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Evidence that soil depth and clay content control the post-disturbance regeneration of balsam fir and paper birch under heavy browsing from deer[1]

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Abstract: It is not well understood why successful regeneration of balsam fir and paper birch was observed in the south-central portion of Anticosti Island, despite a high-density deer population reputed to severely browse the seedlings of these 2 species. The area where this regeneration occurred was severely affected by a hemlock looper epidemic in the early 1970s and was specifically confined to one geologic formation (Chicotte). We tested whether or not the occurrence of balsam fir and paper birch coincided with a certain range of soil properties (pH, exchangeable cations, soil depth, clay content, and forest floor thickness). Out of 49 plots surveyed, balsam fir and paper birch respectively occurred on 30 and 25 plots, while black or white spruce occurred on all plots. There was co-occurrence of balsam fir and paper birch in 15 plots in which the relative abundance of paper birch was low. Multivariate regression trees (MRT) indicated that balsam fir occurred on shallow soils, whereas paper birch occurred on deep soils. On shallow soils, MRT indicated better regeneration of balsam fir in soils with low clay content. Results suggest 2 concurrent mechanisms related to site fertility leading to the regeneration of balsam fir and paper birch. The first involves low fertility conditions that stimulate balsam fir to produce higher concentrations of anti-herbivore compounds. The second mechanism involves increased tolerance of birch saplings to repeated deer browsing on the deeper and more fertile soils. Future research should strive to confirm these mechanisms and understand why they were efficient on the Chicotte formation but not elsewhere on the island.

Keywords: balsam fir, bottom-up pressures, forest regeneration, paper birch, white-tailed deer.

Résumé : Une bonne régénération de sapin baumier et de bouleau à papier a été observée dans certains secteurs situés au centre-sud de l'île d'Anticosti, en dépit d'une pression de broutement élevée par le cerf de Virginie. Cette régénération était circonscrite à une seule formation géologique (Chicotte) et située dans un secteur ayant été affecté par une épidémie d'arpenteuse de la pruche en 1971. Une étude de terrain a été entreprise pour voir si la présence de ces deux espèces coïncidait avec certaines propriétés du sol (pH, cations échangeables, profondeur, % d'argile et épaisseur de la couche morte). Le sapin baumier et le bouleau à papier ont été observés respectivement dans 30 et 25 des 49 parcelles étudiées, alors que les épinettes blanche ou noire étaient présentes dans toutes les parcelles. Le sapin baumier et le bouleau à papier étaient présents ensemble dans 15 parcelles, mais dans tous ces cas l'abondance relative du bouleau à papier était très faible. Des arbres de régressions multivariées (ARM) nous indiquent que le sapin baumier est favorisé sur les sols superficiels, et le bouleau à papier sur les sols profonds. Pour les sols minces, les ARM indiquent une meilleure régénération du sapin baumier dans les sols contenant peu d'argile. Les résultats suggèrent l'existence de deux mécanismes reliés à la fertilité du sol qui permettent la régénération du sapin baumier et du bouleau à papier. D'une part, une faible fertilité pourrait stimuler le sapin baumier à produire plus de composés secondaires impliqués dans la défense contre l'herbivorie. D'autre part, il se peut que les sols plus profonds et fertiles confèrent au bouleau à papier une meilleure tolérance au broutement. Les études futures devraient tenter de confirmer ces deux mécanismes et de comprendre les raisons de leur efficacité sur la formation Chicotte et pas ailleurs sur l'île.

Mots-clés : bouleau à papier, cerf de Virginie, pressions « bottom-up », régénération forestière, sapin baumier.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

Large herbivore populations can modify plant communities via selective foraging, trampling, and additions of excreta (Côté *et al*., 2004; Terborgh *et al*., 2006). These modifications, in turn, may affect nutrient cycling, soil fertility, and ecosystem productivity (Singer & Schoenecker, 2003; Harrison & Bardgett, 2008). Such "top-down" pressures on ecosystem functioning are especially prevalent in predator-free situations with high stochastic variability, where herbivore populations can reach very high densities (Saether, 1997). For example, a white-tailed deer (*Odocoileus virginianu*) population that was introduced to Anticosti Island (Canada) over a century ago has subsequently risen to > 50 deer·km^{-2} in some areas

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(Tremblay, Huot & Potvin, 2007), resulting in the widespread eradication of deciduous shrubs and the conversion of forests dominated by balsam fir (*Abies balsamea*) either to white spruce (*Picea glauca*) stands (Potvin, Beaupré & Laprise, 2003) or to parkland communities (Barrette, Bélanger & De Grandpré, 2009). Balsam fir is the principal winter forage for deer on Anticosti Island (Lefort *et al*., 2007) and is unlikely to regenerate at such elevated deer densities.

Despite a high-density deer population, Chouinard and Filion (2005) noted successful regeneration of balsam fir stands in certain locations within the south-central portion of Anticosti Island. In the course of the present study, we also found successful regeneration of another browse-susceptible species, paper birch (*Betula papyrifera*). The portion of the island where this regeneration occurred had previously been dominated by mature balsam fir stands, but was subsequently ravaged in 1971-72 by an eastern hemlock looper (*Lambdina fiscellaria fiscellaria*) epidemic covering 1165 km^2. Using a GIS platform, closer inspection of the region of Anticosti Island that had experienced severe defoliation revealed that balsam fir regeneration was mainly confined to the disturbed area within one specific geologic formation known as the "Chicotte" (Figure 1). This formation, which covers approximately 700 km^2, dates from the Silurian (upper Llandovery, Telychian) and is characterized paleontologically as a speciose, crinoid-rich, sand-shoal complex (Petryk, 1981; Desrochers, 2006). The strong association between balsam fir/paper birch regeneration and geologic formation suggested that a "bottom-up" mechanism, such as edaphic properties that were possibly controlling forage quality, may dominate over top-down pressures in the Chicotte formation. Regeneration of balsam fir and paper birch on the Chicotte formation remained patchy, however, despite the relative uniformity of the pre-disturbance vegetation (MRNF, 1973). This led us to hypothesize that specific soil characteristics within some parts of the Chicotte formation controlled the regeneration of balsam fir and paper birch.

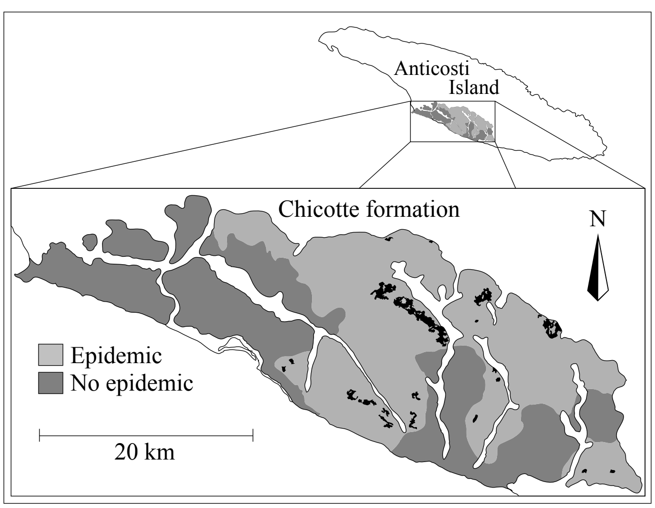

FIGURE 1. Map of Anticosti Island outlining the Chicotte geologic formation. Black areas in the magnified map at the bottom refer to the 24 polygons containing study plots.

Considering the time that had elapsed since the epidemic disturbance (*i.e.*, 35 y), our study focused on physico-chemical properties of the mineral soil rather than on forest floor properties, since the latter are strongly related to stand composition. We thus measured base cation concentrations, pH, clay content, and mineral soil depth. Forest floor thickness was used as an indicator of drainage class, because indicator understory plant species were likely to have been overbrowsed (Tremblay, Huot & Potvin, 2006). Based on the carbon-nutrient balance model (Bryant, Chapin & Klein, 1983), we hypothesized that low fertility conditions, such as shallow soils, low pH, low clay content, or low base cation concentrations, would confer to plants stronger anti-herbivore chemical defences and correlate, therefore, with successful balsam fir and paper birch regeneration.

Methods

STUDY SITE DESCRIPTION AND FIELD SURVEY DESIGN

Anticosti Island (7943 km^2) is located in the Gulf of St. Lawrence (49.1–50.0° N, 61.7–64.5° W), in eastern Canada. It is classified as part of the eastern balsam fir–paper birch bioclimatic zone (Grondin *et al*., 1996). The island supported no large herbivores prior to the introduction of ~ 220 white-tailed deer in the late 19th century. In the absence of predators, the deer population increased rapidly and has remained at high densities since about 1930. The latest official survey estimates the overall density at 20 individuals·km^{-2} (Rochette & Gingras, 2007), although densities > 50 deer·km^{-2} have been unofficially reported in some areas (Tremblay, Huot & Potvin, 2007).

Prior to our field work, we were not aware of successful paper birch regeneration anywhere on Anticosti Island, except within fenced deer exclosures. We located, therefore, all mature balsam fir stands (> 9 m) within the Chicotte formation where total mortality occurred after the hemlock looper outbreak in 1971. For this analysis, we used 1:20 000 maps from the first provincial forest inventory of the island (MRNF, 1973). Using ArcView GIS v. 3.3 (ESRI, 2002), we formed polygons to delineate balsam fir stands and generated random sampling locations in each polygon according to the following criteria: (1) polygons large enough to contain a 100-m^2 circular plot at each sampling location; (2) minimum distance of 30 m between sampling plots and roads, and between sampling plots and polygon boundaries; (3) a minimum distance of 100 m between sampling plots within a polygon. We thus obtained 388 potential sampling plots distributed in 122 polygons. From these, we selected all sampling plots that were located ≤ 350 m from a road or trail. The resulting 49 sampling plots were located in 24 polygons that varied in size from 7 to 131 ha, with balsam fir abundance varying from 0 to 80% according to aerial photo-interpretations from 1997 (MRNF, 1998).

FIELD SAMPLING AND SOIL ANALYSES

In June 2008, we counted all tree stems ≥ 2 m in each sampling plot, which is considered by Chouinard and Filion (2005) to be the minimum free-to-grow height on Anticosti Island. The surveyed tree species (*i.e.*, dependent variables) included balsam fir, paper birch, white spruce, and black spruce (*Picea mariana*). Forest floor thickness and mineral soil depth were measured at four cardinal points set at 2.5 m from the centre of each plot. We collected B horizon mineral soil from each sampling location along the entire profile, avoiding only the surficial eluvial Ae horizon (Soil Classification Working Group, 1998). These were bulked into one composite sample per plot and transported to the laboratory for analyses. The pH of air-dried and sieved (2 mm) mineral soil was measured in 1:2 (w:w) mixtures with deionized water. Air-dried samples were extracted in Mehlich III solution to which 2% lanthanum oxide had been added (Tran & Simard, 1993), and the extracts were analyzed for base cations (Ca^{2+}, Mg^{2+}, K^+) using an AAnalyst 100 atomic absorption spectrometer (Perkin Elmer Corp., Norwalk, CT). Mineral soil samples were ashed in a muffle furnace (400 °C for 24 h) to remove the organic matter, aggregates were manually destroyed with a mortar and pestle and chemically dispersed with sodium hexametaphosphate, and clay content was subsequently determined by the hydrometer method (Bouyoucos, 1936).

STATISTICAL ANALYSES

Preliminary univariate correlation and regression analyses revealed only 1 significant relationship between the abundance of regeneration and soil properties (log-paper birch *versus* % clay content: $r^2 = 0.363$, $P < 0.001$), suggesting that most relationships between response and predictor variables were not linear. Moreover, transformation of the variables did not alleviate problems of non-normality in the data. We thus implemented a regression tree approach that extends CART (Classification and Regression Trees; Breiman *et al*., 1984) from the univariate to the multivariate case (De'Ath, 2002). We constructed multivariate regression trees (MRT), using the mvpart library in R statistical software (R Development Core Team, 2009).This flexible nonparametric technique allowed us to repeatedly and dichotomously split the response data in a stepwise fashion to form progressively more homogenous groups based on the predictor variable that explained the greatest amount of variation in the dependent variable ensemble at each iteration (De'Ath, 2002; Larsen & Speckman, 2004). We created a first MRT in which we used tree counts per species in each plot as dependent variables and soil properties as the predictor variables, performing 500 cross-validations to ensure the validity of the final Tree. We subsequently created a second MRT in which we included only the plots in which balsam fir and/or paper birch occurred along with white and/or black spruce ($n = 40$).

Results

Soil properties were variable across the plots, with 10- to 30-fold differences (> 5000-fold in soil acidity) between the lowest and highest values. Forest floor thickness varied between 2.6 and 25.8 cm, mineral soil depth between 0.9 and 12.6 cm, clay content between 0.6 and 18.4%, mineral soil pH between 4.6 and 8.3, extractable K^+ between 18 and 149 $mg \cdot kg^{-1}$, extractable Mg^{2+} between 18 and 180 $mg \cdot kg^{-1}$, and extractable Ca^{2+} between 935 and 18 648 $mg \cdot kg^{-1}$ (Table I). Most correlations among the soil properties were weak or insignificant, except for Ca^{2+} *versus* pH ($r = -0.636$, $P < 0.001$), Ca^{2+} *versus* Mg^{2+} ($r = -0.524$, $P < 0.001$), and K^+ *versus* clay content ($r = 0.478$, $P = 0.001$).

Balsam fir was present in 30 of 49 plots, with a relative abundance varying between 11 and 97% (mean = 65%, SD = 23%) in plots where it was present (Figure 2). Paper birch was present in 25 plots, with a relative abundance varying between 1 and 91% (mean = 24%, SD = 33%) in plots where it was present. Balsam fir and paper birch co-occurred in 15 plots, with a relative abundance of balsam fir varying between 47 and 92% and that of paper birch between 1 and 16%. However, there was no significant positive or negative association between these 2 species based on their presence or absence (Phi-coefficient: $\phi = -0.026$, $P = 0.86$). White spruce was present in all plots, with a relative abundance varying between 2 and 100% (mean = 38%, SD = 33%). Black spruce was present in 31 plots, with a relative abundance varying between 1 and 80% (mean = 16%, SD = 20%) in plots where it was present.

The first MRT, which included all 49 plots, produced a single split that explained 16.1% of the variance (CV error = 1.14, SE = 0.27). The decision rule at this node partitioned the responses into 2 more homogenous groups on the basis of soil depth, with a threshold value of 8.75 cm (Figure 3). Balsam fir regeneration was more abundant on the shallower soils (*i.e.*, < 8.75 cm deep) of 35 plots, whereas paper birch was more abundant on the deeper soils (≥ 8.75 cm) of 14 plots. Nine of the plots contained neither balsam fir nor paper birch. The second MRT, which only included plots containing fir or birch ($n = 40$), produced the same split as above on the basis of soil depth, but this node explained 22.3% of the variance (CV error = 1.05, SE = 0.276) in the reduced data set. Among the 28 plots located on shallow soils, the second MRT generated a second split on the basis of clay content, which explained an additional 13.85% of variation in the response data (CV error = 1.07, SE = 0.260). Balsam fir regeneration was thus more abundant on shallower soils with clay contents that were < 5.85% (Figure 4). We found no differences in mean concentrations of base cations (K^+, Ca^{2+}, Mg^{2+}) among the 3 terminal sample groups (Kruskal–Wallis tests, $P > 0.14$).

TABLE 1. Mean values of forest floor properties measured in 49 sampling plots on the Chicotte formation; values in parentheses = SD.

Forest floor thickness (cm)	7.5	(6.2)
Mineral soil depth (cm)	14.7	(6.1)
Clay content (%)	5.3	(3.0)
Mineral soil pH	6.4	(0.8)
Extractable K^+ (ppm)	75.0	(35.4)
Extractable Mg^{2+} (ppm)	73.4	(32.7)
Extractable Ca^{2+} (ppm)	6253	(4573)

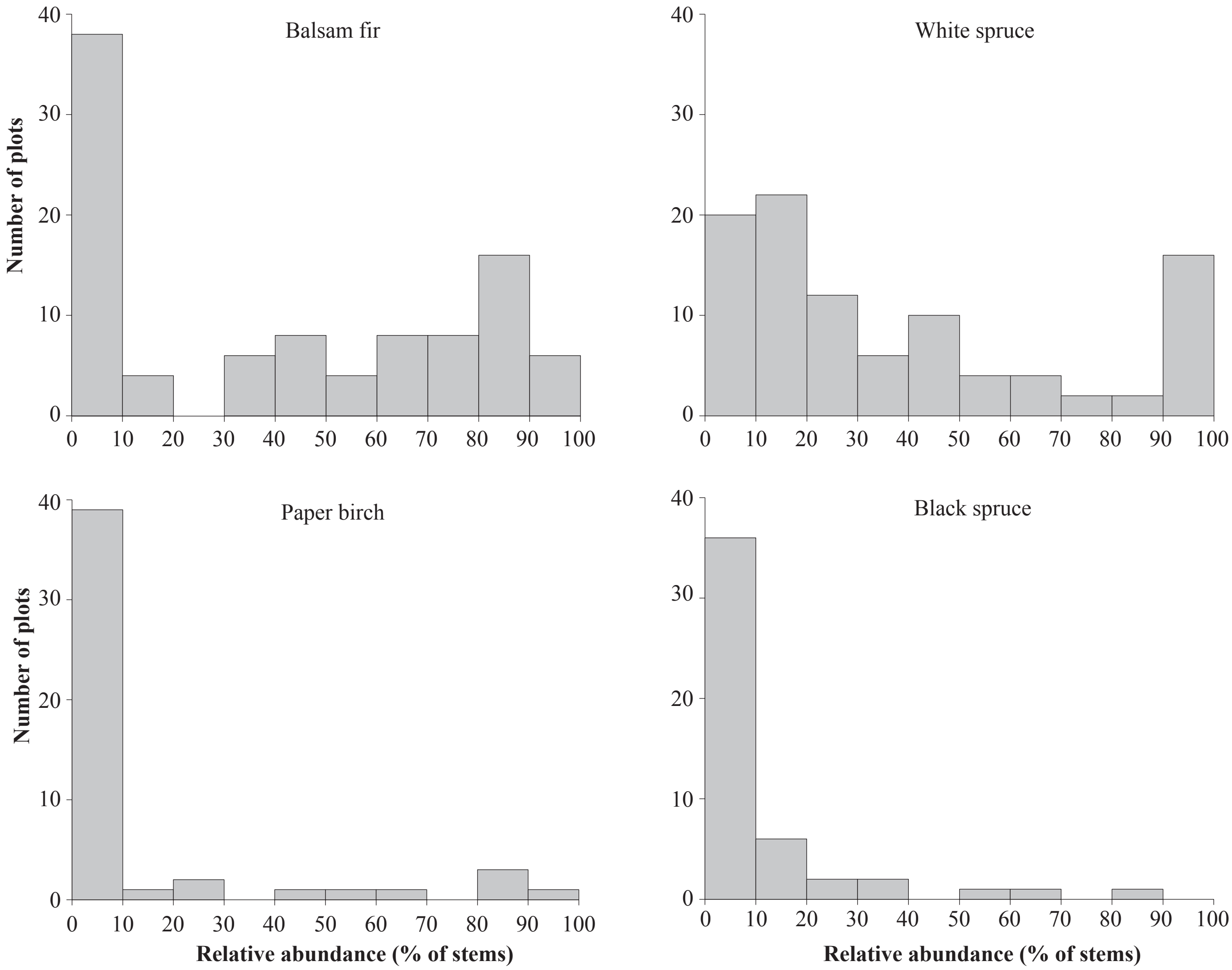

FIGURE 2. Frequency distribution of study plots (n = 49) according to the relative abundance of balsam fir, paper birch, white spruce and black spruce.

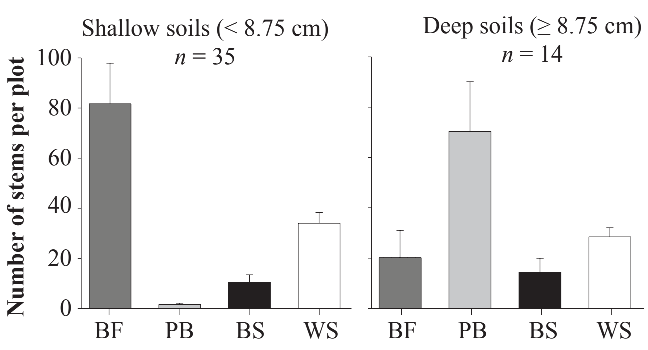

FIGURE 3. Mean abundances of balsam fir, paper birch, black spruce and white spruce (> 2 m) in the two groups of plots that were segregated by multivariate regression tree (MRT) according to soil depth. The MRT explained 16.1% of the total variance. Whiskers represent + 1SE.

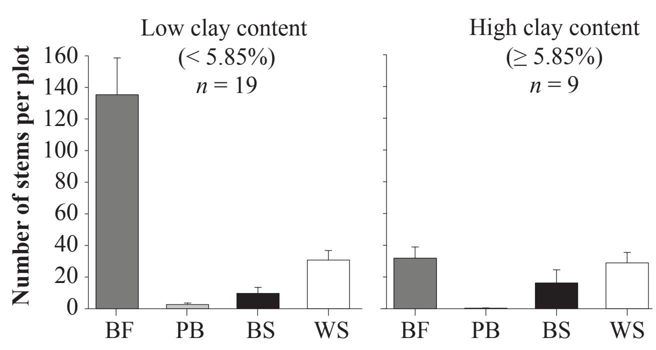

FIGURE 4. Mean abundances of balsam fir, paper birch, white spruce and black spruce (> 2 m) in a second MRT split defined by soil clay content. This MRT used only the plots containing at least one balsam fir or paper birch stem (n = 40). The first and second splits of this MRT respectively explained 22.3% and 13.9% of the total variance. Whiskers represent + SE.

Discussion

Mineral soil depth reflects site nutrient capital, whereas clay content is related to soil cation exchange capacity. As balsam fir occurs mainly on shallow soils with low clay content, we suspect that successful balsam fir regeneration partly depended on low soil nutrient availability. In accordance with carbon-nutrient balance theory (Bryant, Chapin & Klein, 1983), soil nutrient limitations increase the proportion of photosynthates used to produce carbon-based secondary compounds in woody plants. For example, production of phenolic constitutive defences, such as foliar condensed tannins, is known to increase under conditions of low soil fertility (*e.g.*, Donaldson, Kruger & Lindroth, 2006). These tannins have been shown to correlate with lower palatability and digestibility of foliage to deer (Sauvé & Côté, 2006) and other ruminants (Butler, 1989). Nutrient stress–mediated differences in foliar quality were not verified in our study, because secondary metabolites are not only synthesized in response to variation in soil fertility, but also can be expressed in response to herbivory that occurred during stand development in previous years (*e.g.*, Schultz & Baldwin, 1982; Vourc'h *et al*., 2002). It is, nevertheless, a reasonable hypothesis that browsing during early stand development, combined with shallow soils with low clay content, could increase anti-herbivore compounds that eventually deter deer before fir saplings attain the maximum browsing height (Donaldson, Kruger & Lindroth, 2006). This observation is supported by data from Chouinard and Filion (2005), who recorded an average browsing height of 90 cm on the Chicotte formation, which is 50% lower than elsewhere on the island.

We did not expect to find paper birch in our plots, as this deciduous species is preferred by deer over balsam fir, and is rarely found on Anticosti Island outside of deer exclosures (Tremblay *et al*., 2005). The observation that paper birch occurred mainly on deeper and, therefore, richer soils runs counter to the mechanism previously proposed to explain balsam fir regeneration. This may be because paper birch, unlike balsam fir, cannot produce the same quantity or quality of secondary metabolites that would deter deer herbivory. For example, Howard and Howard (1993) found that nearly 3 times more tannin-protein precipitates formed from extracts of fir than from those of birch leaves when these were made to react with protein. If paper birch, by this criterion, is ostensibly incapable of defending itself chemically against large herbivores, then its survival on the Chicotte formation would have depended on another strategy.

In order to survive strong browsing pressures, plants must either deter herbivores through various physical or chemical defensive traits (*i.e.*, resistance to browsing) or display compensatory traits that allow them to regrow following herbivory (*i.e.*, tolerance to browsing). Although there remains doubt that traits conferring resistance and those conferring tolerance can evolve independently of each other (Puustinen *et al*., 2004), both strategies involve direct fitness costs, which suggests tradeoffs between the 2 strategies (Fineblum & Rausher, 1995). Thus, if paper birch is unlikely to be as resistant to browsing as balsam fir, it is more likely to display traits that may provide sufficient tolerance to deer browsing during early stand development. Strauss and Agrawal (1999) provided a comprehensive review of mechanisms that provide tolerance to browsing, several of which might apply to this species:

1. Inherently high vertical growth rates, as with pioneer tree species such as paper birch, favour escape from deer browsing;
2. Allocation of root C reserves to aboveground parts after browsing will also favour recovery. For birch species, this mechanism is especially effective early or late in the growing season (Kays & Canham, 1991);
3. A high rate of photosynthesis, as with pioneer tree species, favours rapid recovery of partially browsed saplings;
4. Paper birch displays an indeterminate growth habit such that leaves are produced throughout the growing season. This enables new leaf emergence following deer browsing;
5. Many graminoid plant species respond to browsing by producing tillers (*e.g.*, Mullahey, Waller & Moser, 1991), which help the plant recover after it has lost apical dominance of the main shoot. Analogously, paper birch saplings whose shoots are repeatedly killed back respond by regenerating new sprouts at the base of the stems (James & Courtin, 1985).

The fact that paper birch regeneration was mainly confined to the deeper, richer soils is further evidence of a tolerance strategy by this species. High soil nutrient concentrations, coupled with high light intensity and few plant competitors after the hemlock looper disturbance, are factors that increase vertical growth rates, root C reserves, and photosynthesis (*i.e.*, mechanisms 1, 2, and 3 listed above) and that are known to facilitate plant tolerance to herbivory (Strauss & Agrawal, 1999).

In summary, we found opposite relationships between indices of soil fertility and the successful regeneration of balsam and paper birch on the Chicotte formation. These observations led us to hypothesize higher resistance to browsing by balsam fir at low fertility, and higher tolerance to browsing by paper birch at high fertility. We posit that both strategies would be facilitated by coarse woody debris on the forest floor, originating from mortality of the previous stand. For example, Casabon and Pothier (2007) found that coarse woody debris offered provisional safe sites against deer herbivory and increased recruitment of tree seedlings by 650% in 8-y-old clearcuts on Anticosti Island. The question remains, however, as to why balsam fir and paper birch successfully regenerated on the Chicotte formation but not on adjacent geologic formations that succumbed to the same hemlock looper epidemic. Future research should attempt, therefore, to compare soil fertility, fir needle chemistry, and tolerance traits of paper birch within experimental deer enclosures established on the Chicotte formation and adjacent geologic deposits.

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