

DISCUSSION / DISCUSSION

Comment on “Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?”¹

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Abstract: In a recent rapid communication, Duchesne and Ouimet (2009. *Can. J. For. Res.* **39**: 2273–2282) reported that the current expansion of American beech (*Fagus grandifolia* Ehrh.) in Quebec is mainly caused by soil base cation depletion due to atmospheric acid deposition. They based their conclusions on an examination of the relationships between stem densities in the sapling and tree strata compared against canopy composition and the availability of base cations in 426 sample plots. Here in this comment, we raise some shortcomings with their study and provide a more prudent and complete perspective on the complex dynamics associated with fluctuations in American beech and sugar maple (*Acer saccharum* Marsh.).

Résumé : Dans un article publié récemment, Duchesne et Ouimet (2009. *Rev. Can. Rech. For.* **39**: 2273–2282) rapportent que l'épuisement des cations basiques dans le sol dû aux dépôts atmosphériques acides serait en grande partie responsable de l'expansion actuelle du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) au Québec. Ils basent leur conclusion sur un examen des relations entre la densité des tiges dans la strate des gaules et celle des arbres comparativement à la composition du couvert et à la disponibilité des cations basiques dans 426 placettes échantillons. Dans cette communication, nous soulevons certaines lacunes de leur étude et nous proposons une perspective plus complète et plus prudente de la dynamique complexe associée aux fluctuations du hêtre à grandes feuilles et de l'érable à sucre (*Acer saccharum* Marsh.).

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Reports of changes in the relative abundance of sugar maple (SM) (*Acer saccharum* Marsh.) and American beech (AB) (*Fagus grandifolia* Ehrh.) near their northern range limits and investigations of the possible causes of such fluctuations are important questions both ecologically and in terms of forest management. The dynamics of these species in beech–maple forests have been the subject of numerous studies in recent years (e.g., Beaudet et al. 1999; Brisson and Bouchard 2003; Duchesne et al. 2005; Duchesne and Ouimet 2008; Nolet et al. 2008; Takahashi and Lechowicz 2008; Gravel et al. 2010; Takahashi et al. 2010). In a recent

rapid communication, Duchesne and Ouimet (2009) (hereafter D&O) reported that “American beech is currently expanding in the sugar maple range of Quebec” and that “soil base cation depletion, caused in part by atmospheric acid deposition, is among the main factors involved in the present-day expansion of American beech”. Their conclusions are based on an examination of the relationships between stem densities in the sapling and tree strata compared against canopy composition and the availability of base cations at 426 sample plots in southern Quebec. In their paper, D&O argued that overstory SM tree health declined as a re-

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sult of atmospheric acid deposition and concomitant soil acidification, leading to an opening of the canopy and increased light transmission to the understory that favored the recruitment of AB over SM. They contended that SM is undergoing a regeneration failure, while AB, being less sensitive to soils low in base cations, is benefiting from the decreased competition with SM as well as increased understory light associated with SM decline. Although some of the results reported by D&O might be consistent with this hypothesis, we argue that their overall conclusions are based on some logically flawed interpretations and an unrepresentative sample, comprise several overstatements, and offer a misleading and oversimplified explanation of a rather complex phenomenon. The purpose of this comment is to provide a more prudent and complete perspective on the complex dynamics associated with fluctuations in AB and SM abundance.

Expansion of American beech and regeneration failure of sugar maple

D&O related the increase of AB to site characteristics, and more particularly to soil properties. While we agree that there have been reports of increases in AB abundance locally (e.g., Beaudet et al. 1999) and regionally over relatively short time scales (Duchesne et al. 2005), we argue that the methodology employed by D&O is inappropriate to document and, most of all, locate increases in AB abundance relative to SM. Their conclusion of an increase in AB at the expense of SM is based on static observations of relatively small differences in the relative abundance of species between saplings (14.5% for AB and 40.1% for SM) and trees (9.7% for AB and 46.6% for SM) in a subjectively selected set of plots (D&O's Fig. 1). Such static information, and in D&O's case for only two size classes, cannot support inferences of past or future change in species composition. Condit et al. (1998) demonstrated from both theory and empirical data that "static information on the size distribution is not a good predictor of future population trends". Concluding that the relative abundance of saplings determines the future relative abundance of trees assumes that transition rates are the same for all species and over all life history stages, which is unsupported by empirical data (Pacala et al. 1994; Kobe et al. 1995; Kneeshaw et al. 2006; Gravel et al. 2008).

SM decline in Quebec caused by atmospheric acid deposition and soil acidification

D&O proposed that atmospheric acid deposition reduced soil base cation reserves, affecting SM nutrition and health. While there is strong evidence for an adverse effect of acid deposition on soil base cation reserves in northeastern North America (e.g., Likens et al. 1996; Bélanger et al. 2002; Thiffault et al. 2007), the sampling design in D&O was not developed to show the extent of soil acidification in Quebec, nor do their data document this phenomenon. The design simply offers information regarding a range of sites with contrasting productivities, including different availabilities in Ca and Mg that are correlated with sapling and tree abun-

dance of AB and SM. This is insufficient basis to conclude that soil acidification due to air pollution is causing a widespread SM decline and regeneration failure in Quebec. Only a few studies in the northeastern United States (Pennsylvania) linked SM decline to low base cation availability, and these were done on acidified, unglaciated soils (e.g., Horsley et al. 2000; Bailey et al. 2004). Others have argued that SM nutrition and health are less affected by air pollution on younger, glaciated soils (Drohan et al. 1999, 2002; Miller and Watmough 2009), although there seems to be widespread SM decline in western Pennsylvania (Hall et al. 1999). In the latter case, however, the decline was not associated with Ca and Mg deficiencies, but rather to severe drought, late spring frosts, and unusual defoliation events. Finally, although the observation that experimental liming improves crown vigor, nutrition, and growth (Moore et al. 2000, 2008) is consistent with a hypothesis that SM decline can be caused by soil base cation depletion, this is not decisive evidence that soil acidification induced by air pollution is causing SM decline *so long as there are reasonable alternative explanations*. For example, a response of SM to fertilization could simply indicate that trees are limited by base cations because they are found on soils developed from bedrock with intrinsically low base cation levels (e.g., Precambrian Shield granitic rocks). Moreover, D&O did not sample in the southwestern part of Quebec where the SM decline was reported to be the most severe (e.g., Paré and Bernier 1989; Ouimet and Camiré 1995) or from the region south and east of Montreal in the St. Lawrence River Valley, which is characterized by base cation rich soils developed from the Champlain Sea lacustrine sediments (e.g., Beaudet et al. 1999).

Relative basal area of dead SM trees used as a proxy to SM decline

D&O observed that the relative basal area of dead SM was nearly double on sites where AB was present among saplings compared with sites where AB was absent. Based on this and on the fact that this same variable explained 10%–12% of the variance in the basal area and relative basal area of AB in the sapling stratum, they claim that "AB was favoured by the decline of SM canopy trees". Such reasoning is based on assumptions that the "Relative basal area of dead SM integrates stand health over a fairly long period of time" and that relative basal area of dead SM is an adequate proxy for the presence of SM decline. Although SM decline might indeed lead to an increased percent basal area of dead SM, an increased percent basal area of dead SM is not necessarily caused by maple decline. Ice storm damage, insect and disease outbreaks, or simply age-dependent mortality all can account for an increased relative basal area of dead SM. For instance, in the D&O study, data from stands at all successional stages were combined within a data set containing a wide range of basal area typical of recently logged forests (lowest basal area = 0.3 m²·ha⁻¹) to mature forests (basal area >40m²·ha⁻¹). The higher proportion of dead SM observed in the presence of AB saplings might simply be related to the tendency for AB to be present at later successional stages and a higher rate of SM mortality related to overall greater tree age in late-successional

stages. There clearly are other causal factors and alternative interpretations that were not considered by D&O, which undermines their conclusions.

SM sapling distribution and abundance as a function of soil base cation availability

D&O claimed that “failure of SM regeneration was higher on base-poor sites”, but their data do not support a relationship between SM sapling distribution and soil exchangeable base cation concentrations. The results presented in their Table 2 do not show any significant difference in Ca and Mg availability between sites where SM saplings are present versus absent, a point overlooked in the discussion. D&O apparently based their conclusion instead on results from Table 3 where they reported that SM relative basal area in the sapling stratum increased with soil Ca and Mg concentrations. However, the correlations supporting their conclusion were weak (Spearman’s r of 0.113 and 0.111 for Ca and Mg, respectively) and only marginally significant ($p < 0.071$). Here, one should further note that no Bonferroni or other correction to the level of significance was considered despite the large number of correlation tests (54) in Table 3. D&O also overlooked the fact that there was no correlation between SM *absolute* basal area in the sapling stratum and base cations (Spearman’s r of 0.017 and 0.018 for Ca and Mg, respectively; Table 3). Finally, D&O failed to mention the many contradictory observations on the relationships between SM–AB abundance and soil properties (e.g., van Breemen et al. 1997; Beaudet et al. 1999; Schwarz et al. 2003; Arie et al. 2005; Gravel et al. 2008). In our opinion, D&O did not have sufficient quantitative and statistical evidence to support their conclusion of a *SM regeneration failure* associated with base-poor sites, nor therefore their inferences attributing AB increases to a negative impact of atmospheric acid deposition on soil base cation status.

Conclusion

We believe that D&O should have considered and discussed published studies that do not concur with their main hypothesis, been more careful in the interpretation of their results, and tested alternative explanations for their observations. They also should have better explained why they had selectively excluded parts of the most southern ranges of AB and SM in Quebec that are highly relevant to the question. There have been several reports of recent local or more global increases in AB abundance in the temperate forests of eastern North America (e.g., Beaudet et al. 1999; Forrester et al. 2003; Duchesne et al. 2005; Busby et al. 2008) as well as in SM (Siccama 1971; McIntosh 1972; Abrell and Jackson 1977; Runkle 1990; Fain et al. 1994; Poulson and Platt 1996; Foré et al. 1997). Several interacting factors can play a role in determining the abundance of AB, including its low palatability to deer, its ability to reproduce vegetatively, its susceptibility to beech bark disease, and its response to various types of disturbances including ice storms and human activities such as harvesting (e.g., Rhoads et al. 2002; Brisson and Bouchard 2003; Leak 2006; Beaudet et al. 2007; Long et al. 2007; Runkle 2007; Busby et al. 2008; Takahashi and Lechowicz 2008; Takahashi et al. 2010). A recent study also suggests that the distribution of SM and

AB is related to a major change in small-scale disturbance history (Gravel et al. 2010). Moreover, the high shade tolerance of AB puts it at an advantage in long-term successional trends (Kobe et al. 1995). Supporting this view is the fact that presettlement abundance of AB has been repeatedly shown to be higher than modern abundance (Siccama 1971; McIntosh 1972; Simard and Bouchard 1996; Brisson and Bouchard 2003).

Similarly, many other factors and mechanisms can be involved in a decrease in SM density and an associated increase in AB density; with the exception of harvest impacts, none of these factors were mentioned by D&O. We suggest that both local and large-scale variations in the relative abundance of AB and SM most likely result from multiple interacting factors. Oversimplified explanations and overstatements retard rather than advance our scientific understanding of this important aspect of the long-term dynamics of eastern North American forests.

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