that value. If the median size class of a site was class 1 or 2 (reflecting seedlings), then the growth potential of a site was considered to be the exact height (accuracy of 1 cm) of the site's tallest recruit observed in that size class. However, if the median size class was a sapling, then the growth potential of the site was expressed as a DBH interval. To compare the growth potential between all sites, we had to convert the DBH intervals into tree height intervals. Therefore, we derived the 2.5% and 97.5% quartiles of tree height that corresponded to each of the four DBH classes. This was done using dominant or co-dominant postfire individuals from six fires of 10-30 years that were gathered by several of our lab co-workers in northern Quebec (north of 49°N). In total, 1343 spruce trees and 689 pine trees were used for the DBH-height conversions (Appendix C).

Classifying a site's growth potential into "good" or "bad"

For the three types of response variables (total, black spruce, and jack pine), postfire growth was classified as good or bad using the following method based on the SI system. The SI system is one of the oldest and most widely used methods of estimating wood volume production and relies on the assumption that there is a direct correlation between the height growth of a forest stand and its volume growth (Skovsgaard and Vanclay 2008). Because SI curves are typically used to evaluate the growth performance of adult (individuals that have well exceeded a height of 130 cm) stands, we had to construct a height-time reference curve for young black spruce and jack pine individuals (Fig. 3). To construct this curve, we used two reference points: (*i*) the time by which the individual should have reached 1.0 m height and (*ii*) the minimum SI used in forestry (7.5 for black spruce (Johnston 1977) and 9 for jack pine (Pothier and Savard 1998)).

The first reference points consider the initially slow growth of most seedlings in natural forests because of species-specific physiology (e.g., spruce invests first in establishing a wide root network (Sims et al. 1990)), edaphic factors, or competition with the already established ground-layer vegetation (Mallik 2003; Thiffault and Jobidon 2006). For black spruce, the cutoff value between good and bad growth was set at 25 years to reach 1.0 m, a value based on several studies in the greater boreal forest region of Quebec and Newfoundland (Mallik 2003; Ruel et al. 2004; Rheault 2013). For jack pine, the cutoff value was set at 11 years. This threshold was based on Vasiliauskas and Chen (2002), who showed that under postfire conditions and considering variability in site conditions, it takes a jack pine seedling, on average, 56% less time to reach 1.0 m height compared with black spruce. For the second reference points, we constructed the height-time curves corresponding to a SI of 7.5 for black spruce and 9 for jack pine, thereby considering species-specific growth trends (e.g., at an early age, pine already shows a rather linear height growth; Pothier and Savard 1998) (Fig. 3). For each TSF between 10 and 30 years, the tree height threshold was derived from the constructed curves (Table 3).

To compare the observed data with these curves, we plotted the growth potential of each site, represented by a height value or a height interval (derived from a DBH-height conversion; see Appendix C) as a function of time (TSF). For instance, a black spruce site was considered to have a good growth potential when it exceeded a height of 45 cm after 15 years and 149 cm after 30 years, compared with 147 and 316 cm, respectively, for jack pine (Table 3). For mixed sites containing both black spruce and jack pine recruits, the growth quality was considered good as soon as one of the two species met its species-specific threshold. Although DBH-height conversions were often needed to evaluate the growth potential of jack pine sites, Figure 3 illustrates that our classification is not sensitive to the conversion from height to DBH (most sites' height growth intervals were plotted substantially above or below the threshold curve), indicating that we have a robust classification of good and bad growth according to our definition settings.

Productivity

Postfire site productivity was considered to be the combined quality of stocking and growth (Fig. 1) and was determined for all sites (referred to as "total", irrespective of the dominant tree species), black spruce sites, and jack pine sites. Sites that met both stocking and growth thresholds were considered productive (class P), whereas all others were classified as unproductive as a result of bad stocking (class BS), bad growth (BG), or bad stocking and bad growth (BB). It should be noted that our thresholds were especially defined to minimize the chance of classifying productive sites as unproductive. Therefore, sites classified as unproductive are very unlikely to be productive, whereas sites classified as Fig. 3. Height-time curves developed as a reference for growth quality. These curves serve as a threshold line and divide (a) black spruce and (b) jack pine sites into good (points above curve) and bad (points below curve) growth. The two criteria on which the curve construction is based are indicated in the figure: (i) the time that it takes to reach 1.0 m and (ii) the site index, i.e., the height that the dominant trees of a site have reached after 50 years. All site values for which size was expressed in DBH were converted into corresponding height intervals according to Appendix C and are plotted in this figure as grey vertical bars. The mean value of the 95% CI is indicated by a thin horizontal line in the middle of the grey bar. Sites that had a size value that needed to be converted into a height interval were plotted as the median value of the grey bar, and when there were several sites with the same height interval and age, sites were plotted next to each other on the thin line representing the median value.



productive (P) were assumed to have the potential to grow into commercially productive sites.

Statistical analysis

The three main response variables, i.e., stocking, growth, and productivity, were computed for total, black spruce, and jack pine sites, resulting in a total of nine response variables. For stocking and growth response variables, we used binomial logistic regression to identify the best predictors. For productivity, both ordinal and multinomial logistic regressions were used. Productivity class BS (bad stocking but good growth) could not be considered for

| | Minimal height, cm (size class) | |
|-------------|------------------------------------|-------------|
| TSF (years) | Black spruce | Jack pine |
| 10 | 25 (1) | 90 (2) |
| 11 | 29 (1) | 101 (2) |
| 12 | 33 (1) | 112 (2) |
| 13 | 37 (1) | 123 (2) |
| 14 | 41 (1) | 135 (2) |
| 15 | 45 (1) | 147 (2) |
| 16 | 50 (1) | 159 (2) |
| 17 | 55 (1) | 171 (2) |
| 18 | 60 (1) | 183 (2) |
| 19 | 65 (2) | 169–317 (3) |
| 20 | 70 (2) | 169–317 (3) |
| 21 | 75 (2) | 169–317 (3) |
| 22 | 81 (2) | 169–317 (3) |
| 23 | 87 (2) | 169–317 (3) |
| 24 | 93 (2) | 169–317 (3) |
| 25 | 100 (2) | 169–317 (3) |
| 26 | 108 (2) | 169–317 (3) |
| 27 | 117 (2) | 169–317 (3) |
| 28 | 126 (2) | 169–317 (3) |
| 29 | 137 (2) | 169–317 (3) |
| 30 | 149 (2) | 316-524 (4) |

Table 3. Time–height threshold values for growth quality of black spruce and jack pine.

Note: The values in this table are derived from the growth curves in Fig. 3 and reflect the minimum height (cm) that a seedling should have reached at each year to be considered "good growth". Time is expressed as time since fire (TSF) and is assumed to correspond to tree age. Sites classified as good growth have potential to reach the minimal site indices presented above, whereas sites classified as bad growth are less likely to attain these minimal limits. The values in parentheses correspond to different size classes: 1, height 15–60 cm; 2, height > 60 cm, but DBH < 1.0 cm; 3, DBH [1.0–2.9 cm]; 4, DBH [3.0–4.9 cm], etc.). Starting from a size value of 3, size of postfire individuals was only measured in DBH and corresponds, therefore, to a height interval (see Appendix C).

further analysis as it was too rarely observed (n = 3). As a result, the three remaining productivity classes (P, BG, and BB) had a clear ordinal character (P > BG > BB), which allowed us to use ordinal logistic regression. The advantage of this type of analysis is that it allows for identifying the variables that best predict the degree of productivity of a site.

We also conducted a multinomial regression analysis to identify the combination of predictors that result in the correct classification of the highest number of sites. Identified predictors do not necessarily imply that they promote productivity, but that they contribute to classifying most sites in their correct productivity class.

For all analyses, we first ensured that all assumptions with regards to the dataset were met (Supplementary data).² Not all 116 sites were included in each analysis for various reasons, e.g., the uncertain determination of black spruce postfire stocking and the stratification of sites according to prefire species dominance (i.e., black spruce sites and jack pine sites). The number of sites included in the analysis of each response variable is presented in Table 2. For each response variable, we identified the most parsimonious model by using second-order Akaike's information criterion (AIC_c) in the R package AICcmodavg (Mazerolle 2013). AIC_c considers the sample size of each analysis and also ensures a more parsimonious model compared with AIC by applying a higher

penalty for adding a new predictor to the model (Mazerolle 2013). Once we had identified the predictors of a model, we used different combinations of these predictors to predict the response variable of the model, and the resulting AIC_c values allowed us to rank the predictors according to their strength. This methodology was also used to determine which class of predictors best succeeded in correctly predicting a model's response outcome, i.e., whether combined climatic predictors contributed more to the model than combined edaphic or site history related predictors.

Finally, we used the prediction profiler function in JMP (SAS Institute Inc. 2008) to (*i*) visually and statistically explore the importance of every predictor relative to each response outcome (productivity class) expressed by the slope of the functions and (*ii*) determine the probability of finding a productive site (P) for a set of optimized predictors. The profiler function is especially useful in multiple-response models as it identifies predictor values that optimize a complex set of criteria in the dataset. By taking into account interaction or cross-product effects in the model and using simulation and defect profiling features, it allows for robust and high-quality predictions of the desired response class (SAS Institute Inc. 2008). Except for the prediction profiler (JMP; SAS Institute Inc. 2008), the software R (version 2.15.3; R Core Team 2013) was used for all analyses.

Results

Observation on postfire stocking, growth, and productivity

Figure 3 shows that growth quality was poor in the study area: for 61% of the sites, none of the observed tree species met its growth threshold (see "total"), and the species-specific analyses indicated that 54% of black spruce sites and 78% of jack pine sites did not meet their growth threshold. In sharp contrast, stocking was predominantly classified as good: 77% of total sites and 80% of black spruce sites had stocking $\geq 60\%$ (Fig. 4). Even when considering that young (≤20 years) black spruce sites with bad stocking were generally excluded from the analysis because of an uncertain stocking determination resulting in a potential bias towards an increased proportion of sites with a good stocking (see Material and methods), we found that the proportions of older (>20 years) sites with good total stocking and black spruce stocking were also high, amounting to 65% and 74%, respectively (horizontal broken lines in Fig. 4). However, for jack pine sites, stocking was not as good, with only 45% of the sites having stocking $\geq 60\%$.

Combining stocking and growth quality, we found that only 28% of total sites were classified as productive, i.e., they met both stocking and growth thresholds (Fig. 5). Species-specific analysis showed that black spruce sites had a higher proportion of productive sites compared with jack pine sites (29% vs. 12%, respectively). Interestingly, total site analysis indicated that sites with good growth but bad stocking were almost nonexistent, representing <4% of all sites (class BS; Fig. 5). Specifically, in 24 of 27 cases, sites with good growth also had good stocking and thus good productivity.

The dominant productivity class was BG, i.e., sites with bad growth but good stocking, and this class represented 52% of all sites. The least productive class BB, i.e., sites showing both bad growth and bad stocking, represented 16% (Fig. 5).

Potential drivers

Our response models revealed that the best predictors were, in order of importance, climatic, edaphic, and site history related factors. Of a total of nine stocking, growth, or productivity response variables, the predictive effect of climatic factors was dominant: 7 of 9 response variables were best predicted by a climatic

²Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0273.

Fig. 4. Total and species-specific stocking and growth quality. The number of sites is indicated at the top of each column and is clarified in Table 2. The left part of each double column represents stocking quality, whereas the right part shows growth quality. The white parts of the stacked columns represent bad stocking (left column) or bad growth (right column). Total growth was considered good as soon as one of the two tree species had attained the growth threshold assumed to reflect the minimal acceptable growth for commercially viable sites. The broken horizontal lines in the columns of total stocking and black spruce stocking represent the proportion of sites with a good ($\geq 60\%$) stocking when only considering older sites (TSF > 20 years, n = 38 (total) and 33 (black spruce)) for which no potential bias towards "good stocking" sites was expected (cf. Table 2). Exact values represented by the columns are presented in Supplementary data.²



factor, whereas for the two other response variables, the predictive power of climatic predictors was ranked second (Table 4). Edaphic factors were the best predictor for one model and second for four, whereas site history related factors were first for only one model (Table 4).

Whereas growth quality was found to be uniformly poor for all three types of sites, it was also found to be uniformly controlled by the same predictor class, i.e., climate (Table 4). More specifically, black spruce growth and total growth were mostly promoted by DD, whereas jack pine growth was mostly affected by altitude and aspect. In terms of stocking, each response variable was best predicted by different sets of factors: total stocking was most related to site history, black spruce to climatic factors, and jack pine to edaphic factors (Table 4).

As a result of the strong effect of DD on the postfire growth of both total and black spruce growth, this climatic variable also best predicted the level of productivity (P > BG > BB) of these two response variables (Table 4). However, the productivity level of jack pine sites was mostly promoted by a high fraction of sand in the mineral soil. Nevertheless, DD was found to be only slightly less predictive (Δ AIC_c = 1.47), and for all three productivity response variables, climatic variables (primarily DD) best determined their productivity level (Table 4).

The multinomial regression results for total productivity (Table 4; Fig. 6) show that, in order of importance, slope, latitude, the fraction of sand in the mineral soil, and altitude were the four predictors that resulted in a correct productivity classification for the highest number of sites. The confusion matrix shows that 71% of all sites were correctly classified using these predictors (Table 5). The model was particularly successful in predicting unproductive sites (BG and BB) with 90% (n = 52 of 58) of unproductive

Fig. 5. Total and species-specific site productivity. The number of sites is indicated at the top of each column and is clarified in Table 2. Four productivity classes were distinguished in correspondence to Fig. 1: one productive class (P = productive, both stocking and growth are good) and three unproductive classes: BS = bad stocking, but good growth; BG = bad growth, but good stocking; and BB = bad stocking and bad growth. Exact values are presented in Supplementary data.²



tive sites being classified as unproductive and 76% (n = 44 of 58) of unproductive sites classified in the correct unproductive class being BG or BB (Table 5). For the productive sites (n = 24), 58% (n = 14) were correctly predicted and the remaining 42% (n = 10) were classified as BG, a more productive class compared with BB.

The prediction profiler further shows that in an area with a growing season of 1150 DD, the probability to find a productive site was 61%, whereas at 1000 and 900 DD, probabilities decreased to 21% and 9%, respectively. Similarly, at latitude 51.0°N, the probability of finding a productive site still amounted to 69%, whereas at latitudes 52.0°N and 53.0°N, probabilities decreased to 29% and 3%, respectively (Fig. 6).

The most unproductive sites (BB) were best predicted by altitude: at higher altitudes, sites tended to have both bad stocking and bad growth; sites with an altitude greater than 450 m a.s.l. had a probability of 55% to be classified as BB, whereas at 291 m a.s.l., which is the mean altitude of all sites, this probability was only 16% (Fig. 6).

Of all parameters, slope was found to be the best predictor for our productivity square classification because it correctly classified most sites as belonging to BG, the most common productivity class. The prediction profiler indicates that sites on flat terrain generally had bad growth but were well stocked. Similar to slope, the fraction of sand in the mineral soil classified well the common BG class: sandy soils were generally associated with bad growth but good stocking.

Discussion

Defining productivity thresholds for young postfire stands

In this study, we defined thresholds for both stocking and growth to classify young (<30 years) postfire sites into productive and unproductive ones. All thresholds were defined with the sole aim of evaluating the likeliness of a site to (*i*) attain a closed canopy and (*ii*) have a growth rate that may allow recruits to reach a minimal commercial stem volume. For the first criterion, we linked suggested minimal tree density to minimal stocking, and

Table 4. Identification of predictors of postfire stocking, growth, and productivity.

| | No. of sites | Logistic regression type | Ranking of significant ($P < 0.05$) predictors via AIC _c ^{<i>a</i>} | Ranking of predictor classes via $AIC_c^{\ b}$ | AIC _c of model |
|--------------|--|--------------------------------------|--|--|--|
| Stocking | | | | | |
| Total | 85 | Binomial | 1. Prefire total stocking (+): $P = 0.005$ 2. Altitude (–): $\Delta AIC_c = 2.14$; $P = 0.026$ | 1. Site history 2. Climatic: $\Delta AIC_c = 2.14$ | 77.95 (<i>P</i> < 0.001) |
| Black spruce | 52 | Binomial | 1. Degree days (+): <i>P</i> = 0.001 2. Drainage (–): ΔAIC _c = 0.23; <i>P</i> = 0.013 3. Latitude (–): ΔAIC _c = 5.89; <i>P</i> = 0.006 | 1. Climatic 2. Edaphic: $\Delta AIC_c = 4.61$ | 40.82 (<i>P</i> = 0.001) |
| Jack pine | 55 | Binomial | 1. % Sand (+): <i>P</i> = 0.001 2. Degree days (+): DAIC _c = 5.51; <i>P</i> = 0.013 | 1. Edaphic 2. Climatic: ΔAIC _c = 5.51 | 66.83 (<i>P</i> < 0.001) |
| Growth | | | | | |
| Total | 113 | Binomial | 1. Degree days (+): $P = 0.003$ 2. Slope (+): $\Delta AIC_c = 1.75$; $P = 0.015$ 3. Burn severity (–): $\Delta AIC_c = 3.01$; $P = 0.002$ | 1. Climatic 2. Edaphic: $\Delta AIC_c = 1.75$ 3. Site history: DAIC _c = 3.01 | 135.99 (<i>P</i> < 0.001 |
| Black spruce | 68 | Binomial | 1. Degree days (+): <i>P</i> = 0.001 | 1. Climatic | 70.42 (P < 0.001) |
| Jack pine | 50 | Binomial | 1. Slope (+): $P = 0.028$ 2. Altitude (-): $\Delta AIC_c = 0.67$; $P = 0.034$ 3. Aspect (south): $DAIC_c = 0.98$; $P = 0.040$ | 1. Climatic 2. Edaphic: $\Delta AIC_c = 0.46$ | 51.32 (<i>P</i> = 0.001) |
| Productivity | c | | | | |
| Total | P = 24; BG = 44; BB = 14 (n = 82) | Ordinal Multinomial | 1. Degree days (+): $P < 0.001$ 1. Slope (+): $P = 0.001$ 2. Latitude (-): $\Delta AIC_c = 8.71$; $P = 0.009$ 3. Altitude (-): $\Delta AIC_c = 10.02$; $P = 0.010$ 4. Sand (+): $\Delta AIC_c = 12.21$; $P = 0.019$ | Climatic Edaphic Climatic: ΔAIC_c = 7.56 | 154.20 (<i>P</i> < 0.001 140.35 (<i>P</i> < 0.001 |
| Black spruce | P = 15; BG = 25; BB = 11 (n = 51) | Ordinal | 1. Degree days (+): <i>P</i> < 0.001 | 1. Climatic | 104.12 (<i>P</i> < 0.001 |
| Jack pine | P = 6; BS = 5; BG = 19; BB = 20 (<i>n</i> = 50) | Ordinal (3 classes: P; BS+BG; BB) | 1. Sand% (+): $P = 0.015$ 2. Degree days (+): DAIC _c = 1.47; $P = 0.029$ 3. Aspect (south): DAIC _c = 1.61; $P = 0.046$ | 1. Climatic 2. Edaphic: ΔΑΙC _c = 0.19 | 94.08 (P = 0.001) |

^aPredictors were ranked according to importance determined via AIC_c. The sign of relationship between the predictor and the response variable is listed after each predictor in parentheses.

bTo know whether climatic, edaphic, or site history related variables were most predictive, the cumulative AIC_c values of the three predictor classes were compared. The predictor class in bold is the one that contributed most to predicting the response variable. In two cases, the difference between the best and second-best predictor class was negligible (Δ AIC_c < 1.00) and both classes are indicated in bold.

For productivity, both ordinal and multinomial logistic regression analyses were performed. The best predictor class determined via ordinal logistic regression analysis is presented in bold for its importance in predicting a site's degree of productivity. Multinomial regression analysis rather identifies the variables that result in a correct productivity classification for the highest number of sites. The obtained best overall predictive model is further analysed in Fig. 6 and Table 5. The abbreviations P, BS, BG, and BB refer to those in Fig. 1.

for the second one, we used minimal SI values as reference for growth quality. Although stocking is frequently determined using 4 m² microplots with a 40% or 60% threshold (Arnup et al. 1988; Côté and Walsh 2008), we preferred to use 9 m² microplots with a 60% threshold for the following reasons: (*i*) for early-stage stands, several studies have shown that microplots with a bigger surface area, typically around 10 m², provide a better estimate of future tree density (Bella 1976; Bella and DeFranceschi 1978; Doucet 1988), and (*ii*) a 60% threshold corresponds (in the case of 9 m² microplots) to a minimal tree density of 666 stems ha⁻¹, which is considered to be the lowest tree density that may still allow for a closed canopy with black spruce (Newton 1998; Sharma and Zhang 2007).

A similarly conservative threshold was applied for evaluating growth quality; whereas minimum SI values of 7.5 (black spruce) and 9 (jack pine) assume a time span of ca. 9 and ca. 6 years, respectively, to reach a tree height of 100 cm (Pothier and Savard 1998), our threshold times to reach this height were set at 25 and 11 years, respectively. Our results (Fig. 3) show that ignoring the time period that it takes a stand to reach a height of 100 (or 130) cm has important consequences: 50 years following fire, observed harvest volumes should show a delay of 16 (25 – 9 years, see above)

to 25 years for black spruce and 5 (11 – 6 years) to 11 years for jack pine stands.

Our thresholds were set to minimize the chance of classifying a productive site as unproductive, implying that sites in the productive class P are potentially productive. Factors such as inter- and intra-specific competition before and at the time of sampling, as well as future mortality of the recruits, are likely to affect our productivity estimates (Carmean and Lenthall 1989; Goelz and Burk 1992). Also, when applying SI curves as growth reference, we assume that wood volume production of well-stocked stands can be estimated based on height growth and that sites with the same growth potential or tree height will produce the same wood volume (Eichhorn's rule; Eichhorn 1902; for a review, see Skovsgaard and Vanclay 2008). Thus, even though we applied conservative thresholds for both stocking and growth and found our growth classification not to be too sensitive to the chosen thresholds (the majority of sites with bad growth were plotted substantially below the threshold curve in Fig. 3), some sites might have been misclassified when compared with the effectively realized harvest volumes.

Fig. 6. Prediction profiler for total productivity. This figure shows the combination of the four significant (P < 0.05) variables, in order of importance from left to right, that resulted in a correct productivity classification for the highest number of sites (cf. Table 4, total productivity, multinomial regression). Although DD was not selected as predictor in this most parsimonious multinomial model, it was more successful in predicting a site's degree of productivity than its collinear variable latitude and was therefore plotted on top of latitude in a lighter shade. For each predictor, the probability curves of the three productivity classes that were modelled (P, BG, and BB) are plotted for the range of predictor values observed in the 82 sites. For instance, at latitude 51.0° N, the probability of finding a productive site amounted to 69%. The dotted horizontal lines show the "observed" distribution of the three productivity classes for the average value of all predictors indicated by the dotted vertical lines. Similarly, the stacked column to the right (values in parentheses) shows the "modelled" distribution of the three classes.



Table 5. Confusion matrix for total productivity.

| | Predicted (n) | | | | | | |
|-------------------------|---------------|----------|------|------|-------|--|--|
| Observed (n) | Р | BS | BG | BB | Total | | |
| (a) Absolute n | umber | of sites | | | | | |
| P | 14 | | 10 | 0 | 24 | | |
| BS | | | | | | | |
| BG | 4 | | 38 | 2 | 44 | | |
| BB | 2 | | 6 | 6 | 14 | | |
| Total | 20 | (3) | 54 | 8 | 82 | | |
| (b) Proportion of sites | | | | | | | |
| P | 58.3 | | 41.7 | 0 | 100 | | |
| BS | | | | | | | |
| BG | 9.1 | | 86.4 | 4.5 | 100 | | |
| BB | 14.3 | | 42.9 | 42.9 | 100 | | |

Note: This matrix is based on the multinomial model listed in Table 4 and presented in Fig. 6. Sites with successfully predicted productivity classes can be found on the diagonal and are presented in bold. Note that the model does not consider productivity class BS because of too few replicates (three sites). For clarity, the table is plotted twice: once with the absolute number of sites (part *a*) and once with the proportion of sites (part *b*).

Findings and implications

We found that only 28% of the young postfire sites were assumed to have a potential to reach the minimal acceptable harvest volume within the expected time period.

The productivity square concept identified that the large proportion of unproductive sites was mainly a result of poor growth of both black spruce and jack pine. Moreover, this concept showed that good growth was associated with good stocking in 24 of 27 cases, further indicating that growth quality holds the key to productive sites in our study area. For an area situated in the closed-crown forest just north of the managed forest area, these findings are rather surprising. Although the climatic range between southern and northern sites varied only by about 250 DD (from 1140 to 890 DD, respectively), this gradient significantly predicted variability in site productivity, a finding suggesting that, in northern areas, the growth of adult trees (e.g., Jarvis and Linder 2000), as well as young 10- to 30-year-old individuals, may already be limited by climate. Furthermore, as DD was also the best predictor of black spruce postfire stocking, climate may also limit black spruce seed maturation and resulting seedling recruitment, particularly in areas with a growing season limited to 900 DD or less, as shown by Meunier et al. (2007).

In addition to climatic and edaphic factors, historical legacies affected postfire regeneration success: total prefire stocking highly determined total postfire stocking (Table 4; Greene and Johnson 1999; Splawinski et al. 2014). This finding suggests that once stands have become more open, they tend to stay open, as identified in several previous studies (e.g., Chapin et al. 2004; Jasinski and Payette 2005). In our study area, the lack of productivity due to the opening of stands was primarily a feature of jack pine sites. Our differential stocking analysis confirmed that this process is still ongoing: jack pine lost its dominance following fire in 17 of 42 sites (40%) in favour of black spruce (14 sites) or sites that have become treeless (3 sites) (Supplementary data).²

These observations are in concordance with the aerial and space-borne results of Rapanoela et al. (2015), which suggested that jack pine sites often have a low density and more frequent regeneration accidents compared with black spruce sites. On dry sites, in particular, jack pine may be less resilient to fire than previously thought (Rapanoela et al. 2015; Gauthier et al. 2015; Pinno et al. 2013).

However, as we identified that postfire stocking was not only a function of prefire stocking, but also of climatic and edaphic factors, low tree density is unlikely to be an exclusive result of past site history. Therefore, in our study area, afforestation of currently treeless or open woodland areas may not be the main solution to increasing forest productivity. Moreover, tree growth was highly limited by climatic factors, thereby further reducing our action potential to increase productivity. As a result, plans to afforest dry northern woodlands with jack pine, known for its generally more rapid growth and higher resilience to fire compared with black spruce, may need to be considered with caution (Rapanoela et al. 2015), even if preliminary studies have shown some early successes (Tremblay et al. 2013; Hébert et al. 2014; Côté et al. 2014).

Poor growth is likely to be a widespread problem of northern forests and raises questions about the potential of both sustainable forestry and climate change mitigation projects in the circumboreal north. However, in areas with better growing conditions, a northward expansion of forestry and afforestation projects might become possible. Forest management for fibre or carbon stocking of northern forests and woodlands should therefore be planned while paying particular attention to the reasons for the observed productivity of the sites. In this context, we suggest that the productivity square used in this case study is a useful tool to help define areas where such projects could be sustainable. However, the success of the tool is directly dependent on the quality of the productivity thresholds used. More studies should therefore focus on the link between young and commercial-sized forest stands to ensure more rigorous earlystage productivity thresholds for different tree species around the world.

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Appendix A. Collection procedure of the 22 predictors

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To identify the controlling factors of the stocking, growth, and productivity response variables, a total of eight climatic, eight edaphic, and six site history related predictors were collected (see Table 1).

Climatic predictors

Because of the sparse distribution of meteorological stations over central and northern Quebec, climatic variables were estimated using the BioSIM 9 software package (Régnière and Saint-Amant 2008), a sophisticated interpolation program that has proven its validity in bioclimatic research in northern areas (e.g., Mansuy et al. 2012; Boiffin and Munson 2013; Boulanger et al. 2013; Terrier et al. 2013). In this study, the software was used to estimate the following climate variables known to affect both plant regeneration and growth after fire (Zasada et al. 1987; Johnson 1996; Boiffin and Munson 2013): mean summer (June to August) temperature and precipitation, DD, and the weather during the first 3 years after fire (drought code and drought code relative to deposit type) (Table 1). In addition to these five climatic variables estimated by BioSIM, we also considered latitude, altitude, and aspect as climatic predictors. This classification is supported by the fact that in our study area, factors such as latitude and altitude varied more with climatic parameters (e.g., DD) than with edaphic or site history related ones (MRN 2014, appendix 6). All of these predictors except for aspect were measured in situ by a GPS with a calibrated aneroid altimeter. Aspect was measured in degrees and then converted into three ordinal categories: cold, neutral, and warm. WNW to ESE (292.5°–112.4°) aspects were considered "cold", taking into account that east-facing slopes tend to be colder than west-facing slopes, whereas ESE to WNW (112.5°–292.4°) aspects were considered "warm". If the site was located on flat terrain, aspect was classified as "neutral" (Table 1).

Edaphic predictors

Edaphic factors were determined in situ (Table 1). Thickness of both residual soil organic layer (rOL) and mineral soil (in mm), the fraction of sand, silt, and clay in the mineral soil, drainage, and stoniness were recorded in one soil pit placed at the centre of each plot, whereas slope was determined considering the entire transect length (for more details, see Berger et al. 2008). The organic layer was considered to extend from the ground surface up to the mineral layer or bedrock. Drainage was determined according to a predefined scale of seven classes (details in Berger et al. 2008) that were afterwards grouped into three ordinal classes (good, moderate, and poor drainage). Slope was measured with an inclinometer and expressed as percentage (Table 1).

Site history related predictors

Site history related factors were determined either from cartographic data or in situ.

Time since the last fire (TSF) and fire cycle (the time required to burn an area equal in size to a study area; see Gauthier et al. 2015) were derived from the MFFP database, which provides detailed information on time and size of forest fires since 1972 (MRN 2014).

Dominant tree species before fire, crown fire severity, and stand age at the time of the last fire were determined in situ (Table 1). The dominant tree species before fire was defined as the species with the highest prefire stocking. Crown fire severity was defined as high or low, with high meaning that all trees at the site had died and low meaning that one or more tree individuals had survived the fire (observed in 29 of 116 sites). Finally, to explore if a potentially short interval between the most recent fire and the previous one had reduced the regeneration capacity of some stands due to high mortality before reaching sexual maturity (Brown and Johnstone 2012), we identified the stand age at the time of the last fire. Therefore, a minimum of two trees per site that belonged to the dominant size (DBH) class were sampled. Stem disks were taken at the height of the root collar and annual rings were counted under a microscope. In 85% of the cases (n = 99/116), the age of the individuals was similar (±5 years) and stand age was assumed accurately determined. In some cases (n = 17), it was not possible to estimate precisely the age of the dominant prefire cohort. For these sites, a minimum stand age was attributed based on the age of the oldest tree.

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Appendix B. Determination of black spruce postfire stocking

Because black spruce is a slow-growing tree species and seedlings <15 cm were not recorded (Berger et al. 2008), we found a significant relationship between postfire stocking and TSF for the 105 sites that had black spruce in pre- or post-fire stocking counts ($R^2 = 0.134$, P < 0.001; Fig. B1). The correlation was no longer observed if we excluded all sites with a TSF of \leq 20 years ($R^2 < 0.001$, P = 0.971, n = 37; Fig. B1). Therefore, black spruce stocking sites were included in the analysis based on our ability to correctly classify them as bad or good.

Sites that met the following criteria were able to be correctly classified: (*i*) a TSF of >20 years (all "good"), (*ii*) younger sites but with a postfire stocking that had already surpassed the threshold (>60%; all "good"), and (*iii*) sites with a TSF of 17–20 years and postfire stocking determined as <60% with all counted seedlings greater than 60 cm (all "bad") (Table 2). The same reasoning was applied for total stocking, although, in addition, if young (TSF of \leq 20 years) sites were exclusively occupied by jack pine (>15 cm) both before and after fire, total stocking was also considered as correctly classified (see Table 2 for the number of sites used).

Fig. B1. Relationship between postfire stocking of >15 cm black spruce seedlings and time since fire (TSF). (*a*) The positive linear relationship for the entire TSF period (10–30 years) for the 105 sites (total number of sites that contained black spruce before and (or) after fire). Note that not all sites are visible in the plots as several sites had an identical stocking and TSF. (*b* and *c*) The relationships for the TSF periods of (*b*) 10–20 years and (*c*) 21–30 years. Although five sites aged 10–20 years had stockings of 0% of >15 cm black spruce seedlings (three sites with a TSF of 11 years had stockings of 0%), 0% stockings were not observed for TSF >20 years. Similarly, 21 sites had ≤10% stocking; 19 of those sites had a TSF of ≤20 years compared with only two sites with a TSF of >20 years.



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Appendix C. Conversion of DBH classes into height classes

To compare the growth potential between all sites, we had to convert DBH intervals into tree height intervals; therefore, we derived the 2.5% and 97.5% quartiles of tree height that corresponded to each of the DBH classes (Table C1). This was done using dominant or co-dominant postfire individuals from six fires of 10–30 years north of 49°N gathered by several of our lab co-workers. In total, 1343 spruce trees and 689 pine trees were used for the DBH–height conversions.

Table C1. Conversion of diameter at breast height (DBH) classes into height classes for black spruce and jack pine.

| | DBH (cm) | | Height quartiles | | |
|------------|----------|------|-------------------|--------------------|----------------|
| Size class | Range | Mean | Minimum (2.5%) | Maximum (97.5%) | Sample size |
| Black spru | ice | | | | |
| 3 | 1.0-2.9 | 2.14 | 1.91 | 2.77 | 253 |
| 4 | 3.0-4.9 | 3.07 | 2.46 | 4.31 | 789 |
| 5 | 5.0-6.9 | 5.96 | 3.41 | 5.57 | 301 |
| Jack pine | | | | | |
| 3 | 1.0-2.9 | 2.05 | 1.59 | 3.17 | 121 |
| 4 | 3.0-4.9 | 4.10 | 3.16 | 5.24 | 120 |
| 5 | 5.0-6.9 | 5.92 | 4.2 | 6.5 | 165 |
| 6 | 7.0-8.9 | 7.97 | 5.2 | 7.7 | 185 |
| 7 | 9.0-10.9 | 9.87 | 6.2 | 8.9 | 99 |

Note: Size classes: 1, height 15–60 cm; 2, height > 60 cm, but DBH < 1.0 cm; 3, DBH [1.0–2.9 cm]; 4, DBH [3.0–4.9 cm], etc.