

DISCUSSION / DISCUSSION

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

Christian Messier, Nicolas Bélanger, Jacques Brisson, Martin J. Lechowicz, and Dominique Gravel

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.).

[Traduit par la Rédaction]

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-

Received 3 March 2010. Accepted 14 September 2010. Published on the NRC Research Press Web site at cjfr.nrc.ca on 16 February 2011.

C. Messier.² Département des sciences biologiques, Centre d'Étude de la Forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada.

N. Bélanger. Télugu, Centre d'Étude de la Forêt, Université du Québec à Montréal, 100 rue Sherbrooke Ouest, Montréal, QC H2X 3P2, Canada.

J. Brisson. Institut de recherche en biologie végétale, Centre d'Étude de la Forêt, Université de Montréal, 4101 Sherbrooke Est, Montréal, QC H1X 2B2, Canada.

M.J. Lechowicz. Department of Biology, Centre d'Étude de la Forêt, McGill University, 1205 Docteur Penfield Ave., Montréal, QC H3A 1B1, Canada.

D. Gravel. Département de biologie, chimie et géographie, Centre d'Étude de la Forêt, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

¹Appears in *Can. J. For. Res.* **39**: 2273–2282 (2009).

²Corresponding author (e-mail: messier.christian@uqam.ca).

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.

References

- Abrell, D.B., and Jackson, M.T. 1977. A decade of change in an old-growth beech–maple forest in Indiana. *Am. Midl. Nat.* **98**(1): 22–32. doi:10.2307/2424712.
- Arie, K., Hamel, B.R., and Lechowicz, M.J. 2005. Environmental correlates of canopy composition at Mont St. Hilaire, Quebec, Canada. *J. Torrey Bot. Soc.* **132**(1): 90–102. doi:10.3159/1095-5674(2005)132[90:ECOCCA]2.0.CO;2.
- Bailey, S.W., Horsley, S.B., Long, R.P., and Hallett, R.A. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. *Soil Sci. Soc. Am. J.* **68**(1): 243–252. doi:10.2136/sssaj2004.0243.
- Beaudet, M., Messier, C., Paré, D., Brisson, J., and Bergeron, Y. 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Bois-des-Muir old-growth forest, Quebec. *Ecoscience*, **6**(2): 264–271.
- Beaudet, M., Brisson, J., Gravel, D., and Messier, C. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. *J. Ecol.* **95**(3): 458–467. doi:10.1111/j.1365-2745.2007.01219.x.
- Bélanger, N., Courchesne, F., Côté, B., Fyles, J.W., Warfvinge, P., and Hendershot, W.H. 2002. Simulation of soil chemistry and nutrient availability in a forested ecosystem of southern Quebec. Part II. Application of the SAFE model. *Environ. Model. Softw.* **17**(5): 447–465. doi:10.1016/S1364-8152(02)00008-7.
- Brisson, J., and Bouchard, A. 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Quebec. *Ecoscience*, **10**: 236–246.
- Busby, P.E., Motzkin, G., and Foster, D.R. 2008. Multiple and interacting disturbances lead to *Fagus grandifolia* dominance in coastal New England. *J. Torrey Bot. Soc.* **135**(3): 346–359. doi:10.3159/08-RA-004.1.
- Condit, R., Sukumar, R., Hubbell, S.P., and Foster, R.B. 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. *Am. Nat.* **152**(4): 495–509. doi:10.1086/286186.
- Drohan, P., Stout, S.L., and Petersen, G.W. 1999. Spatial relationships between sugar maple (*Acer saccharum* Marsh.), sugar maple decline, slope, aspect, and atmospheric deposition in northern Pennsylvania. In *Proceedings of an International Symposium, June 2 to 4, 1998, Warren, Pennsylvania: Sugar Maple Ecology and Health*. Edited by S.B. Horsley and R.P. Long. U.S. For. Serv. Gen. Tech. Rep. NE-261. pp. 46–50.

- Drohan, P.J., Stout, S.L., and Petersen, G.W. 2002. Sugar maple (*Acer saccharum* Marsh.) decline during 1979–1989 in northern Pennsylvania. *For. Ecol. Manag.* **170**(1–3): 1–17. doi:10.1016/S0378-1127(01)00688-0.
- Duchesne, L., and Ouimet, R. 2008. Population dynamics of tree species in southern Quebec, Canada: 1970–2005. *For. Ecol. Manag.* **255**(7): 3001–3012. doi:10.1016/j.foreco.2008.02.008.
- Duchesne, L., and Ouimet, R. 2009. Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter? *Can. J. For. Res.* **39**(12): 2273–2282. doi:10.1139/X09-172.
- Duchesne, L., Ouimet, R., Moore, J.-D., and Paquin, R. 2005. Changes in structure and composition of maple–beech stands following maple decline in Québec, Canada. *For. Ecol. Manag.* **208**(1–3): 223–236. doi:10.1016/j.foreco.2004.12.003.
- Fain, J.J., Volk, T.A., and Fahey, T.J. 1994. 50 years of change in an upland forest in south-central New York: general patterns. *Bull. Torrey Bot. Club*, **121**(2): 130–139. doi:10.2307/2997164.
- Foré, S.A., Vankat, J.L., and Schaefer, R.L. 1997. Temporal variations in the woody understory of an old-growth *Fagus–Acer* forest and implications for overstory recruitment. *J. Veg. Sci.* **8**(5): 607–614. doi:10.2307/3237364.
- Forrester, J.A., McGee, G.G., and Mitchell, M.J. 2003. Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest 1985 to 2000. *J. Torrey Bot. Soc.* **130**(2): 70–78.
- Gravel, D., Beaudet, M., and Messier, C. 2008. Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. *Ecology*, **89**(10): 2879–2888. doi:10.1890/07-1596.1.
- Gravel, D., Beaudet, M., and Messier, C. 2010. Large-scale synchrony of gap dynamics and the distribution of understory tree species in maple–beech forests. *Oecologia (Berl.)*, **162**(1): 153–161. doi:10.1007/s00442-009-1426-6.
- Hall, T.J., Unger, J.S., Bast, T.C., and Regester, B.S. 1999. Factors associated with rapid mortality of sugar maple in Pennsylvania. *In Proceedings of an International Symposium, June 2 to 4, 1998, Warren, Pennsylvania: Sugar Maple Ecology and Health. Edited by S.B. Horsley and R.P. Long. U.S. For. Serv. Gen. Tech. Rep. NE-261. pp. 51–54.*
- Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., and Hall, T.J. 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. *Can. J. For. Res.* **30**(9): 1365–1378. doi:10.1139/cjfr-30-9-1365.
- Kneeshaw, D.D., Kobe, R.K., Coates, K.D., and Messier, C. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *J. Ecol.* **94**(2): 471–480. doi:10.1111/j.1365-2745.2005.01070.x.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **5**(2): 517–532. doi:10.2307/1942040.
- Leak, W.B. 2006. Fifty-year impacts of the beech bark disease in the Bartlett Experimental Forest, New Hampshire. *North. J. Appl. For.* **23**: 141–143.
- Likens, G.E., Driscoll, C.T., and Buso, D.C. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science*, **272**(5259): 244–246. doi:10.1126/science.272.5259.244.
- Long, Z.T., Pendergast, T.H., IV, and Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech–maple forest. *For. Ecol. Manag.* **252**(1–3): 230–238. doi:10.1016/j.foreco.2007.06.034.
- McIntosh, R.P. 1972. Forests of the Catskill Mountains, New York. *Ecol. Monogr.* **42**(2): 143–161. doi:10.2307/1942261.
- Miller, D.E., and Watmough, S.A. 2009. Air pollution, climate, soil acidity, and indicators of forest health in Ontario's sugar maple forests. *Can. J. For. Res.* **39**(11): 2065–2079. doi:10.1139/X09-124.
- Moore, J.-D., Camiré, C., and Ouimet, R. 2000. Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Quebec, Canada. *Can. J. For. Res.* **30**(5): 725–732. doi:10.1139/cjfr-30-5-725.
- Moore, J.D., Duchesne, L., and Ouimet, R. 2008. Soil properties and maple–beech regeneration a decade after liming in a northern hardwood stand. *For. Ecol. Manag.* **255**(8–9): 3460–3468. doi:10.1016/j.foreco.2008.02.026.
- Nolet, P., Bouffard, D., Doyon, F., and Delagrangé, S. 2008. Relationship between canopy disturbance history and current sapling density of *Fagus grandifolia* and *Acer saccharum* in a northern hardwood landscape. *Can. J. For. Res.* **38**(2): 216–225. doi:10.1139/X07-160.
- Ouimet, R., and Camiré, C. 1995. Foliar deficiencies of sugar maple stands associated with soil cation imbalances in the Quebec Appalachians. *Can. J. Soil Sci.* **75**(2): 169–175. doi:10.4141/cjss95-024.
- Pacala, S.W., Canham, C.D., Silander, J., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* **24**(11): 2172–2183. doi:10.1139/x94-280.
- Paré, D., and Bernier, B. 1989. Origin of the phosphorus deficiency observed in declining sugar maple stands in the Quebec Appalachians. *Can. J. For. Res.* **19**(1): 24–34. doi:10.1139/x89-004.
- Poulson, T.L., and Platt, W.J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology*, **77**(4): 1234–1253. doi:10.2307/2265592.
- Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. *Can. J. For. Res.* **32**(10): 1763–1775. doi:10.1139/x02-089.
- Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.* **20**(5): 632–641. doi:10.1139/x90-085.
- Runkle, J.R. 2007. Impacts of beech bark disease and deer browsing on the old-growth forest. *Am. Midl. Nat.* **157**(2): 241–249. doi:10.1674/0003-0031(2007)157[241:IOBBD]2.0.CO;2.
- Schwarz, P.A., Fahey, T.J., and McCulloch, C.E. 2003. Factors controlling spatial variation of tree species abundance in a forested landscape. *Ecology*, **84**(7): 1862–1878. doi:10.1890/0012-9658(2003)084[1862:FCSVOT]2.0.CO;2.
- Siccama, T.G. 1971. Presettlement and present forest vegetation in northern Vermont with special reference to Chittenden County. *Am. Midl. Nat.* **85**(1): 153–172. doi:10.2307/2423919.
- Simard, H., and Bouchard, A. 1996. The precolonial 19th century forest of the upper St. Lawrence region of Quebec: a record of its exploitation and transformation through notary deeds of wood sales. *Can. J. For. Res.* **26**(9): 1670–1676. doi:10.1139/x26-188.
- Takahashi, K., and Lechowicz, M.J. 2008. Do interspecific differences in sapling growth traits contribute to the co-dominance of *Acer saccharum* and *Fagus grandifolia*? *Ann. Bot. (Lond.)*, **101**(1): 103–109. doi:10.1093/aob/mcm259.
- Takahashi, K., Arii, K., and Lechowicz, M.J. 2010. Codominance of *Acer saccharum* and *Fagus grandifolia*: the role of *Fagus* root sprouts along a slope gradient in an old-growth forest. *J. Plant Res.* **123**(5): 665–674. doi:10.1007/s10265-010-0312-y.
- Thiffault, E., Bélanger, N., Paré, D., Hendershot, W.H., and Munson, A.D. 2007. Investigating the soil acid–base status in man-

ged boreal forests using the SAFE model. *Ecol. Model.* **206**(3–4): 301–321. doi:10.1016/j.ecolmodel.2007.03.044.

van Breemen, N., Finzi, A.C., and Canham, C.D. 1997. Canopy

tree – soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. *Can. J. For. Res.* **27**(7): 1110–1116. doi:10.1139/cjfr-27-7-1110.