

American beech and sugar maple sapling relative abundance and growth are not modified by light availability following partial and total canopy disturbances

Kim Bannon, Sylvain Delagrangé, Nicolas Bélanger, and Christian Messier

Abstract: Studies have reported divergent results on the effect of soil fertility and canopy opening on understory density and growth of sugar maple (AS; *Acer saccharum* Marsh.) and American beech (FG; *Fagus grandifolia* Ehrh.). The main objective of this study was to evaluate the effect of a gradient of canopy opening and soil fertility on the density and growth of AS and FG saplings in southwestern Quebec, Canada. We investigated 56 stands containing both AS and FG that were subjected to different disturbance history types (DHTs) (UF, unmanaged forest; PC, partial cut; and CC, clearcut) on various soil types. AS and FG absolute and relative sapling density varied greatly among the 56 stands; however, no significant effects of DHT, soil nutrient availability, or their interaction were found. Both species responded positively in terms of radial growth to canopy openings, with FG growth being slightly better than AS growth in PC stands compared with other canopy treatments. Contrary to our hypothesis, AS did not show significantly higher growth than FG following clear-cutting. These results do not support the idea that AS abundance and growth could be promoted by increasing the intensity of the canopy opening during harvest, at least on the generally acidic and base-poor soils that were investigated.

Key words: *Fagus grandifolia*, *Acer saccharum*, soil nutrient availability, light availability, saplings, clearcut, partial cut.

Résumé : Des études font état de résultats divergents concernant l'effet de la fertilité du sol et de l'ouverture du couvert forestier sur la densité et la croissance de l'éclaircie à sucre (AS; *Acer saccharum* Marsh.) et du hêtre d'Amérique (FG; *Fagus grandifolia* Ehrh.) sous couvert. L'objectif principal de cette étude était d'évaluer l'effet d'un gradient d'ouverture du couvert forestier et de la fertilité du sol sur la densité et la croissance des gaules d'AS et de FG dans le sud-ouest du Québec, au Canada. Nous avons échantillonné 56 peuplements contenant des AS et des FG ayant été soumis à différents types d'historique de perturbation (THP) (FN, forêts non aménagées; CP, coupes partielles; CT, coupes totales) sur différents types de sol. La variation des densités absolue et relative des gaules d'AS et de FG entre les 56 peuplements était importante, mais nous n'avons trouvé aucun effet significatif du THP, de la disponibilité des nutriments du sol ou de leur interaction. La croissance radiale des deux espèces a réagi positivement à l'ouverture du couvert, mais la croissance de FG était légèrement supérieure à celle d'AS dans les CP comparativement aux autres traitements du couvert forestier. Contrairement à notre hypothèse, la croissance d'AS n'était pas significativement plus grande que celle de FG à la suite d'une CT. Ces résultats n'appuient pas l'idée qu'on puisse favoriser l'abondance et la croissance d'AS en augmentant l'intensité des ouvertures par la coupe, à tout le moins sur les sols généralement acides et pauvres en bases qui ont été étudiés. [Traduit par la Rédaction]

Mots-clés : *Fagus grandifolia*, *Acer saccharum*, disponibilité des nutriments du sol, disponibilité de la lumière, gaules, coupe totale, coupe partielle.

Introduction

Throughout the last century, forest management has changed the structure and composition of temperate deciduous stands within the forested landscapes of Quebec. Most notably, results from several experiments have indicated that management practices affect the coexistence (i.e., the replacement patterns) of sugar maple (AS; *Acer saccharum* Marsh.) and American beech (FG; *Fagus grandifolia* Ehrh.) in deciduous forests (Forcier 1975; Kelty and Nyland 1981; Horsley 1994; Poulson and Platt 1996; Beaudet et al. 1999; Nolet et al. 2008a). A key factor determining replacement patterns in AS–FG forests is the competitive regeneration of AS and FG in the understory (Arii and Lechowicz 2002), particularly how each species responds to the biotic and abiotic factors. These patterns have been investigated by a number of authors

(Runkle 1990; Brisson et al. 1994; Poulson and Platt 1996; Beaudet et al. 1999; Arii and Lechowicz 2002; Nolet et al. 2008a; Gravel et al. 2010); however, the biotic and abiotic factors that are responsible for this replacement have yet to be fully elucidated.

Environmental factors such as light availability and soil water and nutrient availability have been individually shown to influence AS regeneration patterns. Their effects on AS regeneration, however, have rarely been studied in interaction with each other (Arii and Lechowicz 2002; Nolet et al. 2008a). AS regeneration, growth, and vigour appear to be controlled by two principal factors and their interaction: (i) light availability, which varies according to previous forest management and canopy characteristics (Canham 1985; Kobe et al. 1995); and (ii) soil nutrient availability (Kobe 1996; Dijkstra and Smits 2002; Bailey et al. 2004). It seems

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likely that these two dominant factors and their interaction govern the temporal and spatial patterns of AS–FG coexistence (Nolet et al. 2008a).

Dieback, defoliation of the crown, increased mortality, and decreased recruitment and growth of AS trees due to atmospheric acid deposition, which acidifies soils (thus leading to increased aluminum (Al) and manganese (Mn) activity in the soil solution) and leaches the base cations (notably calcium (Ca)), was reported over the last 20 years (Likens et al. 1996; Bailey et al. 2004; Schaberg et al. 2006; Long et al. 2009). Soil acidification and the subsequent leaching of Ca is also, in part, thought to be responsible for the decreasing AS population and the changing composition of deciduous forests in Quebec (Moore et al. 2000; Duchesne et al. 2005, 2006; Duchesne and Ouimet 2009). This is due to the fact that AS is a Ca-demanding tree species and that its health and vigour (Long et al. 1997; Juice et al. 2006; Huggett et al. 2007) and distribution (Kobe 1996; van Breemen et al. 1997) are controlled by soil acidity and Ca availability. At the same time, the relative dominance of FG appears to have been increasing in these ecosystems — apparently, FG saplings are gradually gaining dominance in the understory (Doyon et al. 2005; Gravel et al. 2010), and in turn, the structure and composition of AS stands are being modified (Duchesne et al. 2005). Another important factor that can shift the dominance of the two species is beech bark disease. Because FG is capable of vegetative reproduction (Beaudet and Messier 2008), this disease can trigger sprouting, a mechanism that apparently maintains or perhaps augments FG sapling proportions (Houston 2001; Hane 2003; Nyland et al. 2006). Bohn and Nyland (2003) also suggested that herbivory, climate change, and wind and ice storms influence FG sapling proportions in deciduous forests and, therefore, replacement patterns between AS and FG.

The performance and coexistence of AS and FG was previously studied as a function of disturbance history types (DHTs) and light and nutrient availability (Arii and Lechowicz 2002; Nolet et al. 2008a). Nolet et al. (2008a) have suggested that large gaps (e.g., >30% of total incident light) are necessary to favour growth and regeneration success of AS over FG. Moreover, subsequent and frequent disturbances in those stands would assure continuous AS regeneration (Poulson and Platt 1996) and allow this species to maintain its dominance over FG. However, other studies have suggested that both species respond similarly to an increase in light availability — indeed, following formation of the substantial canopy openings that were caused by the 1998 ice storm event, the hierarchical ranking of both species in the forest understory was not modified (Beaudet et al. 2007).

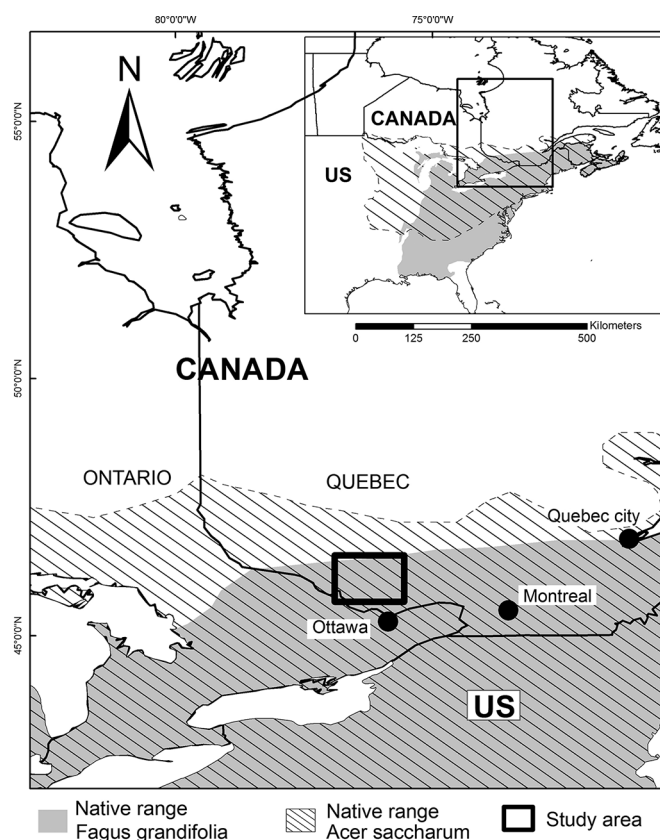
To clarify the possible synergistic effects of light conditions and soil nutrient availability on the regeneration success of both AS and FG, we sampled 56 stands with varying light and soil nutrient availabilities in the Outaouais region of the province of Quebec, Canada. The objectives for the present study were as follows: (i) to verify if variation in AS and FG abundance at the regeneration level is explained by the range in soil nutrient availabilities that are found in the region; (ii) to examine the interaction between soil nutrient availability and DHTs with respect to current AS and FG sapling densities, thereby allowing the testing of Nolet et al.'s hypothesis that AS exhibits greater growth in environments with higher light availability; and (iii) to evaluate radial growth responses of both AS and FG saplings as a function of contrasting intensities of canopy disturbances.

Methods

Study sites

This study was conducted in the Outaouais region of Quebec, Canada (Fig. 1). This region is characterized by the sugar maple – yellow birch bioclimatic domain (Robitaille and Saucier 1998), which is dominated mainly by AS, FG, and yellow birch (*Betula*

Fig. 1. Study area of the 56 sugar maple and American beech stands situated throughout the Outaouais region, Quebec, Canada.



alleghaniensis Britton). Mean annual temperature is 3.7 °C, and annual precipitation ranges from 900 to 1000 mm (Ordre des ingénieurs forestiers du Québec 2009). The Outaouais region sits on the Precambrian Shield and is characterized by thin glacial till soils (Ordre des ingénieurs forestiers du Québec 2009), which are generally Orthic Humo-Ferric Podzols and Eluviated Dystric Brunisols (Soil Classification Working Group 1998). Melanic Brunisol and Gleysols sometimes formed on calcareous deposits (e.g., originating from localized marble rocks) and in poorly drained (low) lands, respectively.

Stand selection

Using a geographic information system (ArcGIS v.9.0), stands were preselected to create an intensity gradient of canopy disturbance and soil nutrient availability. Three levels of DHTs were selected. These included unmanaged forest (UF) stands, which had no record for any management since information was recorded (at least 60 years ago), as a control group; partial cut (PC) stands, which were implemented approximately 20 years ago and resulted in 30% canopy removal; and clearcut (CC) stands, which were implemented about 50 years ago and resulted in more than 75% canopy removal. For each PC and CC stand, we had the exact year of the treatment, whereas the age of UF stands was estimated to be over 100 years, because the mean sapling age was approximately 52 years and the age of some of the canopy trees was up to 200 years. Within each DHT, stands were then roughly sorted into three soil nutrient availability levels based on the particle size distribution of surface deposits that are available in the inventory database of the Ministère des Ressources Naturelles du Québec (MRN). Overall, 72 mature stands dominated by AG and FG with a minimum area of 4 ha were preselected. After field validation, 56 stands (18 UF stands, 18 PC stands, and 20 CC stands) were selected for the study, with the others being eliminated because they did not fit

all criteria (mainly incorrect stand composition or DHT). Although beech bark disease is becoming more common in the Outaouais region, this disease was not observed in the selected stands at the time of the study.

Experimental design

For each stand, we established two sampling areas, which were separated by a minimum distance of 150 m. Each sampling area consisted of five sample plots, one at the centre (A) of an array and four others that were established at a distance of 15 m in each of the four cardinal directions (B, C, D, and E; Fig. 2). AS and FG had to be present in both the understory and the canopy for the area to be sampled. A total of 280 sample plots were measured throughout the region (i.e., 56 stands \times 5 plots).

Field measurements

Basal area, sapling density, and radial growth of AS and FG

In each sample plot A, we took the basal area of each species with a factor 2 prism (metric), whereas we recorded sapling (1 cm < DBH (diameter at breast height) < 9.0 cm) density of both species within a 3.09 m radius (i.e., 30 m²) in all five sample plots. To examine the effect of DHT and soil nutrient availability on radial growth response, we collected a trunk disk at breast height (1.3 m) from one large sapling (7 cm < DBH < 9 cm) of both AS and FG in each plot of the UF and PC stands. In the CC stands, mature trees were cored (one of each species) at breast height to obtain individual growth responses in the early years following disturbance. In total, 112 disks or cores of both species were collected for dendrometric measurements. Disks and cores were air dried for several weeks and sanded up to 600 grit papers. A tree-ring measuring table with 0.01 mm precision (Velmex Inc., Bloomfield, New York) was used to examine each sample. For disks, radial growth (millimetres per year) was evaluated by averaging two radii, one taken along the larger diameter axis and the other taken perpendicular to the first. Only one reading was performed for cores from the CC stands. For PC and CC stands, radial growth measurements were compiled for a period that encompassed the 5 years prior to the disturbance event (i.e., harvest) and the 10 years following it, including the year of disturbance. We used different terms for each time period; BP, before perturbation, AP1, 0–5 years after perturbation, and AP2, 6–10 years after perturbation. For the UF stands, we measured the 15 years of radial growth that corresponded to the period of disturbance in the PC stands that occurred 20 years ago.

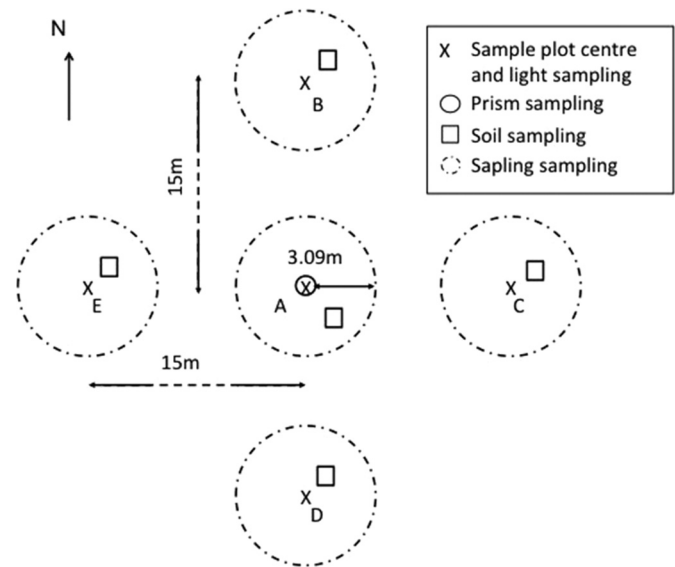
Light measurements

One hemispherical photograph was taken at the centre of all sample plots at 1 m aboveground to characterize light availability in each sampling area. We used a digital Nikon Coolpix 990 digital camera (Nikon Corporation, Tokyo, Japan) that was equipped with a hemispheric lens Fisheye Converter FC-E8. In total, 280 pictures were taken and analyzed with Gap Light Analyser v.2.0 software (Simon Fraser University, Cary Institute of Ecosystem Studies, Millbrook, New York. Available from <http://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla>) (Frazer et al. 1999).

Soil characteristics

In all sample plots, we collected soil from the top 15 cm of the B horizon with a Dutch soil auger. Samples were put in Ziploc bags for transportation to the laboratory where they were air dried for several weeks and then sieved through a 2 mm mesh. The five samples were pooled by volume in the laboratory to yield a total of 56 soil samples (i.e., one sample per stand). Carbon (C) and nitrogen (N) concentrations were determined by high temperature combustion (960 °C) and thermoconductometric detection (Vario MACRO, Elementar Analysensysteme, Haan, Germany). Base calcium and magnesium cations (Ca²⁺ and Mg²⁺, respectively) and

Fig. 2. Sampling design representing the five sample plots (A, B, C, D, and E), with \times representing the centre of the sample plot. All sapling measurements were made in all five plots (radius = 3.09 m).



orthophosphate (PO₄³⁻) were extracted with a Mehlich-3 solution as described in Sen Tran and Simard (1993). Concentrations of Ca²⁺ and Mg²⁺ were determined by atomic absorption spectroscopy (AAAnalyst 100, PerkinElmer, Norwalk, Connecticut). Orthophosphate concentrations were determined by manual colorimetry using Murphy–Riley reagent (Sen Tran and Simard 1993) and then converted to free phosphorus (P). Lastly, soil pH was measured in water with a soil to water ratio of 1:2 (Hendershot et al. 2007).

Data analysis

The basal area (BA) was calculated for the whole stand (BA_{Stand}) and then for AS (BA_{AS}) and FG (BA_{FG}) separately. For light and soil nutrient availability, measurements that were taken from each sample plot were averaged to provide a single estimate for each of the 56 stands. Sapling density per hectare (whole stand and then for AS and FG separately) and the relative sapling density of AS and FG were calculated.

Linear models were used to test for differences in stand and soil characteristics among the DHTs (Tables 1, 2, and 3). Dependent variables were BA_{AS}, BA_{FG}, BA_{Stand}, sapling density (SD) of AS (SD_{AS}) and FG (SD_{FG}), relative sapling density (SD_{Rel}) of both species, light availability, soil C, nutrients, and pH. Linear mixed-effects models were used independently to test for relationships between SD_{AS}, SD_{FG}, and SD_{Rel} and soil chemical properties and DHT. Soil Ca, Mg, P, C, and C:N were of most interest as they offered the greatest range of values. These soil data were used as continuous variables, whereas DHT was a categorical variable. Because the experimental design was nested and saplings of both species were measured in the same sample plot of the stand, a random effect parameter (i.e., stand) was added to maintain independence between observations. Pearson correlation coefficients were also calculated between SD_{AS}, SD_{FG}, and SD_{Rel} and each of the continuous soil variables among the DHT categories.

Linear mixed-effects models were used to compare the effects of different time periods, i.e., before perturbation (BP) compared with 0–5 years after perturbation (AP1) and BP compared with 5–10 years after perturbation (AP2) (among the DHTs), on the radial growth responses of AS and FG saplings. The dependent variable that was used was the direct gain in radial growth for the PC and CC stands, which was obtained by subtracting AP1 from BP and AP2 from BP, respectively.

Table 1. Characteristics of stand composition according to disturbance history type (DHT) in the Outaouais region, Quebec.

DHT	n	Stand characteristic			
		BA _{AS} (m ² .ha ⁻¹)	BA _{FG} (m ² .ha ⁻¹)	BA _{Stand} (m ² .ha ⁻¹)	LA (%)
Unmanaged forest (UF)	18	13.7a	1.6b	22.3a	9.1a
Partial cut (PC)	18	9.1b	4b	19.2a	6.5b
Clear-cut (CC)	20	7.9b	8a	20.8a	8.1a

Note: Values within a column with different lowercase letters are significantly different among DHTs at $\alpha = 0.05$. BA_{AS}, basal area of *Acer saccharum*; BA_{FG}, basal area of *Fagus grandifolia*; BA_{Stand}, basal area of stand.

Table 2. Characteristics of stand understory composition according to disturbance history type (DHT) in the Outaouais region, Quebec.

DHT	n	SD (stems.ha ⁻¹)			SD _{Rel} (%)	
		AS	FG	Total	AS	FG
Unmanaged forest (UF)	18	448a	726a	1174a	47.70a	52.30a
Partial cut (PC)	18	792a	959a	1751a	45.69a	54.31a
Clear-cut (CC)	20	527a	670a	1197a	50.21a	49.79a

Note: Values are the means. Values within a column with different lowercase letters are significantly different among DHTs at $\alpha = 0.05$. SD, sampling density; SD_{Rel}, relative sampling density; AS, *Acer saccharum*; FG, *Fagus grandifolia*.

Log transformations were applied to the dependent variables when needed to meet the assumption of normality of the residuals. For all analyses, R statistical software (R Development Core Team 2008) was used. Post hoc Tukey tests were completed by using the multcomp package after running the models. Models were considered significant at $\alpha = 0.05$.

Results

Stand characteristics

BA_{AS} was significantly higher in UF stands than in PC and CC stands, whereas BA_{FG} was significantly higher in CC stands than in UF and PC stands (Table 1). Although there was no significant difference for BA_{Stand} among DHTs, BA_{AS} was clearly greater than BA_{FG} in both PC and UF stands. There was no significant difference between AS and FG in terms of absolute SD and SD_{Rel} among DHTs (Table 2). In CC stands, the proportion of AS and FG appeared similar for both canopy trees (BA) and understory saplings (SD) (Tables 1 and 2). UF and CC stands had a significantly higher light transmission than PC stands (Table 1).

Soil characteristics

Except for Mg, all soil nutrients showed significant differences among some or all of the DHTs (Table 3). Soil C levels were higher in CC stands compared with UF and PC stands, whereas C to N ratios significantly increased with the severity of DHT (i.e., severity increases from UF to PC to CC). Soil Ca decreased as DHT severity increased. Similarly, soil P concentrations were significantly lower in CC stands than in UF and PC stands; however, there was no significant difference between PC and UF stands. Soil pH was significantly higher in UF stands than in PC and CC stands.

Interactions between SD_{AS} and SD_{FG} and DHT and soil fertility

Upper B horizons were generally acidic (pH < 4.5) and nutrient poor in all stands (Table 3). For example, average soil Ca concentrations ranged from 325 to 641 mg Ca.kg⁻¹ among DHTs. These Ca values can be considered very low, as they fall below Mehlich-3 values of acidic upper B horizons of Ferro-Humic Podzols supporting cedar and hemlock in British Columbia (945–1273 mg Ca.kg⁻¹; Cade-Menun et al. 2000). With respect to P levels ranging from 20 to 51 mg.kg⁻¹ among DHTs, this is slightly above the Mehlich-3 P values measured for other upper podzolic B horizons in Canada

(3–20 mg P.kg⁻¹ in Simard et al. (2001) and 6.1–10.2 mg P.kg⁻¹ in Cade-Menun et al. (2000)). The average C to N ratios ranged from 14 to 17 among DHTs, which is typical for surface mineral soil horizons in hardwood stands of eastern Canada (McLaughlin 2012). Such C to N ratios compare better with agricultural soils with fast N turnover (C:N = 10–15) than with boreal forests with recalcitrant conditions that immobilize N (C:N > 30). Therefore, the results suggest that the sandy loam forest soils sampled in this study are at the lowest spectrum of optimum tree growth values for Ca and to a lesser extent for P.

Overall, none of the soil chemical properties was related to variation in SD_{AS}, SD_{FG}, or SD_{Rel} (data not shown). All Pearson correlations showed no significant relationships between relative SD_{AS} and soil chemical properties, except for the C to N ratio in CC stands ($r = -0.5$, $P < 0.001$).

Radial growth response of AS and FG

Growth of both species responded positively and significantly among periods of the DHT in the PC stands (BP–AP1, $P < 0.002$; BP–AP2, $P < 0.004$) and CC stands (BP–AP1, $P < 0.001$; BP–AP2, $P < 0.001$) (Fig. 3). As expected, there was no growth difference among periods for UF stands (Fig. 3A). In PC stands, there was already a slight difference BP between the two species, which significantly increased following the perturbation to the advantage of FG (Fig. 3B). In CC stands, both species significantly gained in terms of radial growth from BP to AP1, and there was enhanced growth of both species that was sustained during AP2 (Fig. 3C).

Discussion

Growth response of AS and FG saplings to canopy disturbances

Few differences were reported between AS and FG in terms of absolute radial growth among the three DHTs that were studied. The only appreciable difference was that FG responded better than AS following partial cutting. Such a growth difference between AS and FG in PC stands was also reported for larger trees (i.e., DBH > 9 cm) by Forget et al. (2001). This response reinforces the idea that partial canopy disturbances favour FG regeneration relative to AS in the northern part of their distributional range (Nolet et al. 2008a).

Several studies have reported the inability of AS to outgrow FG under light availability levels less than 30%, whereas AS can outgrow FG under higher light availability levels (Beaudet et al. 2007; Nolet et al. 2008a, 2008b). In our study, light availability could not be measured at the time of the DHT (i.e., 20 and 50 years ago for PC and CC stands, respectively), but it is safe to assume that light availability levels were higher than 50% of total incident radiation following clear-cutting. Nevertheless, following clear-cutting, radial growth of AS and FG saplings was similar. Under closed canopy conditions, the higher growth potential of FG relative to AS has been attributed to its vegetative reproduction capabilities, especially root sprouting (Beaudet et al. 1999; Arii and Lechowicz 2002). In this study, the origin of FG saplings in the UF stands was impossible to determine, but no particularly higher FG performance was observed under this DHT. However, FG showed a significantly higher radial growth potential than AS under partial cutting. This result highlights the importance of partial canopy openings in increasing FG dominance of the regeneration, especially on lower fertility sites such as the ones that were sampled in this study. However, it is possible that on more fertile sites, greater enhancement of AS growth rates relative to FG growth rates may occur after very large canopy openings are formed (cf. McClure et al. 2000), making AS capable of outgrowing FG (Nolet et al. 2008a).

AS and FG regeneration dynamics and DHT

The regeneration dynamics described in this study do not cover the whole population of AS-dominated stands, but instead, they

Table 3. Characteristics of the B horizon according to disturbance history type (DHT) in the Outaouais region, Quebec.

	Soil characteristic						
	N (mg·kg ⁻¹)	C (mg·kg ⁻¹)	C:N (mg·kg ⁻¹)	P (mg·kg ⁻¹)	Ca (mg·kg ⁻¹)	Mg (mg·kg ⁻¹)	pH
Unmanaged forest (UF)							
Mean	2.42a	33.64a	14.03a	50.90a	640.92a	31.90a	4.3a
Minimum	1.59	18.27	10.89	5.42	67.35	8.16	3.7
Maximum	4.04	58.52	21.19	157.44	1770.75	66.15	4.7
SD	±0.58	±8.43	±2.23	±39.06	±455.47	±15.77	±0.3
Variance	0.33	71.01	4.98	1525.96	207 456.26	248.62	0.1
Partial cut (PC)							
Mean	2.13a	32.69a	15.37b	45.65a	493.66b	27.38a	4.2b
Minimum	1.40	22.13	12.23	4.32	50.40	8.06	3.8
Maximum	3.26	50.09	19.93	164.99	1 346.61	48.39	4.7
SD	±0.44	±7.99	±2.05	±47.54	±388.71	±12.20	0.2
Variance	0.19	63.82	4.22	2260.33	151 096.18	148.85	0.1
Clear-cut (CC)							
Mean	2.33a	39.70b	16.88c	18.96b	276.62c	21.54a	4.1b
Minimum	1.63	21.35	13.07	0.33	56.45	8.03	3.6
Maximum	3.62	78.51	25.60	164.96	916.67	46.00	4.5
SD	±0.53	±12.78	±2.97	±36.20	±266.91	±11.69	0.2
Variance	0.28	163.35	8.81	1310.67	71 240.42	136.77	0.0

Note: Values within a column with different lowercase letters are significantly different at $\alpha = 0.05$, as a function of DHT (UF, PC, and CC). N, nitrogen; C, carbon; C:N, carbon to nitrogen ratio; P, phosphorus; Ca, calcium; Mg, magnesium.

cover the AS-dominated stands where the presence of both AS and FG saplings were found in the understory at the time of the study. Such stands are relatively common in our region where UF stands are typically dominated by AS with a small proportion of FG in the overstory (Bouffard et al. 2003). Our study clearly shows that the proportion of FG has increased as the intensity of canopy disturbance increases from UF to CC stands. Such a drastic increase in FG compared with AS is also seen in the sapling bank in all stands independently of the DHT. Such results suggest that DHT is not the main factor causing the increase in FG in our AS-dominated stands but that it tends to accelerate it. Several other factors not considered in this study such as climate change, air pollution, and soil acidification (Bouliane 1969; Duchesne et al. 2005) may have interacted with DHT to produce the observed changes in both the overstory and understory composition (Poulson and Platt 1996; Nolet et al. 2001, 2008a; Arii and Lechowicz 2002; Bouffard et al. 2003). However, these interactions need further investigation to be confirmed.

SD_{AS} and SD_{FG}, DHT, and soil fertility

Relative sapling densities of FG and AS did not reflect their relative canopy composition. Basal area of both species in all stands was clearly at the advantage of AS, whereas in the understory, the situation was the other way around. This concurs with several recent studies that have shown a relative increase in understory FG compared with AS in many AS-dominated stands in northeastern North America (Doyon et al. 2005; Gravel et al. 2010). Surprisingly, we found no difference in SD_{Rel} that could be attributed to DHT, soil fertility, or the interaction of the two factors. This contradicts other findings that have linked diverging sapling abundances of AS and FG with soil fertility and, more specifically, with soil Ca availability (Arii and Lechowicz 2002; Duchesne and Ouimet 2009). However, it is possible that the gradient in soil nutrient availability across our sampling of 56 stands was too narrow, e.g., most of the sites generally had soils with low pH or Ca levels. Indeed, we had to reject areas with apparently richer soils because of the absence of FG in the stands. This suggests that the occurrence of FG competition in AS stands in the Outaouais region may be presently restricted to lower fertility sites in respect to pH and Ca, thereby restricting our ability to detect relationships between SD and soils. The acidic and Ca-poor nature of the soils that were sampled likely reflects: (i) a dominance of

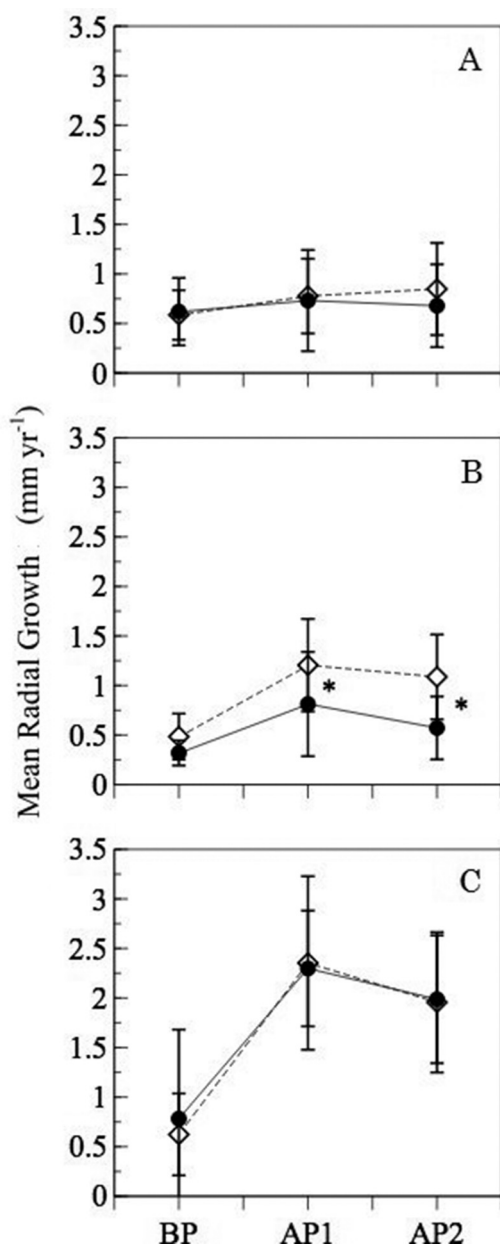
base-poor Precambrian Shield rocks (e.g., granitic gneiss) in the parent material from which the soils developed, and (ii) a limited influence of the sparse metamorphosed limestone and dolomitic rocks (i.e., marbles) that occur in the area. Based on the particle size distribution of surface deposits taken from the inventory of the Ministère des Ressources Naturelles du Québec (MRN), our sampling clearly covered some areas where soils had developed from lacustrine deposits (proglacial lakes). However, our Ca and Mg data suggest that the deposits were either low in calcite and dolomite or that these minerals were leached out from the upper B horizons since deposition about 12 000 years ago.

Furthermore, soil pH and nutrient levels can be affected by DHT. The high nutrient demand of fast-growing or aggrading stands was often associated with lower pH and base cation levels in the mineral soil, including Ca, due to a pumping effect by the roots in exchange for protons (Alban 1982; Binkley and Richter 1987; Knoepp and Swank 1994). Base cations are eventually transferred back to the surface soil through biocycling. Our results suggest a decrease in pH and Ca, as well as P, after clear-cutting. Also, harvesting is associated with a net flux of C from residues such as leaves, branches, and twigs, which leads to the C enrichment of the soil (mostly the forest floor but also occasionally the upper mineral soil) and an increase in C to N ratios relative to undisturbed stands (see meta-analysis by Johnson and Curtis (2001)). Our results corroborate with the possible response of upper mineral soils to harvesting in regard to increased C levels and C to N ratios under clear-cutting. Likely because it maintained a canopy and preserved some biocycling, soils at PC stands appear to fall closer to soils at UF stands for most variables except Ca and C to N ratios, which seemed to be intermediate between UF and CC stands.

Conclusion

Our results do not support the hypothesis of Nolet et al. (2008a) that AS sapling growth potential on poorer soils is promoted when more severe DHTs occurred. In contrast, limited below-ground resources may have greatly constrained the ability of AS to respond to higher light availability, minimizing differences in growth competitiveness between AS and FG (Beaudet and Messier 2008). However, considering the narrow and low fertility range

Fig. 3. Mean radial growth response ($\text{mm}\cdot\text{year}^{-1}$) for *A. saccharum* (solid circles) and *F. grandifolia* (open diamonds) according to disturbance history type (DHT) for each time period (BP, before perturbation; AP1, 0–5 years after perturbation; and AP2, 6–10 years after perturbation), with A representing an unmanaged forest (UF) stand, B representing a partial cut (PC) stand, and C representing a clearcut (CC) stand. Asterisks indicate significant differences at $\alpha = 0.05$ between species within a given time period. For CC, PC, and UF, BP is 5 years of growth prior to (i) the clear-cutting some 50 years ago, (ii) the partial cutting that occurred 20 years ago, and (iii) about 5 years before the year 1989, respectively.



that we sampled, we cannot conclude that such AS growth enhancement is absent on richer soils (Nolet et al. 2008a).

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