How do natural disturbances and human activities affect soils and tree nutrition and growth in the Canadian boreal forest?[1]

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Abstract: There are concerns about the effect of increasing resource extraction and other human activities on the soils and vegetation of the boreal zone. The review covers published papers between 1974 and 2012 to assess the effects of natural disturbances and human activities on soils and tree nutrition and growth of the Canadian boreal zone. Changes in soil and foliar nutrients following disturbance were also analyzed by meta-analysis. When sufficient replicated studies were not available for a given disturbance or nutrient, response assessments or narrative summaries are presented. The majority of fertilization studies in the boreal zone showed a positive tree growth response to nitrogen (N) and phosphorus (P) fertilization either individually or in combination. Large amounts of N may be lost through volatilization following fire depending on the severity and frequency of the fire. This may contribute to N limitation in the boreal zone. Available soil P and extractable calcium (Ca) and magnesium (Mg) increased in the surface horizons following fire. In contrast, extractable P decreased following harvest. Harvesting had no effect on total or inorganic N except in mixedwoods where total N decreased in the surface organic horizon following harvest. These are potential areas of concern given tree growth responses to N and P fertilization. Potassium (K) in the forest floor did not change following fire or harvesting; thus, K availability for tree nutrition should not be at risk, since its cycle is rapidly restored. Mercury (Hg) cycling may be altered in the boreal zone as a result of flooding and if fire return intervals and intensities increase. Interactions of multiple disturbances may increase the risk of nutrient depletions, but there is currently little information on these interactions in the boreal zone. Evidence to date suggests the soils of the Canadian boreal zone have not been adversely affected except in localized areas. However, there is the risk of nutrient loss if soils are not considered in our forest management strategies, particularly where multiple disturbances may interact. The potential for off-site movement of nutrients and contaminants into the atmospheric and aquatic ecosystems, in addition to on-site environmental issues, is also a concern.

Key words: boreal, disturbances, nutrient cycling, nitrogen, phosphorus, base cations, mercury, soils.

Résumé : En région boréale, l'augmentation du nombre de projets d'extraction des ressources ainsi que des autres activités humaines soulève des inquiétudes quant aux impacts sur les sols et la végétation. Cette synthèse traite des articles publiés sur ce sujet entre 1974 et 2012 afin d'évaluer l'effet des perturbations naturelles et d'origine anthropique sur les sols et sur la croissance et la nutrition des arbres de la zone boréale canadienne. Les changements au niveau des sols et de la nutrition foliaire à la suite des perturbations ont aussi été analysés par méta-analyse. Lorsque le nombre d'études répétées n'était pas suffisant pour évaluer de manière statistique un type de perturbation ou de nutriment, l'évaluation se limite à la présentation des résultats ou à un résumé de la situation. La plupart des études de fertilisation en zone boréale ont montré une réponse positive de la croissance des arbres à la fertilisation en azote (N) et en phosphore (P) appliqué individuellement ou ensemble. Des quantités importantes de N peuvent être perdues par volatilisation lors des feux de forêt, tout dépendants de l'intensité et de la fréquence de ces feux. Ceci pourrait contribuer à maintenir l'azote dans un état limitatif en forêt boréale. La disponibilité en P, ainsi qu'en calcium (Ca) et en magnésium (Mg) extractibles augmente dans les horizons de surface à la suite d'un feu. À l'opposé, le P extractible décroît à la suite de la récolte. On n'a pas observé d'effets de la récolte sur le N total ou inorganique, sauf dans le cas des forêts mixtes où le N total décroît dans l'horizon organique de surface après la récolte. Ceci peut être considéré comme étant préoccupant si l'on considère la réponse du taux de croissance des arbres à la fertilisation en N et P. Le potassium (K) de la couche organique du sol n'a pas changé à la suite de feu ou de la récolte, indiquant ainsi que la disponibilité de K pour la nutrition des arbres ne devrait pas être à risque puisque son cycle est rapidement restauré. Le cycle du mercure (Hg) peut être altéré par l'ennoiement et lorsque l'intensité et la fréquence des feux de forêt augmentent. L'effet combiné de plusieurs perturbations peut augmenter les risques de baisse de la disponibilité des nutriments, mais il n'existe que très peu d'information à ce sujet en zone boréale. À ce jour, il n'y a pas d'évidences que les sols de la zone boréale canadienne ont été affectés négativement, sauf dans certains endroits bien précis. Cependant, il y a un risque d'appauvrissement des sols si ceux-ci ne sont pas considérés dans nos stratégies d'aménagement, tout particulièrement dans les situations où de multiples perturbations peuvent interagir entre elles. En

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plus des enjeux à l'échelle du site, le déplacement potentiel de nutriments et de contaminants hors des sites forestiers vers l'atmosphère ou vers les écosystèmes aquatiques est aussi une source de préoccupations.

Mots-clés : boréal, perturbation, cycle des nutriments, azote, phosphore, cations basique, mercure, sols.

1. Introduction

Soil (pedosphere) is part of the Earth's critical zone where inter-action occurs with the lithosphere, atmosphere, hydrosphere, and biosphere (Yaalon 2007; National Research Council 2009). The ecological processes of nutrient cycling through soil and vegetation provide adequate and balanced supplies of nutrients necessary for life that underpin all other ecological services (Millennium Ecosystem Assessment 2005).

Soils are formed from the combined effects of climate, biotic activities, topography, parent material, and time (Jenny 1941). The soils of the boreal zone are of a similar age with most developing since the end of the last glaciation at about 10 000 – 6 000 years ago (young in geological terms), with some pockets of much older soils predating that glaciation (e.g., on the Gaspésie peninsula of Quebec). However, differences in the other four factors of soil formation have resulted in a mosaic of soils across the boreal landscape (Fig. 1). In eastern Canada, coarse-textured acidic soils of the Podzolic order predominate, with the exception of the clay belt, with its Luvisolic soils in east-central Ontario and western Quebec. In western Canada (e.g., Boreal and Taiga Shield West ecozones), fine-textured Luvisolic soils and lesser developed Brunisolic soils are the major soil types. Cryosolic soils with continuous permafrost dominate in the Taiga and Hudson Plains. Interspersed throughout the boreal zone are Gleysolic (mineral) and Organic soils (e.g., peats, bogs, and fens) in low-lying areas with fluctuating water tables and Regosols that formed from more recent deposition of parent materials such as alluvial deposits in floodplains. Black Chernozems occur on the southern edges of the Boreal Plain Ecozone (Rennie 1978; Kabzems et al. 1986).

The productivity of the boreal zone is influenced by soil type (Rennie 1978). On the Canadian Shield in the northern part of the boreal zone (Taiga Shield East and West ecozones), the soils generally support very low forest productivity (<1 m³·ha⁻¹·year⁻¹) (Bickerstaff et al. 1981). Podzols are the dominant soil type, except for in the northwest, which is predominantly Brunisols. The Luvisolic soils in the Boreal Plain and Boreal Shield West, along with areas of Chernozemic soils in the southern part of these ecozones, are low to moderately productive (0.6–1.5 m³·ha⁻¹·year⁻¹). The southern sections of Ontario and Quebec, primarily consisting of Podzols, are the most productive (1.2–3.0 m³·ha⁻¹·year⁻¹) areas of the boreal zone (Rennie 1978; Bickerstaff et al. 1981). Podzols and Brunisols have a wide range of physical and chemical properties under various climatic regimes, so sites associated with these soils range widely in mean annual growth increment (Sanborn et al. 2011; Smith et al. 2011). In general, Brunisols and Podzols in the boreal regions of Canada are often coarse-textured and would be less productive and more susceptible to nutrient depletions than associated fine-textured Luvisolic or Chernozemic soils (Lavkulich and Arocena 2011; Pennock et al. 2011; Sanborn et al. 2011; Smith et al. 2011).

The natural process of soil formation occurs slowly during a prolonged period of time (Yaalon and Yaron 1966). In undisturbed conditions, changes to the soil profile and chemical properties in the short term (i.e., decades) are nearly imperceptible; however, natural disturbances such as wildfire, insect and disease outbreaks, windthrow, landslides, and erosion alter soil nutrient cycles in boreal ecosystems. The partial or complete removal of aboveground biomass is the most obvious effect of most disturbances; soil processes may be affected as well, resulting in impacts on soil quality and other ecosystem services that may be either positive or negative (Maynard 2002). A wide range of potential responses of soil nutrients to disturbance has been observed in various forest ecosystems, although nutrient loss is often considered the norm (Turner 2010). The extent of loss and long-term effects are dependent on a combination of factors such as the disturbance regime (e.g., frequency, type, and severity), climate, tree species, and soil properties.

Environmental change, including soil formation and disturbance, occurred naturally during the Holocene following glaciation in the boreal zone. Since the Industrial Revolution (1750–1850), human actions (e.g., forestry operations, mining, and other resource extractions) have been considered the main drivers of global environmental change (Rockström et al. 2009). Currently, the boreal zone remains relatively undisturbed by human activity. It has been estimated that 3% of the Canadian boreal zone has been converted to other land use and 31% has been accessed by industrial development (Anielski and Wilson 2009), but access varies considerably among ecozones. The increasing pressures of resource extraction and other human activities have raised concerns about the long-term function of the boreal zone (Wells et al. 2010; Brandt et al. 2013). Influence on soils can either be local or regional from the effects of activities such as resource extraction (e.g., mining) or activities occurring at larger scales (e.g., climate change, Hg inputs, acid deposition, and N saturation) potentially compromising soil productivity. Although much of our knowledge is based on singular disturbances, interactions of multiple disturbances (natural or anthropogenic) can create conditions of extreme severity or of novel characteristics, resulting in unpredictable recovery pathways (Buma and Wessman 2012). Unfortunately, there is a paucity of empirical data on these interactions.

This review synthesizes data on nutrient limitation and how natural disturbances and human activities affect soils and tree nutrition and growth in the Canadian boreal forest and Alaska (as defined by Brandt 2009). In some cases, studies from boreal forests outside of North America or boreal species growing in temperate forests were also considered where there was insufficient data from North America. Formal meta-analyses, response assessments, or a narrative summary of the effects of disturbances on boreal soils were conducted depending on the availability of data.

The boreal forest is considered nutrient limited and results of fertilizer studies show tree growth response to various nutrients. The effect of the major natural disturbances, fire, insect and disease on soil nutrient cycling is compared with changes in soil nutrients as a result of human activities in the boreal, harvesting and site preparation, acid deposition, and flooding. The implications of global climate change on soil processes (e.g., permafrost and C budgets) are discussed elsewhere (Price et al. 2013; Kurz et al. 2013; Lemprière et al. 2013). Disruption of soil nutrient cycles can potentially affect other ecosystems services within the boreal zone. Water quality and biodiversity, some of the key ecosystems services and disturbances not covered in this review, are discussed in Kreutzweiser et al. 2013 and Vernier et al. Manuscript in preparation, respectively.

2. Methods

Data were compiled from the primary literature using Scopus between 13 December 2010 and 7 January 2011. Keyword search strings combined the main terms Boreal soil and soil + Taiga with the following keywords: fertilization, mining, oil, exploration, fire, acid rain, air pollution, pollutant, permafrost, insect, disease, fire, wildfire, site preparation, disturbance, climate change, biogeochemistry, soil quality, soil resilience, logging, and harvesting.

Fig. 1. Dominant texture, parent material, and soil orders of the boreal ecozones. Soil orders are not shown for the six ecozones (Pacific Maritime, Southern Arctic, Montane Cordillera, Subhumid Praires, Arctic Cordillera, and Atlantic Maritime) that each represent <2% of the total boreal ecozone area. Pie charts show the three dominant soil orders. In all cases these represent >95% of the total ecozone area. The data for the map were obtained from the Department of Agriculture and Agri-food soils web site http://sis.agr.gc.ca/cansis/index.html.
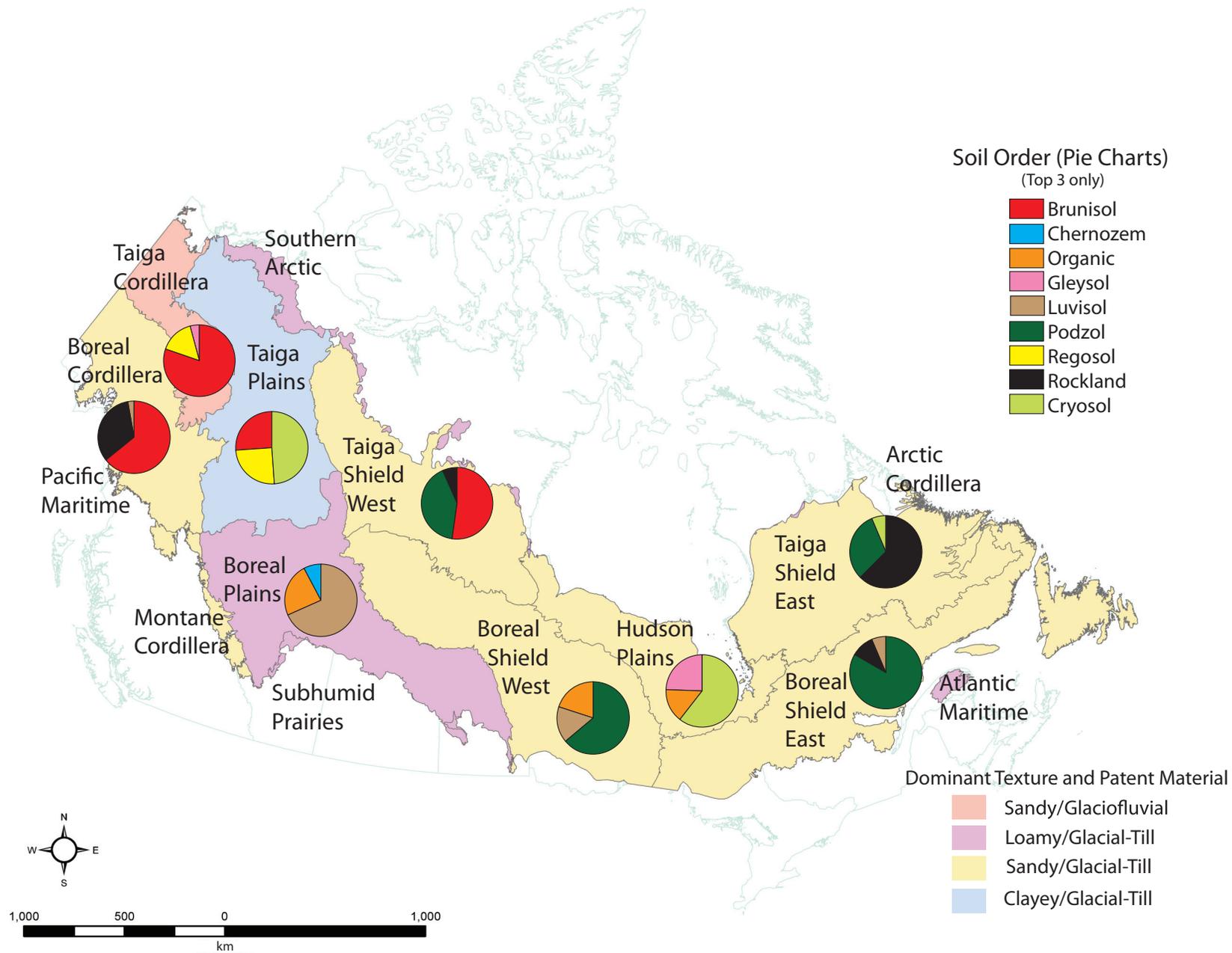
Data were obtained from the original articles. When presented in graphic form, Graphclick (version 3.0; Arizona Software 2008) was used to derive means and error terms. We considered studies conducted at distinct sites from the same publication to be separate entries, as well as each year for multiyear measurements (one datum input per year) for studies that spanned more than one year.

2.1. Fertilizer studies as a tool to evaluate limiting nutrients

Studies on the effects of fertilization on tree growth have provided the best evidence for assessing a soil's ability to provide nutrients in relation to tree demand (Foster and Morrison 1983). We compiled the results from published fertilization trials that had been conducted in the boreal zone on native Canadian tree species to give an indication of the nutrient limitations of forest productivity. We reported the natural log of fertilized to unfertilized growth ratios for N only, P only, and N and P fertilization. It was not possible to find a significant amount of data for other nutrients, either alone or in combination. A growth ratio, ln(fertilized + 1)/ln(unfertilized + 1) > 1, indicated an increase in growth (for various parameters) following fertilization. Only one growth parameter was retained per experimental trial to avoid duplication. Parameters were selected in the following order, giving priority to those that were more integrative of stand growth response: biomass growth > height growth > diameter at breast height (DBH) growth > root biomass > branch biomass. Thirty-four publications and 218 experimental trials were found for N only fertilization, 11 publications and 37 experimental trials for P only fertilization, and 9 publications and 29 experimental trials for N and P (the papers used in this analysis are listed in the supplementary data[2]).

2.2. Natural and anthropogenic (human-induced) disturbance studies

We conducted meta-analysis on soil nutrients following disturbances using the methods of Hedges et al. (1999) and Nave et al. (2010). We chose to use a weighted meta-analysis; therefore, only publications reporting error terms and sample size or sample size and significance level (p or t value) could be included. We limited studies to sites from the Canadian boreal forest and the boreal zone in Alaska defined in Brandt (2009). In addition to treatment means of soil nutrient concentration or content, error terms, sample size, and p or t value, we also extracted measurement units and categorical variables that can be potentially useful predictors of variation in the soil nutrient responses to disturbance.

Disturbance effects were analyzed using a weighted mixed-effects model (Hedges et al. 1999; LeBauer and Teseder 2008; Borenstein et al. 2009). All meta-analyses were carried out with comprehensive meta-analysis software (Borenstein et al. 2009). Overall and categorical results are reported as response ratios (ln(R)) calculated as the natural log of a given nutrient in treated (e.g., harvested or fire) and control plots:

$$\ln(R) = \text{Nutrient}_{treated}/\text{Nutrient}_{control}$$

The ln(R) was calculated from each study to obtain a single unitless response metric. This allowed comparison of data among experiments reporting nutrient responses in different units (Hedges et al. 1999; Nave et al. 2010). Data reported were then back-transformed $\ln(R)(e^{\ln(R)})$ with 95% confidence intervals (CIs) and degrees of freedom (df). Effects of disturbance were significant at $p = 0.05$ if CIs did not include $R = 1$.

We tested categorical variables that were potential predictors of variation in the soil nutrient responses to disturbances. We followed the approach of Nave et al. (2010) and detailed in Jablonski et al. (2002) in a procedure analogous to partitioning of variance in analysis of variance (ANOVA). The total heterogeneity (Q_t) for a group of comparisons was partitioned into within-groups (Q_w) and between-groups (Q_b) heterogeneity. A categorical variable with a large Q_b is a better predictor of variation than a variable with a small Q_b (Nave et al. 2010). Meta-analysis was run on the entire database and then divided into categories by the categorical variable that had the lowest p value. Within each of these groups, meta-analysis was run again for each categorical variable. Further partitioning was not done because of limited sample sizes for several of the categories. Many potential variables were not included in the analysis because too few studies reported a given category to be statistically useful or there was insufficient information to properly categorize studies as in Knorr et al. (2005).

The first meta-analysis comparison was of soil nutrients in unburned and burned sites. Unburned sites included unharvested and harvested stands that were not burned as controls because of the limited number of studies available. We categorized the database into potential predictor variables: soil layer (horizon) sampled (i.e., forest floor (organic horizons) and mineral (top 20 cm)), time since fire (arbitrarily set at <5 years and 5–20 years), experimental versus wildfires, and forest type.

We also compared soil nutrients between uncut controls and harvested treatments. Studies that did not report nutrient data for uncut stands were excluded. We did not distinguish among harvesting systems because of limitations with the number of studies. We used four predictor variables: soil layers (i.e., forest floor and mineral), time since harvest (i.e., <5 years and 5–20 years), soil order (according to the Soil Classification Working Group (1998)), and forest type. There were five soil orders included in the studies (Podzols, Luvisols, Brunisols, Regosols, and Gleysols); the studies were predominantly on Luvisols (followed by Podzols), so the meta-analysis categorized by soil order was limited because there were few studies on the other soil orders (in some categories only Luvisols were sampled). We categorized forest types as coniferous, deciduous, and mixedwood.

There were eight publications containing between 35 and 58 comparisons that met our criteria for fire versus unburned controls and 28 publications containing between 30 and 61 comparisons that met our criteria for the harvested versus uncut control (see supplementary data[2] for the papers used in these analyses). The nutrients analyzed were total N, inorganic ammonium (NH_4^+-N), and nitrate (NO_3^--N) (only for harvested versus uncut), extractable P, and exchangeable calcium (Ca^{2+}), magnesium (Mg^{2+}), and K^+. Not all nutrients were included in every paper, and there were multiple values per nutrient obtained from most studies.

There were insufficient replicated studies to carry out meta-analysis on insect and diseases disturbances, mercury cycling and erosion following fire, site preparation following harvest, acid deposition and N saturation, and flooding. For these sections, discussion was limited to narrative summaries based on the few studies in the Canadian boreal zone.

3. Results and discussion

3.1. Fertilizer studies as a tool to evaluate limiting nutrients

Fertilizer studies on boreal zone tree species showed a positive growth response to N fertilization on 85% of the experiments (Fig. 2a), 94% for P fertilization (Fig. 2b), and 97% for N + P applications (Fig. 2c). These results indicate the ubiquitous limitation of these nutrients. The boreal forest is generally considered nutrient

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Fig. 2. Fertilized to unfertilized natural log (ln) growth ratio (±SD) of boreal tree species in North America fertilized with (*a*) nitrogen (N), (*b*) phosphorus (P), and (*c*) nitrogen (N) and phosphorus (P). Ratios above 1 indicate a positive growth response to fertilization. Numbers within bars indicate the number of observations. tA, trembling aspen; bS, black spruce; wB, white birch; lP, lodgepole pine; bF, balsam fir; and jP, jack pine.
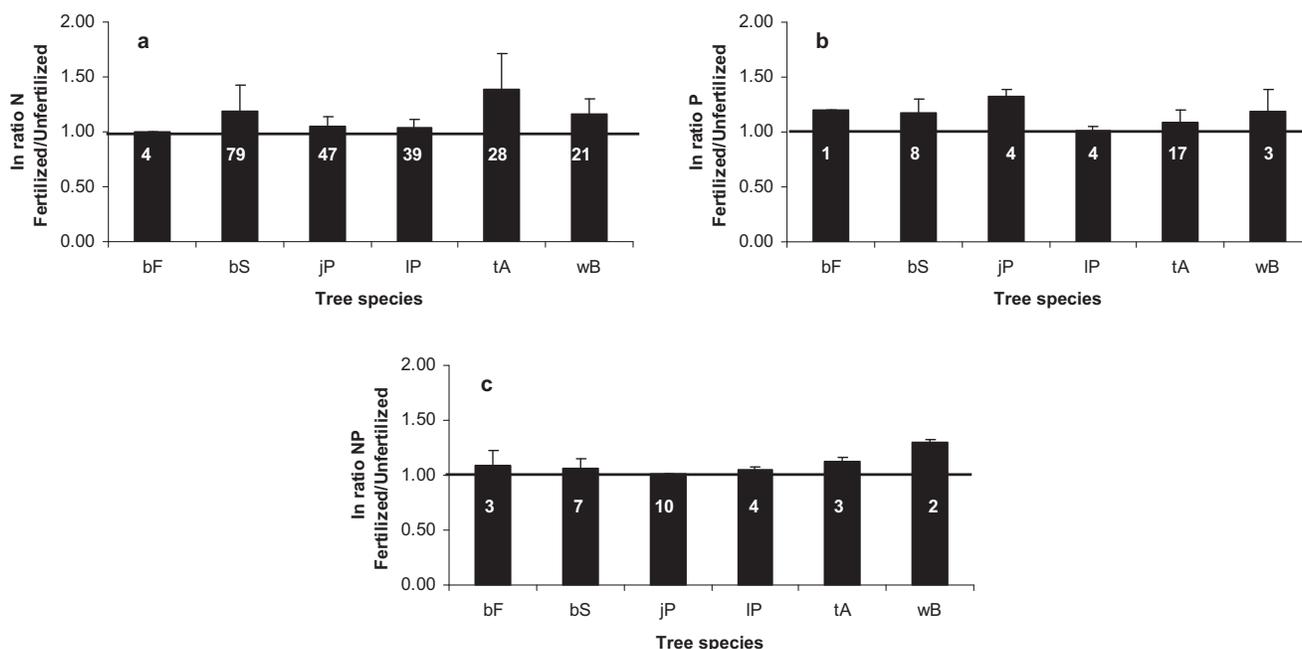
limited, with N the most limiting element (Fisher and Binkley 2000; Magnani et al. 2007). Numerous studies (e.g., Weetman et al. 1979, 1987; Newton and Amponsah 2006) have shown that increased N inputs resulted in increased forest productivity (tree and understory growth). However, our results suggest that P limitations may be as widespread as N limitations.

In boreal zone chronosequence studies with prolonged absence of stand-replacing disturbances, it is hypothesized that the ecosystem may enter a stage of retrogression (stage at which productivity declines) being either co-limited by N and P or primarily by P (Lagerström et al. 2009; Vitousek et al. 2010). Generally, P limitations have not been associated with the relatively young boreal zone soils because P is derived mainly from bedrock and only over much longer time periods, in much older soils does it becomes increasingly depleted or bound in unavailable stable forms (Lagerström et al. 2009). However, in a chronosequence study in Sweden, reduced productivity was observed on islands where fire had been excluded for about 5000 years (Wardle et al. 2004). Long-term absence of fire resulted in decreased P availability and contributed to lower microbial activity (along with N limitations) which in turn could have impaired decomposition and mineralization (Lagerström et al. 2009). In another long-term chronosequence study in the boreal zone (Glacier Bay, Alaska; Chapin et al. 1994), P limitations resulted from high N inputs from the abundant N fixers early in ecosystem development following glaciation. Foliar P concentrations in black spruce 10 years following whole tree harvesting and forest floor removal in the Boreal and Great Lakes St. Lawrence forest regions were within the critical range that suggest P limitations (Long-term Soil Productivity Program; Ponder et al. 2012). These studies and the meta-analysis results (Figs. 2*a* and 2*b*) suggest P limitations in the boreal zone may be more important than previously thought.

The most positive response to N fertilization as indicated by the log-response ratio occurred with trembling aspen (*Populus tremuloides* Michx.), followed by black spruce (*Picea mariana* [Mill.] BSP) and white spruce (*Picea glauca* [Moench] Voss.), whereas balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), and

lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) were less responsive but still positive.

Trembling aspen and white birch (*Betula papyrifera* Marsh.) responded the most to N and P fertilization, whereas the response to P only fertilization was the greatest with jack pine, black spruce, and white birch. These results must be interpreted with caution given the limited number of studies. That being said, several additional factors could contribute to the variation in response ratio. It can be due to the autecology of a species, some species being reactive to changes in their environment, whereas others are more conservative in their growth response (Díaz et al. 2004; Thiffault et al. 2006). It can also be related to the nature of the soil and the environment (i.e., understory vegetation, crop tree age and density, and deficiencies of other nutrients as a result of an imbalance with increased N inputs). For example, in long-term experiments involving annual or periodic N additions, nutrients such as sulfur (S) and boron (B) became limiting, and the greatest growth responses came with additional fertilization that included these elements (Brockley 2000; Högberg et al. 2006). In the Interprovincial Forest Fertilization Program (Weetman et al. 1979, 1987) and black spruce fertilization trials in Newfoundland (van Nostrand 1979), maximum growth increases often occurred on plots with combined N and P or N and P + K treatments, but the interactions were not always statistically significant.

Morrison et al. (1977) observed growth responses in 45-year-old jack pine when several Ca and Mg treatments were added along with N, P, and K. No growth responses to Ca and Mg treatments were found in the absence of N, P, and K fertilization. A meta-analysis conducted for sugar maple (*Acer saccharum* Marsh.) stands (a temperate forest species) indicated a similar trend: i.e., a general strong response to N and a generally greater response to multiple nutrient additions than to a single one (Vadeboncoeur 2010).

3.2. Natural disturbances

3.2.1. Fire

Forest fires are a major large-scale disturbance in the boreal zone (Amiro et al. 2009). Their effect on soil biogeochemical cy-

Fig. 3. Change in total nitrogen (N) following fire. All points are expressed as response ratios ±95% confidence intervals (CIs), with the number of studies in parenthesis. Groups with CIs that overlap 1 (vertical line) show no significant change in total soil N following fire. The response ratio at the top of the figure is the overall effect of fire on total N including experimental burns and wildfires from both soil layers. Within each soil layer, the response ratio across both fire types is shown, as well as within each fire category (experimental burn and wildfire).
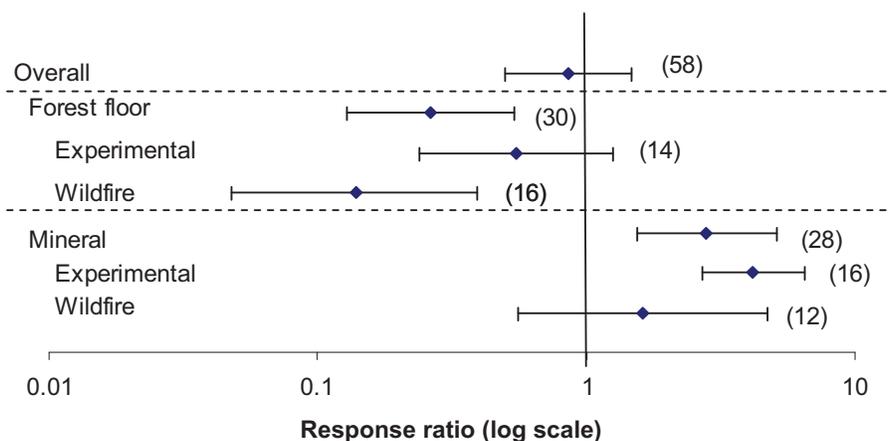
cling depends on their intensity, type, and frequency. Fire is rarely a uniform event and in large burns a variety of intensities will occur across the landscape (Certini 2005). The effect of fire on soil nutrients is complex, as it not only enhances the availability of some nutrients contained in the soil organic matter but also potentially accelerates nutrient losses by volatilization and leaching.

Soil erosion is generally low in undisturbed boreal forests, but there is potential for significant erosion following fire that exposes mineral soil (Neary et al. 2005). Potential increases in surface erosion are related to the availability of readily erodible sediment (i.e., exposed mineral soil), changes in soil infiltration rates, and topography (Wondzell and King 2003; Martin et al. 2010). In addition, the formation of hydrophobic layers can restrict the infiltration of water, resulting in increased surface runoff leading to increased erosion and, in severe cases, mass wasting (Neary et al. 2005).

Carcaillet et al. (2006) found that fires had no significant effect on soil erosion in the eastern boreal forests of Canada with the exception of dry-sandy areas where dune activity is controlled by fire. Under these conditions, the consumption of thin humus layers may result in increased wind erosion. Sand-dune areas cover <0.3% of the total area of Canada (~26 000 km²), with the majority (>90%) in the prairies (David 2011). In the boreal zone, the largest dunes are in the Lake Athabasca area. A large portion of these are active and devoid of vegetation. Elsewhere in the boreal zone, soil erosion as a result of fire on these dry sand-dune areas would be localized.

3.2.1.1. Nitrogen

The nature and frequency of fire potentially play an important role in regulating the N cycle as well as forest productivity because boreal forests are N limited. The meta-analysis comparing burned and unburned sites in the boreal zone found no change in the total soil N (Fig. 3); but when the predictor variables were tested, differences were observed between burned and unburned soils of the forest floor and mineral layers. Forest floor total N was significantly lower following fire, whereas total N in the mineral soils was significantly higher. Those trends were the same regardless of the type of fire, i.e., wildfire or prescribed burn (Fig. 3). The results of our meta-analysis and several others (Johnson and Curtis 2001; Wan et al. 2001; Boerner et al. 2009; Nave et al. 2011) covering various forest types have shown losses were confined to the surface organic layer (i.e., forest floor) as a result of volatilization and did not extend into the mineral soil. Individual studies in the

boreal zone have calculated or modeled N losses equivalent to several centuries of accumulation (e.g., Hardin et al. 2003; Boby et al. 2010). Nave et al. (2011) calculated that forest floors would require 100–130 years to recover lost N (and C) based on their meta-analysis of temperate forests. Thus, the loss of N from the forest floor following fire primarily through volatilization could contribute to N limitation in boreal forests depending on the amount lost and the rate of N accumulation either through atmospheric deposition (see section 3.3.2) or N fixation. Blue green algae associated with mosses have been shown to fix N along with N-fixing shrubs (Zackrisson et al. 2004; Gundale et al. 2011; Ackermann et al. 2012). Markham (2009) found N fixation in *Pleurozium schreberi* ([Brid.] Mitt.) and *Sphagnum capillifolium* ([Ehrn.] Hedw.) and supported work by Zackrisson et al. (2004) that N fixation may be important in late successional boreal forests with significant moss layers.

Increased inorganic N (NH_4^+ and NO_3^-) in soils has been observed postfire (e.g., Wan et al. 2001; Johnson et al. 2004; Boerner et al. 2009; Koyama et al. 2010) in other forest biomes. A meta-analysis of 12 study sites of the Fire and Fire Surrogate Network (primarily temperate forests in USA) found increases in total inorganic N were limited to high-intensity wildfires, were significantly higher during the first year after a fire, but disappeared within a few years (Boerner et al. 2009). Similarly in a meta-analysis of N dynamics in terrestrial ecosystems (including some sites in the boreal zone), NH_4^+ and NO_3^- increased two- to three-fold 1 year after fire and then declined (Wan et al. 2001). Nitrogen losses through increased soil leaching after fire are small relative to the volatilization losses of N in most boreal forests, but they may have implications for aquatic ecosystems such as eutrophication (see Kreutzweiser et al. 2013).

In low-N systems such as the boreal zone, plants appear to use organic N as a N source (Schimel and Bennett 2004; Kielland et al 2006, 2007). Kranabetter et al (2007) found dissolved organic N was the predominant form of extractable N across a range in site potential in the southern boreal zone of British Columbia. Actual rates of organic N uptake and evidence of the significance of organic N to plant nutrition are lacking (Kranabetter et al 2007; Näsholm et al. 2009), although a recent study found 80% of N uptake was as soluble amino acids (Inselsbacher and Näsholm 2012). Thus, future work on N availability following disturbance in the boreal zone needs to consider the role of dissolved organic N.

Fire converts plant biomass into forms of black carbon (C) (e.g., charcoal) that can affect biogeochemical cycles in the boreal zone

Fig. 4. Fire effects on extractable soil phosphorus (P), overall and by soil layer, tree species, and time since disturbance. All points are expressed as response ratios ±95% confidence intervals (CIs), with the number of studies in parenthesis. Groups with CIs that overlap 1 (vertical line) show no significant change in extractable P following fire. The response ratio at the top of the figure is the overall effect of fire on extractable P.
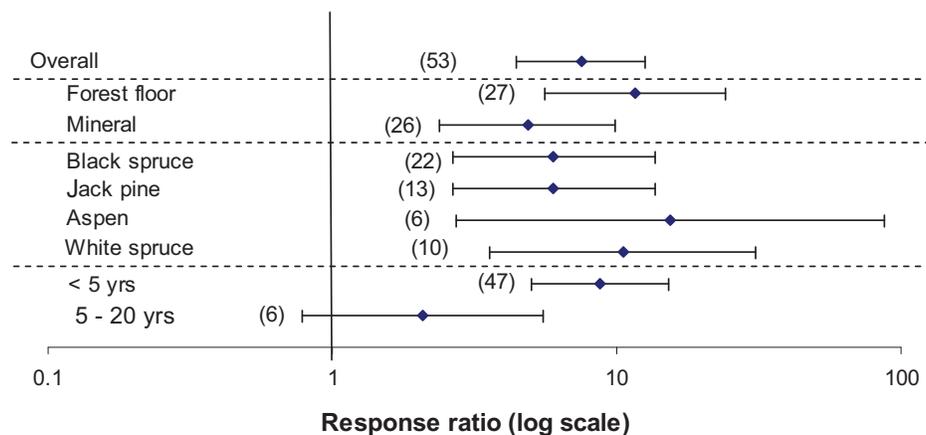
(e.g., Wardle et al. 1998, 2008). Coniferous wood charcoal is C-enriched and N-depleted relative to the unburned wood and has other properties such as organic sorption and cation-exchange capacity which are potentially beneficial to soils (Preston and Schmidt 2006; DeLuca and Aplet 2008). For example, charcoal was found to temporarily improve the availability of nitrogen to some plant species in environments containing high levels of phenolics produced by ericaceous shrubs (Wardle et al. 1998; DeLuca et al. 2002). Water-soluble phenolics in soils treated with charcoal were reduced by as much as 70% in a black spruce stand with *Kalmia* in the understory, but treatment did not affect extractable N and in some treatments seedling biomass decreased (Wallstedt et al. 2002). Thus, a better understanding of the role of charcoal on biogeochemical cycles in boreal forests is needed, particularly as the frequency and intensity of fire are altered under a changing climate.

3.2.1.2. Phosphorus and base cations

Our meta-analysis indicated that extractable P (Fig. 4) and exchangeable Ca and Mg (Figs. 5a and 5b) were significantly higher in the soil following fire. Species, soil layer, or type of fire (wildfire or prescribed burn) had no effect on the response. There was, however, an effect of time since disturbance. Significant increases were found in the studies sampled within 5 years after disturbance; whereas in longer term studies (6–20 years) there were no significant differences between burned and unburned soils, although there were fewer longer-term studies (Figs. 4 and 5).

There was no overall effect of fire on exchangeable soil K (Fig. 5c). When partitioned by soil layer, exchangeable K was significantly higher in the mineral horizons following fire and there was no difference in the exchangeable K of the forest floor. Phosphorus and K are less volatile than N but will volatilize at >774 °C (Raison et al. 1985; Knoepp et al. 2005) while Ca and Mg are nonvolatile elements. The main mechanism for loss of the latter elements is through blowing of fine ash or surface runoff (i.e., erosion). In Quebec, element export rates were more important for the base cations Ca²⁺, Mg²⁺, and K⁺ than for N and P (Lamontagne et al. 2000). Rates of loss were highest in the year following disturbance but remained higher than levels in undisturbed reference drainage areas 3 years after disturbance.

Potassium is a mobile element in soils and higher K in the mineral soils may reflect increased leaching, as K can be more easily displaced than Ca or Mg from most soil colloids. Thiffault et al. (2008) indicated that higher Ca and Mg, but not K, in the forest floor of burned soils could be explained by the mobility of K

and its rapid turnover time relative to divalent base cations. In addition, volatilzation losses for K are likely to be higher than for Ca and Mg (Raison et al. 1985). It appears that exchangeable K was conserved within the upper 20 cm of the mineral soil at least in the short term (<5 years). In the longer term studies (5–20 years), exchangeable K was lower in burned soils compared with unburned sites but the difference was not significant (Fig. 5c). These data should be interpreted with caution, as there was a limited number of longer term studies (R = 0.249, 95% CI 0.051–1.227, p = 0.088, n = 8). Studies of K cycling in forests (including boreal zone aspen stands) have found that K is leached down through the soil, but conserved within the rooting zone, possibly within the microbial (primarily fungal) biomass (Van Cleve and Noonan 1975; Cromack et al. 1975; Louiser and Parkinson 1979; Maynard 1997).

Fire may temporarily increase soil pH and the availability of soil nutrients. These effects are direct, but also indirect through vegetation changes, changes in surface albedo, and change in surface water repellence (Certini 2005). These effects are transitory and generally diminish with time since fire. However, in boreal forests undergoing paludification (the continuous accumulation of an organic layer leading to a peatland), the reduction of the organic layer by fire can have major effects on nutrient cycling and tree growth. Simard et al. (2007) found a reduction in stand-level productivity of 50%–80% with time since fire, comparing postfire cohorts with subsequent ones on the same site. The thickness of the organic layer increased with time directly resulting in productivity decline due to mechanisms and processes including rise of the water table, root distribution (lower proportion of roots in mineral soil), soil temperature, and potentially reduced availability of N, P, and possibly K (Simard et al. 2007). Only a severe fire (Simard et al. 2007) or intensive soil disturbance during forest operations (Lafleur et al. 2010) could restore site productivity. In contrast, on well-drained boreal aspen sites, there were no growth differences between cohorts of fire or harvesting origin despite higher pH and cations in the former (Paré et al. 2001).

3.2.1.3. Mercury

Increased fire frequency in the boreal zone could potentially lead to higher mercury (Hg) emissions to the atmosphere from boreal forest soils (Sigler et al. 2003; Turetsky et al. 2006). The boreal zone appears to be a sink for Hg inputs because of the filtering capacity of the canopy (particularly conifers) and abundance of wetlands (Demers et al. 2007; Driscoll et al. 2007; Friedli et al. 2007; Graydon et al. 2008). In upland soils >95% of the Hg is contained in the surface organic soil layers and boreal peatlands

Fig. 5. Change in exchangeable (*a*) calcium, (*b*) magnesium, and (*c*) potassium following fire, overall and by soil layer, tree species, and time since disturbance. All points are expressed as response ratios ±95% confidence intervals (CIs), with the number of studies in parenthesis. Groups with CIs that overlap 1 (vertical line) show no significant change in exchangeable cations following fire. The response ratio at the top of each figure is the overall effect of fire on individual cations.
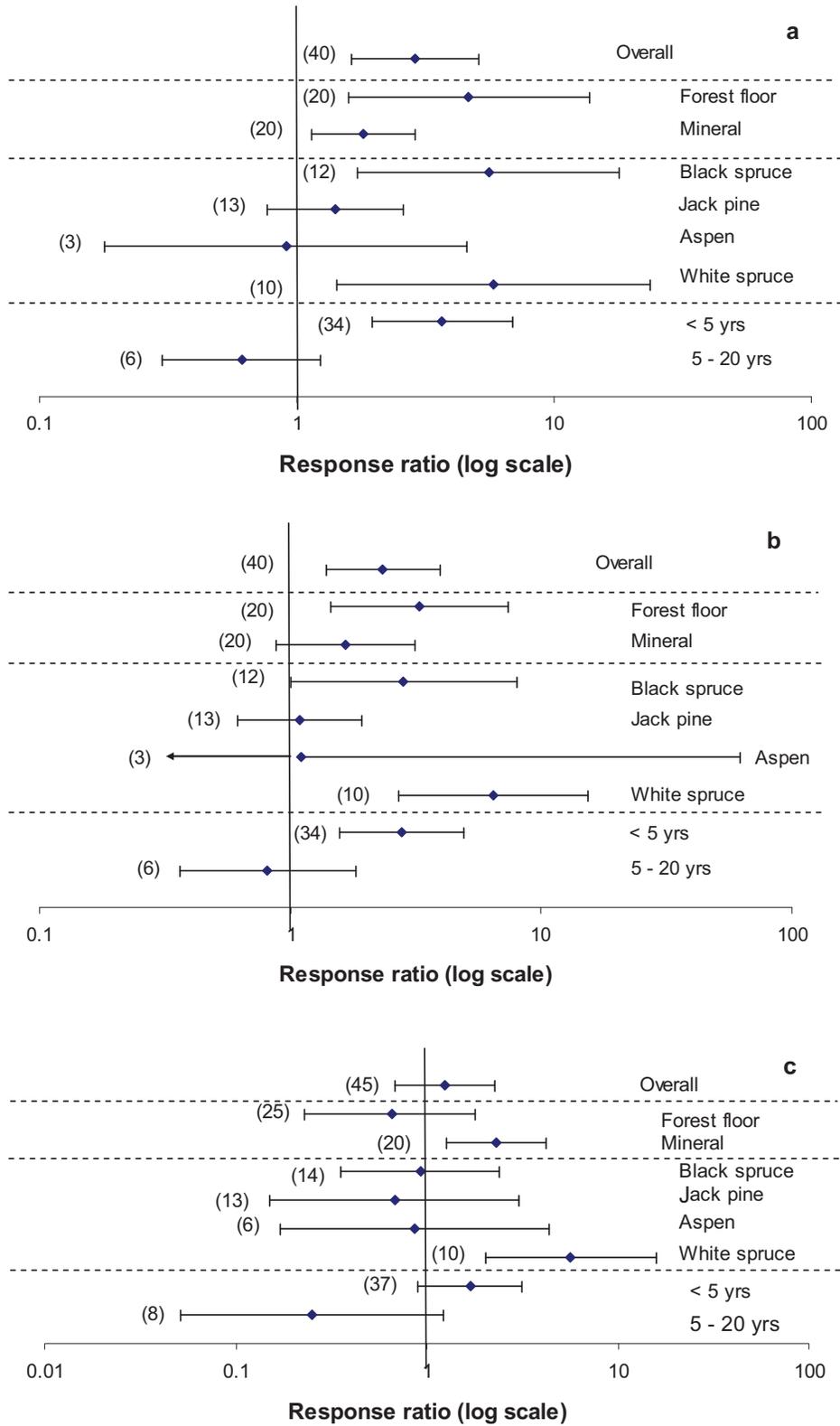
can accumulate up to 10 times more Hg than upland boreal forest soils (Grigal 2003; Turetsky et al. 2006). The relative contribution of various sources of Hg in the boreal zone is uncertain because of insufficient data and knowledge of Hg cycles (Schroeder et al. 2005). The amount of Hg released from boreal zone soils and its distribution (e.g., local, regional, or global) following wildfires will depend on the location of Hg in the ecosystem, the intensity of the fire, the Hg speciation, and the resident time of the emissions in the atmosphere (Engle et al. 2006; Driscoll et al. 2007; Friedli et al. 2007).

There is also evidence that partial losses of forest cover from wildfire may cause elevated Hg as methylmercury (MeHg) in lakes (Garcia and Carignan 2000; Garcia et al. 2007). Methylmercury is a potent neurotoxin produced by microorganisms (primarily bacteria) from inorganic Hg present in soils (Driscoll et al. 2007). The distribution pattern of MeHg in northern pike (*Esox lucius*) and plankton was similar to that of dissolved organic C, a known vector of Hg from soils to lakes (Grigal 2003; Garcia et al. 2007). Thus, the potential for higher MeHg concentrations in lakes and aquatic organisms following fire within a watershed could be predicted as a function of the proportion of the watershed disturbed, the severity of the fire, and the amount of dissolved organic C movement into the lake as a result of the disturbance (Garcia and Carignan 2000, 2005; Garcia et al. 2007).

3.2.2. Insects and diseases

Insect and disease outbreaks may indirectly change soil nutrient dynamics by releasing nutrients sequestered within trees, altering the rate and quantity of nutrients leached or deposited as litter, depositing significant quantities of frass to the soil surface, changing soil microclimates (e.g., soil temperature and moisture and light intensities), reducing competition among plants, altering plant species composition, and stimulating translocation of nutrients from boles and branches to high-turnover components such as leaves, buds, and flowers (Mattson and Addy 1975; Castello et al. 1995; Hunter 2001). In addition, the rates and volumes of woody debris and the manner of tree fall (e.g., uprooted trees versus trees that break off aboveground) generated by increased mortality as a result of insect or disease outbreaks may alter decomposition and nutrient cycles (Gandhi and Herms 2010). The effects of insect and disease outbreaks on nutrient cycles may be short- or long-term; effects on soils may initially increase nutrient availability, but with time can result in decreased availability (Hunter 2001). Soil nutrient properties can also play a role in the rate and severity of insect or disease outbreaks. Studies in temperate and boreal forests have found *Armillaria ostoyae* occurred mostly commonly on coarse-textured (e.g., sandy) soils and drier moisture regimes and nutrient limitations may be responsible (Shaw and Kile 1991; Mallett and Maynard 1998; McLaughlin 2001). Several studies have investigated the relationship between soil drainage and the susceptibility of forest stands to spruce budworm, but results are contradictory (reviewed in McLean and McKinnon 1997).

Lovett et al. (2002) pointed out that defoliation, while enhancing the nutrient flux to the soil, does not necessarily enhance nutrient losses, but may result in nutrient redistribution. A higher C:N ratio in insect frass than in plant as assessed for 130 lepidopteran species (Kagata and Ohgushi 2012) together with a high labile C content of frass (Lovett et al. 2006) contribute to N preservation by the soil microbial communities. Factors that will influence the effects of insects on nutrient cycling include the severity of an attack (i.e., endemic versus epidemic), the type of insect attack (e.g., defoliators versus wood borers), and potential positive feedback mechanisms where increased nutrient availability may stimulate further insect population growth (Hunter 2001). Thus, generalizations on how insect outbreaks may alter

nutrient cycles are difficult given our current understanding of these systems.

In the boreal forest of eastern Canada, spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks are one of the major natural disturbances. In a study of the Lake LaFlamme watershed (70 km north of Quebec City), soil-leaching exports of K^+ and inorganic NH_4^+ and NO_3^- were higher (8.3-, 6.2-, and 30.1-fold, respectively) during the spruce budworm outbreak than during the unperturbed latent period (Houle et al. 2009). The effects persisted for a few years after the outbreak ended. Explanations for the higher leaching losses include lower tree uptake because of increased mortality and reduced growth in balsam fir and increased soil organic matter decomposition rates and the onset of nitrification. Similarly, Lewis and Likens (2007) observed greater nitrate and cation leaching for a 2-year period following insect defoliation in a temperate mixed forest and Stadler et al. (2006) as well as Orwig et al. (2008) observed the same pattern in eastern hemlock (*Tsuga canadensis* (L.) Carrière) forests infested with hemlock woolly adelgid (*Adelges tsugae* Annand). These ecosystems all showed an increased nitrification which was conducive to elemental losses.

Effects of bark beetle disturbance on lodgepole pine forests in Greater Yellowstone persisted for 30 years but were of lesser magnitude than changes observed following stand-replacing fires (Griffin et al. 2011). Available N increased with beetle disturbance as evidenced by a 20%–30% increase in foliar N for surviving unattacked trees; however, the lack of elevated soil nitrate levels suggests leaching losses following bark beetle attack were low. The apparent lack of net nitrate production and potential loss in the lodgepole pine site following mountain pine beetle attack is consistent with studies from other forest types where N deposition is low, the soils are N-limiting, and the disturbance leaves the soil, particularly the forest floor, and understory intact (Prescott et al. 2000; Griffin et al. 2011). Thus, the potential risk of N loss following an insect outbreak will be greater in mixedwood or deciduous boreal forests, where there is higher N availability, and in areas of high N deposition.

3.3. Anthropogenic (human-induced) disturbances

3.3.1. Forest management

3.3.1.1. Harvesting

Harvesting and removal of biomass can result in the depletion of soil nutrients and the redistribution of nutrients from soils to biomass in regenerating forests (Johnson 1994); however, little or no effect on soil nutrient content has been observed in other studies (e.g., Johnson and Curtis 2001; Kreutzweiser et al. 2008; Thiffault et al. 2011). The effects on productivity will depend on the type of harvesting (e.g., whole tree versus stem only or clearcuts versus partial cuts), tree species, soil fertility, weathering rates, and, in the case of N, atmospheric deposition and fixation rates (Kreutzweiser et al. 2008).

Our weighted meta-analysis comparing soil nutrient concentrations between harvested and unharvested (control) areas in the boreal forest of Canada (one study from Alaska) found that the overall changes to soil nutrient concentrations and content were minimal in the short- to medium-term (<20 years). The various nutrients studied, however, had different behaviours according to the characteristics of their specific biogeochemical cycle. Harvesting resulted in significant overall decreases in soil extractable P (Fig. 6). This was observed in the short and long term and was more obvious in the forest floor than the mineral soil. The decrease of extractable P was strongest for mixed stands ($p = 0.002$), followed by conifer stands ($p = 0.05$), whereas it was not significant for deciduous stands ($p = 0.837$). In contrast, harvesting had no significant overall effect on total N (Fig. 7), NH_4^+-N, and NO_3^--N

Fig. 6. Harvesting effects on extractable soil phosphorus (P), overall and by soil layer, soil type, forest type, and time since disturbance. All points are expressed as response ratios ±95% confidence intervals (CIs), with the number of studies in parenthesis. Groups with CIs that overlap 1 (vertical line) show no significant change in extractable P as a result of harvesting. The response ratio at the top of the figure is the overall effect of harvesting on extractable P.
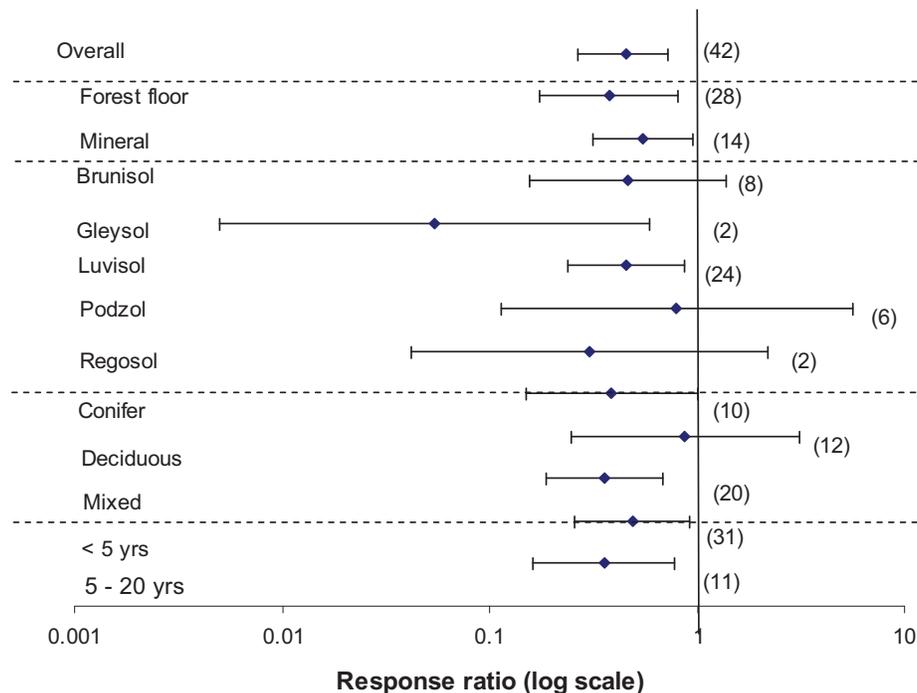

Fig. 7. Change in total nitrogen (N) due to harvesting, overall and by forest type. All points are response ratios with 95% confidence intervals (CIs), with the number of studies in parenthesis. Groups with CIs that overlap 1 show no significant change in total soil N following harvest. The response ratio at the top of the figure is the overall effect of harvesting on total N.
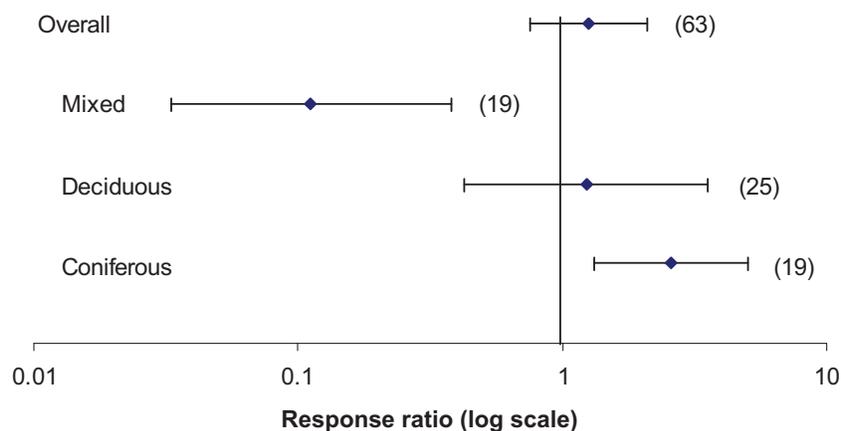
(data not shown), and exchangeable Ca^{2+} (Fig. 8a), Mg^{2+} (Fig. 8b), and K^+ (Fig. 9) in the soil. However, some of the categorical factors did influence the direction and degree of the response depending on the nutrient.

Responses to harvesting for total N (Fig. 7) and exchangeable Ca^{2+} and Mg^{2+} (Fig. 8) were different according to the forest type. Deciduous stands showed no effect of harvesting on those nutrients, whereas in conifer stands there was a significant increase and in mixedwood stands there was a significant decrease. In the conifers, the largest increases in N were attributed to forest floor and longer time since harvest (>5 years). The reasons for the observed differences among forest types are not clear. Johnson and Curtis (2001) found a similar pattern for total N in mineral soils following sawlog harvest across a number of forests types worldwide (i.e., increase in conifers and no effect in deciduous). One

hypothesis may be that harvest creates a more drastic contrast in soil microbial communities and microclimate relative to preharvest conditions in conifer stands, which keep a closed canopy throughout the year because of their perennial foliage, relative to mixed and deciduous stands. The forest canopy controls many ecosystem processes related to nutrient cycling, including transpiration, precipitation interception, and dry deposition (Running and Coughlan 1988). The fate of harvest residues and nutrients may also explain the difference in response to harvest between forest types. In conifer stands, residues are likely incorporated in the forest floor, remain there for a long period of time, and act as a long-term source of nutrients (e.g., Harmon et al. 1990). Microbial immobilization of nutrients (especially N) may also keep nutrients in soils (Vitousek and Matson 1985; Wall 2008). The reason that soil nutrient response to harvest of mixedwood stands is not

Fig. 8. Change in (*a*) exchangeable calcium (Ca) and (*b*) exchangeable magnesium (Mg) due to harvesting, overall and by forest type. All points are response ratios with 95% confidence intervals (CIs), with the number of studies in parenthesis. Confidence intervals that overlap 1 show no significant change in exchangeable soil Ca or Mg following harvest. The response ratio at the top of the figures is the overall effect of harvesting on exchangeable Ca and Mg.
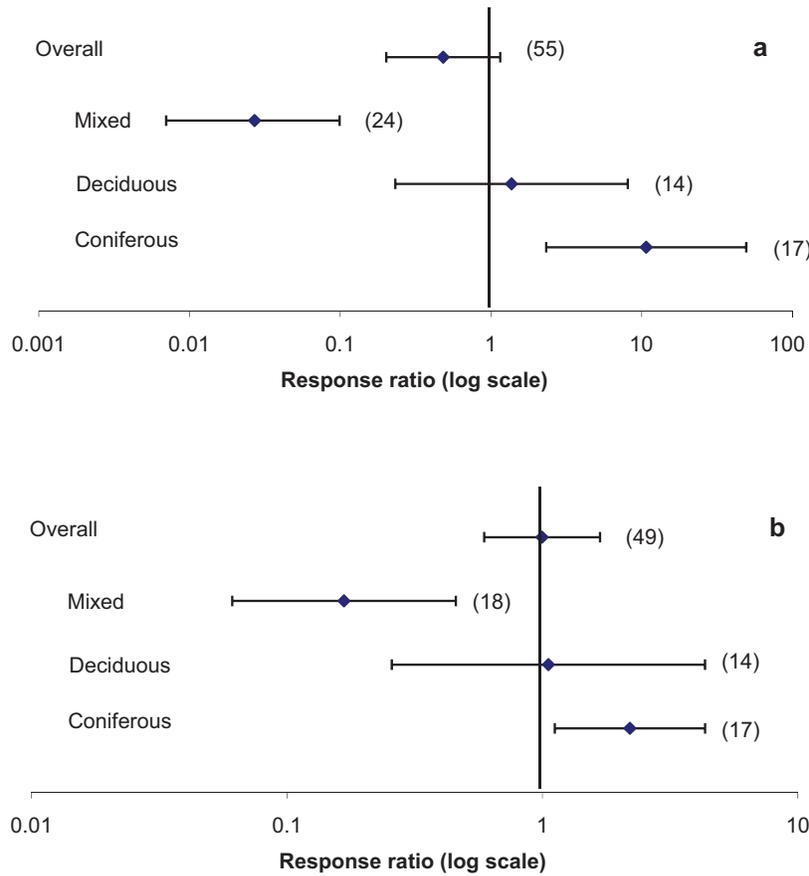

Fig. 9. Change in exchangeable K due to harvesting, overall and by soil layer and time since harvest. All points are response ratios with 95% confidence intervals, with number of studies in parenthesis. Confidence intervals that overlap 1 show no significant change in exchangeable soil K following harvest. The response ratio at the top of the figure is the overall effect of harvesting on exchangeable K.
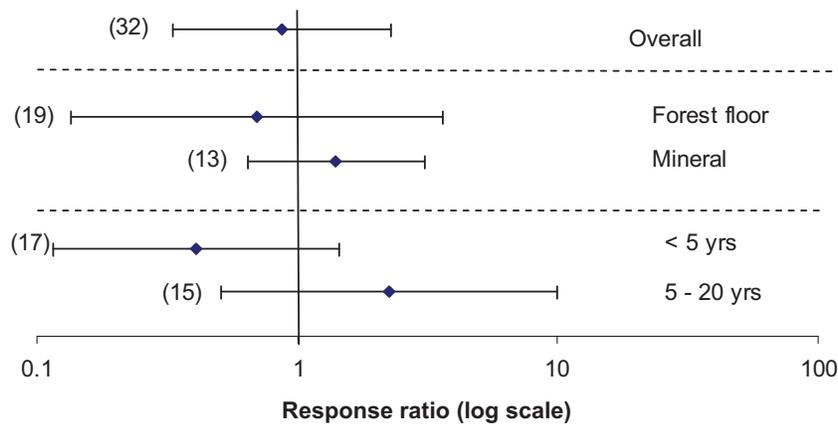
intermediate to responses observed in conifer and deciduous stands remains unclear.

There was no overall effect of harvesting for exchangeable soil K^{+} (R = 0.877, 0.334–2.304 95% CI), and there was no significant effect of any factor following harvest (Fig. 9), although the trend was similar to that found in soils following fire. The response ratio for the forest floor was <1, suggesting a loss of exchangeable K^{+} relative to unharvested sites; and the response ratio of the mineral soil was >1, suggesting an increase in exchangeable K^{+}. In addition, short-term studies showed a decrease in exchangeable K^{+} following harvest, but longer term studies showed an increase in exchangeable K^{+} (Fig. 9). The differences were not significant because of the large variability. Kishchuk et al. (2013) found that forest floor K^{+} was lower 6 years post-harvest than in unharvested controls, but may be retained in surface mineral soil.

Thiffault et al. (2008) found that K does not significantly build up in exchangeable reserves after disturbance, as K^+ may be displaced by other cations (e.g., Ca^{2+} and Mg^{2+}) and leached deeper into the soil profile (Brady and Weil 2008). However, K^+ cycles rapidly through vegetation, litter, and labile organic compounds because it remains as a soluble electrolyte within plant tissues rather than being bound in vegetative structures (Likens et al. 1994). Thus, K^+ availability for tree nutrition should not be at risk with harvest, since its cycle is rapidly restored with the recolonization of vegetation and the input of fresh litter to the soil (Thiffault et al. 2008).

In contrast, the exchangeable pools of Ca^{2+} and Mg^{2+} built from the nutrient flush following disturbance is of crucial importance for nutrient cycling and tree nutrition during the subsequent rotation, as is the capacity of soil to store this pool. In a study of conifer stands of the Boreal Shield East Ecozone, harvesting did not emulate the enhancement of soil Ca^{2+} and Mg^{2+} pools or the deposition of charred organic material with high exchange capacity associated with wildfire, raising concerns about the long-term availability of these two nutrients on harvested sites (Thiffault et al. 2007, 2008). Similarly, the meta-analysis (Figs. 5a and 5b) indicated significant increases were observed for exchangeable Ca^{2+} and Mg^{2+} following fire compared with harvested sites (Fig. 8) where there was no overall effect of harvesting on exchangeable Ca^{2+} and Mg^{2+}.

There were insufficient studies to compare different harvesting systems by meta-analysis. The literature review of Thiffault et al. (2011) suggested that negative impacts of intensive biomass removal practices such as whole-tree harvesting are more frequent in the forest floor than for the mineral soil. In the first years after whole-tree harvesting, influences on tree survival and growth mainly through effects on microclimate and competing vegetation were often positive (i.e., an increase of tree productivity relative to stem-only harvesting). Later in the rotation, however, there is evidence that N and P availability for tree nutrition may be impaired by whole-tree harvesting, resulting in reduced tree growth for as much as 20 years. Whole-tree harvesting can also reduce base cation concentrations in soils and tree foliage, but this has not yet been shown to affect tree growth. Critical determinants of site sensitivity to whole-tree harvesting include climate and microclimate, soil texture, organic matter content, availability of base cations and P, and tree species autecology, although there has been no consistent effect of biomass (whole-tree harvesting) on soil productivity (Thiffault et al. 2011).

3.3.1.2. Site preparation

The objectives of site preparation are to increase nutrient availability, improve soil microclimate, increase early crop-tree performance, create planting microsites, and facilitate planter access. Mechanical site preparation may involve one or more of several different activities, e.g., the removal of forest floor, the raising of mineral soil, the inversion of forest floor and mineral soil, and the mixing of forest floor and mineral soil. There are a limited number of studies that have assessed the effects of site preparation on soil nutrients in the boreal zone of Canada. These few studies and the fact that they encompass various types of site preparation likely explain why the meta-analysis (data not shown) did not show an overall significant effect on soil nutrients.

Mechanical site preparation generally increases N mineralization and nitrification, but may reduce fertility because of net N loss through nitrate leaching and cation losses (Krause and Ramlal 1987). Studies from warm climates have reported such losses (e.g., Vitousek and Matson 1985 and Fox et al. 1986). However, evidence of this phenomenon is lacking in most boreal zone stands. For example, in boreal zone mixedwood stands of northern Alberta, nutrient availability was reduced in soils 2 years after treatment only when the forest floor was completely removed but not with other forms of site preparation compared with harvested stands with no site preparation (Schmidt et al. 1996). Similarly, site preparation did not reduce N availability 10 and 20 years after treatment on a sub-boreal site in northern-central British Columbia (MacKenzie et al. 2005; Boateng et al. 2010). Studies from Scandinavia also showed that, even though site preparation increased N and P leaching from soils, these increases were of short duration (<5 years after treatment) and did not affect overall soil fertility (Piirainen et al. 2007). Leaching losses of other nutrients such as Ca, Mg, and K may also be a concern and the amplitude of losses is related to the extent and intensity of soil disturbance over the treated area (Piirainen et al. 2009). In most cases, disturbance of the entire forest floor has been shown to reduce soil nutrient availability (e.g., Munson and Timmer 1995).

The beneficial effects of mechanical site preparation are usually linked to the exposure of mineral soil or the mixture of organic and mineral soils (Sutherland and Foreman 1995). In boreal forested peatlands with deep (>30 cm) organic deposits, site preparation is often not recommended because of increased risk of rutting (Groot 1998), frost heaving, and flooding (Sutherland and Foreman 1995). Nevertheless, studies in northwestern Quebec showed that site preparation can be effective at creating high-quality microsites despite thick organic layers (Lafleur et al. 2011a). Moderate disturbance of the forest floor has been shown to enhance seedling recruitment, survival, and growth (Morris et al. 2009) and increase N availability and tree nutrition (Lafleur et al. 2011b).

Scarification has also been identified as a silvicultural option to facilitate establishment of plantations on sites dominated by ericaceous shrubs such as *Kalmia angustifolia* L. and *Rhododendron groenlandicum* [(Oeder) Kron & Judd]. Ericaceous shrubs have the potential to rapidly dominate burned or clear-cut sites through vegetative regeneration (Messier and Kimmins 1991; Mallik 1993, 1995), which may convert the sites to unproductive heaths. Ericaceous shrubs can be associated with reduced growth of naturally regenerated and planted conifer seedlings because of competition for nutrients, allelopathy, or low soil temperature (Titus et al. 1995; Zackrisson et al. 1997). Studies in *Kalmia*-dominated sites showed that scarification can reduce *Kalmia* cover and increase the distance from seedlings to the nearest *Kalmia* stem, as well as improve seedling foliar nutrient concentrations relative to unscarified plots (Yamasaki et al. 1998; Thiffault et al. 2005). As scarification does not necessarily enhance soil N availability and may even reduce the availability of other nutrients such as Ca, Mg, and K (Thiffault et al. 2005), improved seedling nutrition following scarification may be explained by either reduced belowground competition from *Kalmia* (Thiffault et al. 2004), or reduced direct (Zhu and Mallik 1994) or indirect (Yamasaki et al. 2002) allelopathic effects, or some combination of these mechanisms.

3.3.2. Acid deposition and N saturation

Acid deposition in the boreal zone can occur via the long-range transport of pollutants from extraneous sources (e.g., eastern Canada (Vet and Ro 2008)) or point sources within the boreal zone (e.g., smelters, sour gas processing plants, or oil sands in northeast Alberta).

Acid deposition, primarily as S and N compounds, can directly or indirectly affect forest ecosystems (e.g., Clair et al. 2011). Direct effects are related to the adsorption of gaseous pollutants by the plant at acute levels. This can also predispose vegetation to other biotic agents or, if mortality occurs, there can be changes in climatic conditions and cycling of nutrients. The possibility of direct effects of pollutants on vegetation is still of concern in high-deposition areas (Cape 1993), but the indirect soil-mediated effects of acidic deposition are considered more important in assessing the effects on forest ecosystems (Roberts et al. 1989). These effects may include increased leaching of base cations (Ca^{2+}, Mg^{2+}, and

K$^+$), increased solubility of toxic elements (e.g., aluminum (Al) or manganese (Mn)), nutrient imbalances because of N (and, to a lesser extent, S) saturation, and changes to the soil microbial community. Nitrogen deposition can lead to eutrophication, excess inputs of other elements into aquatic ecosystems, and shifts in plant species composition (Vitousek et al. 1997; Kothawala et al. 2011. Gundale et al. (2011) found that, at current rates of N deposition for a majority of the boreal forest (<3 kg ha^{-1} year^{-1}), bryophytes (e.g., *P. schreberi*) likely limit the availability of this N to vascular plants, and N enters boreal forests via the same pathways it would otherwise. Under higher N deposition rates, reactive N would bypass the bryophyte layer and be directly taken up by vascular plants (Gundale et al. 2011). Low levels of N deposition have also been hypothesized to stimulate forest growth in N-limited forests such as the boreal (Högberg et al. 2006; Magnani et al. 2007). However, Houle and Moore (2008) found no changes in growth of balsam fir and black spruce after 3 years of N deposition (equivalent to 30 years of N deposition) in mature stands of boreal forests in Québec. Most studies looking at N deposition rates on growth have been short-term and used high N addition rates, making it difficult to predict the impacts of lower levels of N deposition on growth (Högberg et al. 2006).

A critical load approach has been used in Europe as part of emission control strategies and applied more recently in Canada to assess the potential risk of acidic deposition to terrestrial ecosystems (Carou et al. 2008). The United Nations Economic Commission for Europe (UNECE) defined critical loads as "A quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to our present knowledge" (Brodin and Kuylenstierna 1992).

Critical loads were mapped for upland forest soils in Canada (Carou et al. 2008) based on protocol established by the New England Governors and Eastern Canadian Premiers (NEG–ECP) Environmental Task Group on Forest Mapping (NEG–ECP 2001). Soils with critical loads <400 equiv·ha^{-1}·year^{-1} were considered sensitive to acid deposition. A critical load of 400 equiv·ha^{-1}·year^{-1} is used as a reference point because it is analogous to the 20 kg ha^{-1} year^{-1} target load for sulphate deposition originally established in 1983 to protect sensitive lakes in eastern Canada (Carou et al. 2008). Previously, soils were rated on their potential to reduce the acidity of atmospheric deposition based on dominant soil and bedrock features (Environment Canada 1988). In both cases, terrestrial landscapes dominated by organic soils or peatlands were not included.

Areas in the boreal zone at the greatest potential risk for ecosystem damage from acid deposition (i.e., acid-sensitive soils and areas of significant N and S deposition) occur in the southern part of the Boreal Shield East in Ontario and Quebec and Boreal Shield West near the oil sands area in northeastern Alberta, northwestern Saskatchewan, and downwind of smelters in northern Manitoba (Carou et al. 2008). In the Boreal Shield East, soils are moderately sensitive (300–700 equiv·ha^{-1}·year^{-1}) to acid deposition and the high levels of deposition have resulted in the critical load being exceeded (Carou et al. 2008). In areas near the oil sands, deposition is lower relative to eastern Canada but the soils are more sensitive to acid inputs, particularly those in the Boreal Shield West. The risk assessment of acid deposition excludes other disturbances such as forest harvesting and fire, uses a Ca:Al ratio in soil solution of 10 as a critical chemical limit, and assumes all N removal processes from the soil are negligible (Carou et al. 2008). Thus, there are uncertainties associated with these delineations of exceedances of acid input, although it does provide an indication of boreal forest at risk from acid deposition based on the rates of N and S deposition, soil type, or a combination of the two.

There is an indirect effect of N additions to forest soils on decomposition. This can have implications with respect to C sequestration and nutrient availability. Numerous studies on the effect of N additions (either fertilizer or atmospheric deposition) on decomposition have produced variable responses. Knorr et al. (2005) used a meta-analysis of N additions to various ecosystems and found that overall N enrichment had no significant effect on litter decomposition. However, when various factors were partitioned, several significant effects of N additions that could be important in boreal forests were observed. Decomposition of litter was inhibited by the addition of N when the litter quality (e.g., high-lignin litters) was low (Knorr et al. 2005). Thus, decomposition of litter may be inhibited on fertilized sites or areas of high N deposition in boreal forests.

3.3.3. Flooding

The largest areas of flooding of boreal forest soils occur as a result of dam building for hydroelectric development (e.g., Oelbermann and Schiff 2010; Rosenberg et al. 1997). Other significant flooding occurs on areas of flat terrain and hummocky terrain as a result of roads and other construction (Kabzems et al. 1986). There are 1958 dams within the boreal zone (J. Brandt, personal communication, 2013; see also Brandt et al. 2013), and the most obvious effect is the loss of productive land, although the total area affected is unknown. Various biogeochemical cycles (e.g., C) may also be disrupted through changes in the oxidizing and thermal conditions of the soil (Friedl and Wüest 2002). Most of the changes related to soil biogeochemical cycles as a result of flooding will have the greatest influence on the atmosphere, e.g., alter gaseous C and N emissions (Jugnia et al. 2006; Oelbermann and Schiff 2010) and in aquatic ecosystems, e.g., bioaccumulation of methylmercury by fish (Hall et al. 2005; Rosenberg et al. 1997).

Increased emissions of greenhouse gases carbon dioxide (CO_2) and methane (CH_4) are a concern following the flooding of boreal soils, although fluctuating water levels, temperature, soil type, and the quantity and quality of soil organic matter will all influence the microbial processes that control production rates. Labile sources of soil organic matter that are more easily degraded by microbial activity produced greater rates of CO_2 and CH_4 than soil organic matter that was more humified and (or) associated with mineral soil material (Oelbermann and Schiff 2010). In a study of CO_2 emissions during ice-free periods for 3 years after the creation of a reservoir in northern Quebec, total emissions were highest in the first year after flooding, and surface fluxes were spatially heterogeneous. The spatial differences were not random but linked to preflood landscapes (Teodoru et al. 2011). Reservoirs overlaying areas with the largest C stocks such as peatbogs, and mature forests with organic soils, had the highest average emissions. The lowest emissions were associated with the lowest C stocks such as riverbeds and burned soils (Oelbermann and Schiff 2010; Teodoru et al. 2011). The link between surface fluxes of CO_2 and preflood landscapes persisted for at least 2 years following flooding.

In northern Quebec, samples of flooded soil and sediment had higher CH_4 production rates than unflooded soils and these soils also had higher rates of CH_4 oxidation by methanotrophic bacteria that could potentially mitigate increased CH_4 fluxes from flooded forest soils to the atmosphere (Jugnia et al. 2006). Similarly, Teodoru et al. (2011) indicated that CH_4 was not an important emission and accounted for <1% of the total C emissions in the 3 years following flooding.

Methylmercury may be produced by microorganisms, primarily bacteria from inorganic Hg present in soils and vegetation flooded during reservoir creation (Rosenberg et al. 1997; Hall et al. 2005). A positive relationship of MeHg production and accumulation in fish to the terrestrial area flooded and total amount of organic C flooded has been observed for boreal zone reservoirs (Johnston et al. 1991; Hall et al 2005).

3.4. Disturbance interactions

Most studies in the boreal zone have been limited to single disturbances, but the interactions of multiple disturbances should be considered when assessing the overall effects of human disturbance on the boreal zone (Buma and Wessman 2011). For example, N may be retained within the rooting zone under undisturbed conditions; however, following fire or harvesting, significant losses of N could occur before vegetation is re-established. Under conditions of low N deposition, leaching losses of N following wildfire or harvesting would also be low. The risk of N leaching and potential eutrophication of aquatic systems would be higher in areas of relatively high N deposition. This would include the southern boreal zone in Ontario and Quebec, and if the predicted increased N deposition in the oil sands region as a result of expansion occurs, then the potential for N leaching in high-deposition areas is possible here as well. Currently, however, there is little evidence to suggest significant leaching losses of N in the oil sands region is occurring (Cheng et al. 2011; Laxton et al. 2012).

Native insect outbreaks are part of the normal functioning of the boreal forest and the potential implications of enhanced nutrient losses due to pest outbreaks, when such losses occur, are not clear (Vitousek 1990). The consequences of outbreaks of invading pests or pests being active out of their natural ranges are not known. In the Canadian boreal zone, the potential for the expansion of mountain pine beetle east of the Rockies or the northern expansion of spruce budworm into black spruce forests are possible (Régnière et al. 2012). The cumulative losses that may occur during the recurrence of pest outbreaks combined with potential losses associated with other natural and anthropogenic disturbances (fire, harvesting, and acid and N deposition) may enhance nutrient losses. The modelling work of base cation fluxes and soil acid–base status in boreal zone stands of Quebec (Thiffault et al. 2007) suggested that natural disturbances such as spruce budworm outbreaks are minor drivers of soil chemistry in the long term, since they are punctual and their impact subsides a few years after their occurrence. Acid deposition due to air pollution appears to be a much more important driver, as the long-term trajectory of soil chemistry follows trends of deposition and seems less affected by the intensity and return interval of natural disturbances (Thiffault et al. 2007).

The potential cumulative losses of base cations from insect outbreaks combined with tree harvesting and fire (acid deposition for K) may have long-term effects on site productivity (e.g., Houle et al. 2009), but the evidence to date is inconclusive. While increases in K have been measured in soil solution from lysimeters in the rooting zone and estimated using hydrology models on various kinds of disturbances, no decreased K concentrations within the soil have been observed (Figs. 5c and 9).

The interaction of salvage logging following disturbance may also have implications for nutrient cycling and forest productivity (e.g., Cobb et al. 2010; Buma and Wessman 2011). Wood-feeding beetles (*Monochamus scutellatus scutellatus* (Say) (Coleoptera:Cerambycidae)) were relatively abundant in burned sites but absent from a burned and salvaged logged upland mixed stand of white spruce and trembling aspen in the Boreal Plains ecozone (Cobb et al. 2010). Frass from these beetles altered the N availability, decreasing total soluble N and shifting the dominant inorganic N form in the soil from NO_3^- to NH_4^+. Thus, the absence of wood-feeding beetles from salvage logged burned sites may alter soil nutrient dynamics and possibly long-term productivity.

Currently, there is little information on disturbance interactions in the boreal zone with respect to nutrient depletions. Disturbance interactions can potentially cause non-linear and surprising results (Buma and Wessman 2011, 2012). In some cases interacting disturbances may simply increase the magnitude or severity of the response (e.g., nutrient loss), but compounding disturbances may result in novel disturbance conditions (Buma and Wessman 2012). Thus, with changing disturbance regimes in the boreal zone, understanding the interactions of these disturbances on nutrient dynamics is essential (Turner 2010; Buma and Wessman 2012).

4. Summary

- Soils of the boreal zone are varied with an east to west trend with Podzols as the dominant soil in the eastern boreal ecozones and the Boreal Shield West, and Luvisols and Brunisols the dominant soils of the western boreal zones. The Taiga and Hudson Plains are predominantly permafrost (Cryosols) soils.
- Inherent soil properties contribute to the productivity of boreal zone forests. Natural disturbances affect both positively and negatively the cycling of nutrients that are essential to productivity.
- Fertilization studies have shown that the boreal zone is N and P limited. The majority of studies showed a positive growth response to N and P fertilization individually or in combination.
- Large amounts of N can be volatized during fires, although the loss of total soil N was confined to the forest floor. This could contribute to N limitations in the boreal zone, but this depends on the amount lost and the rate of N accumulation through N fixation or atmospheric deposition.
- Extractable P in the soil increased following fire and was consistent (and for most categories significant) for all the categories tested.
- Exchangeable Ca and Mg increased in the soil following fire. Potassium in the forest floor did not change following fire but was higher in the mineral soil. This is consistent with findings from other forest biomes, and elevated K levels at depth may reflect the mobility of K in the ecosystem.
- Mercury can be released from the soil either into the atmosphere or into aquatic ecosystems following fire. Thus, if fire-return intervals and intensities change, there could be increased Hg release from boreal soils.
- Harvesting resulted in significant decreases in soil extractable P. This is the opposite to extractable P following fire and, given the growth response to P fertilization, the P cycle is of concern.
- In contrast, harvesting had no effect on total or inorganic N except that it was lower in harvested mixedwood stands. Exchangeable Ca and Mg followed the same pattern.
- The cumulative effects of natural and anthropogenic disturbances have the potential to affect the vulnerability of boreal zone soils. Currently, however, there is too little information on these cumulative effects on soils to form a clear prediction.
- The evidence to date indicates that, overall, the soils of the Canadian boreal zone have not been adversely affected by anthropogenic disturbances, although there are site-specific cases of adverse effects on nutrient availability and areas of potential concern. There is a risk of nutrient loss and change in forest resilience if we do not consider nutrient depletions in our forest management strategies, particularly where multiple disturbances may interact.
- In addition to on-site environmental concerns, we need to be aware of the movement of nutrients and contaminants (e.g., Hg) into the atmosphere and aquatic ecosystems.

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