

Effects of a spruce budworm outbreak on element export below the rooting zone: a case study for a balsam fir forest

Daniel HOULE^{1,2}, Louis DUCHESNE^{1*}, Robert BOUTIN³

¹ Direction de la Recherche Forestière, Forêt Québec, Ministère des Ressources Naturelles et de la Faune du Québec, 2700, rue Einstein, Québec, Québec G1P 3W8, Canada

² Centre Saint-Laurent, Environnement Canada, 105, rue McGill, Montréal, Québec H2Y 2E7, Canada

³ Centre de Foresterie des Laurentides, Ressources Naturelles Canada, Service Canadien des forêts, 1055, rue du P.E.P.S., C.P. 3800 Sainte-Foy, Québec G1V 4C7, Canada

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Abstract

- Spruce budworm outbreaks are among the major natural disturbances affecting the dynamics and functioning of Canadian boreal forests. However, the element losses potentially associated with spruce budworm outbreaks have not been quantified.
- We evaluated the influence of spruce budworm outbreaks on nutrient export from boreal forest soils by comparing nutrient leaching losses during a spruce budworm outbreaks episode (1981–1984) to an unperturbed period (1999–2003) in a calibrated catchment located in a balsam fir forest.
- Nutrient soil leaching losses were significantly higher during the spruce budworm outbreaks (1981–1984) for N-NO₃ (30.1 fold), K (8.3 fold), N-NH₄ (6.2 fold), Mg (2.7 fold) and SO₄ (2.2 fold), as compared to an unperturbed period (1999–2003). When the recurrence of spruce budworm outbreaks (33 years) and a plausible average length of such events (5 years) are taken into consideration, it is estimated that in the long term, 5.6 more NO₃, 1.5 more K and 1.2 more NH₄ are leached from the soil profile during outbreaks.
- The important leaching losses during spruce budworm outbreaks, when added to the losses due to tree harvesting and fire (and acid deposition for K), may have considerable effects on soil fertility and ecosystem sustainability.

Résumé – Effets d'une attaque de tordeuse des bourgeons de l'épinette sur l'exportation d'éléments au-dessous de la zone racinaire : une étude de cas dans une forêt de sapins baumiers.

- Les épidémies de la tordeuse des bourgeons de l'épinette sont parmi les principales perturbations naturelles qui affectent la dynamique et le fonctionnement des forêts boréales canadiennes. Toutefois, les éléments potentiellement perdus associés à une épidémie de la tordeuse des bourgeons de l'épinette n'ont pas été quantifiés.
- Nous avons évalué l'influence des épidémies de tordeuse des bourgeons de l'épinette sur l'exportation des éléments nutritifs des sols de la forêt boréale, en comparant les pertes par lessivage des éléments nutritifs au cours d'un épisode d'épidémie de la tordeuse des bourgeons de l'épinette (1981–1984) à une période non perturbée (1999–2003) dans un bassin versant calibré situé dans une forêt de sapin baumier.
- Les pertes par lessivage des éléments nutritifs du sol ont été significativement plus élevées au cours de l'épidémie de la tordeuse des bourgeons de l'épinette (1981–1984) pour N-NO₃ (30,1 fois), K (8,3 fois), N-NH₄ (6,2 fois), Mg (2,7 fois) and SO₄ (2,2 fois), de N-NO₃ (par rapport à une période non perturbée (1999–2003). Quand la répétition des épidémies de tordeuse des bourgeons de l'épinette (33 ans) et une durée moyenne plausible de ces événements (5 ans) sont prises en considération, il est estimé que dans le long terme, 5,6 fois plus de NO₃, 1,5 fois plus de K et 1,2 fois plus de NH₄ sont lessivés du profil du sol durant les épidémies.
- Les importantes pertes par lessivage lors des épidémies de tordeuse des bourgeons de l'épinette, ajoutées aux pertes dues à la récolte des arbres et au feu (et des dépôts acides pour K), peuvent avoir des effets considérables sur la fertilité des sols et la durabilité de l'écosystème.

* Corresponding author: louis.duchesne@mrf.gouv.qc.ca

1. INTRODUCTION

Insect outbreaks represent important ecological events that are part of the natural disturbances affecting forest dynamics. Such disturbances may considerably alter the rates of processes that are fundamental to energy, nutrient, and biogeochemical cycling, and drastically reduce uptake by vegetation (MacLean, 1990). In addition to the direct effects on tree growth, increased leaching of nutrients through drainage water has been reported for deciduous forests of the north-eastern United States following insect defoliation (Eshleman et al., 1998; Reynolds et al., 2000; Swank et al., 1981; Webb et al., 1995). The higher leaching losses have been attributed to many factors, including increased rates of return from plants to soil through faecal material (Hollinger, 1986), an increase in nutrients returned to soils in insect cadavers that are more easily decomposed than is leaf litter (Schowalter et al., 1986), an increase in nutrient content in throughfall primarily through increased rates of nutrient leaching from damaged leaves, and reduced interception by the canopy (Tukey, 1982). Changes in the quantity and quality of leaf litter (Risley and Crossley, 1993), and increased soil temperature and litter decomposition rates (Reynolds et al. 2000; Webb et al., 1995) also represent plausible explanations. Inorganic N species, particularly NO_3^- , is the element for which leaching losses are the most often reported. For example, defoliation by the fall cankerworm (*Alsophila pometaria*) in the southern Appalachians in the USA results in marked changes in the export of nitrate in forest streams (Swank et al., 1981). Likewise, infestations of black locust (*Robinia pseudoacacia* L.) by the locust stem borer (*Megacyllene robiniae*) in the same forests coincide with high NO_3^- export in streams (Crossley et al., 1988). A moderate outbreak of the oak-feeding sawfly (*Periclista* sp.) in the Appalachians led to a tripling of average frass inputs and to a five-fold increase in soil nitrate availability (Reynolds et al. 2000). Increases in NO_3^- export have also been observed following gypsy moth (*Lymantria dispar*) defoliation (Eshleman et al., 1998; Webb et al., 1995). Christenson et al. (2002) have shown that the nitrogen comprised within gypsy moth frass can be rapidly immobilized within the soil in northern hardwood stands. Lovett et al. (2002) suggested that most of the nitrogen released from foliage through defoliation by the gypsy moth is redistributed within other forest compartments, and that leaching losses are relatively small.

In the boreal coniferous forests of Canada and in balsam fir (*Abies balsamea* (L.) Mill.) dominated stands of the north-eastern USA, defoliation caused by spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks is one of the major natural disturbances leading to important tree mortality in balsam fir and spruce (*Picea* sp.) stands (Morin, 1994). The spruce budworm outbreaks occurred with a recurrence cycle of 33 years, and their effects on forest productivity cannot be compared with any other insect in eastern North America (Morin, 1994; Morin et al. 2007). The effects of spruce budworm outbreaks on forest productivity are even more important than is fire for many regions of eastern North America (Morin et al. 2007). In the province of Québec, for example, the last outbreak (1975–1985) destroyed annually 139 to

238 million m^3 of softwood on public lands (Boulet et al., 1996) leading to very important economic losses.

Despite the very dramatic aspects of spruce budworm outbreaks, their effects on nutrient export from boreal forests soils are still not well quantified. A calibrated catchment (Lake Laflamme) in the balsam fir forest was heavily affected by the spruce budworm outbreak between 1976 and 1984. Here, after recovery of tree growth, we compared nutrient leaching losses during this spruce budworm outbreak episode to an unperturbed period (1999–2003).

2. MATERIAL AND METHODS

2.1. Study site

The Lake Laflamme watershed (LLW), 68 ha in area, is located 70 km north of Québec City, Canada ($47^\circ 19' 41'' \text{ N}$; $71^\circ 07' 37'' \text{ W}$; 771–864 m a.s.l.). The canopy vegetation ($1092 \text{ stems ha}^{-1}$) is dominated by even-aged balsam fir, with a small component of white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.). Approximately 65% of the watershed is covered by mature stands (49.4 ± 5.5 years, average \pm standard deviation) in which the average annual increment was approximately equal to the current annual increment. The remaining area is a mixture of windthrow and regeneration. The watershed was affected by a severe spruce budworm outbreak from 1976 to 1984. Between 1981 and 2002, the average annual mean temperature and precipitation were 0.6° C and 1284 mm, respectively, with evapotranspiration losses amounting to 463 mm. The soils are classified as Orthic Humo-Ferric Podzols (Haplorthods) in the Canadian classification system which corresponds to Spodosols (Haplorthods) in the American classification. The bedrock consists of Precambrian charnockitic gneiss. More details on study site may be found in previous publications (Houle and Carignan, 1992).

2.2. Water sampling and analysis

Between 1981 and 1998, precipitation was sampled daily using an automatic wet-only collector at an open site located at the border of the watershed. After 1998 precipitation was sampled weekly. Stream flow was continuously monitored for water exports, and sampled weekly at a gauge station located at the lake's outlet. Between 1981 and 1988, mineral soil solutions were sampled at six locations in the watershed using tension ceramic cup lysimeters ($n = 2$ to 4 per location) placed at a depth of 30 cm. Forest floor percolates were also sampled with zero tension lysimeters near the open site ($n = 3$) between 1984 and 1988. In 1999, a study plot ($25 \times 50 \text{ m}$) was established in the watershed in order to monitor nutrient fluxes and vegetation. Since then, forest floor percolates have been sampled with four zero tension lysimeters, while the mineral soil solution was sampled with four tension lysimeters located at a depth of 30 cm and evenly distributed throughout the study plot. Sampling took place weekly from May to October or in the absence of snowpack and frost.

Sample pH was determined potentiometrically. Basic cations were analysed using atomic absorption or emission between 1981 and 1990, and subsequently by inductively coupled plasma emission. Nitrate and SO_4 were analysed by ion chromatography in all solutions between 1981 and 1998, except for SO_4 at the lake's outlet, which

was analysed by colourimetry. Based on paired samples ($n = 42$), values of SO_4 obtained by colourimetric autoanalyser were slightly higher (11%) compared to values obtained by ion chromatography. The colourimetric values were thus adjusted by linear regression ($R^2 = 0.91$). Analyses for NH_4 were done by colourimetry (Technicon AA2).

2.3. Historical tree growth assessment

Tree growth was assessed from dendrochronological analysis. In 1998, 50 dominant and codominant balsam fir trees were sampled at the perimeter of the monitoring plot. For each tree sampled, two increment cores were extracted at breast height (1.3 m above the highest root) from opposite sides of the bole. Cores were dried, mounted in wooden blocks and sanded for dendrochronological measurements. Ring widths of all cores were cross-dated by visual examination of tree-ring sequence before measurement (skeleton plot procedures) (Fritts, 1976; Yamaguchi, 1991). Ring widths were measured to the nearest 0.01 mm with a WinDendro Image Analysis System for Tree-Ring Measurement (Regent Instruments Inc.). Missing and absent rings were added, when necessary, according to standard procedure (Yamaguchi, 1991). Ring width data were verified statistically with the COFECHA program; a quality-control program widely used by dendrochronologists to check the crossdating and overall quality of tree ring chronologies (Holmes, 1996). Cores with rotten heart or cores that could not be cross dated accurately were rejected. A total of 47 trees were used for the subsequent analysis. Previous study has shown that basal area increment (BAI) at breast height is a useful representation of tree vigour and whole-stem growth (Duchesne et al., 2003; LeBlanc, 1990). Annual ring increments were converted to BAI using the formula:

$$\text{BAI} = \pi(R_n^2 - R_{n-1}^2)$$

where R is the tree radius and n is the year of tree ring formation. An average ring basal area chronology was generated by averaging the BAI of each tree over each year. The chronology was truncated when less than ten trees were available.

2.4. Historical spruce budworm defoliation and climate assessment

The Quebec Department of Natural Resources conducts yearly aerial surveys for spruce budworm within Quebec. Parallel (west-east) flight lines, 5–10 km apart, between latitudes 45°N and $50^\circ 30' \text{N}$ are flown at an elevation of 180–250 m. Surveys are conducted from late June in the southwest of the province to early August in the northeast according to regional climate and tree phenology. A code that describes the average level of tree defoliation (0: no defoliation; 1: low defoliation 1–34%; 2: moderate defoliation 35–69%; high defoliation 3: $\geq 70\%$) was assigned to each 5 min (longitude) by 5 min (latitude) cell, and cells were identified by the coordinates of their centers. Average cell size was 58 km^2 (Gray et al., 2000). In the present study, we used mid-class values for computations.

Long term daily air temperature and precipitation (1948–1999) were computed using BioSIM, a system designed to estimate local weather variables from surrounding meteorological stations. This system performs two main functions: (1) matching geo-referenced sources of weather data to the specified locations, and (2) adjusting

data from the selected stations for differences in latitude, longitude, elevation, slope and aspect between the source of weather data and a specified location (Régnière, 1996). The BioSIM model performed very well over a wide range of climatic conditions (Régnière and St-Amant, 2007). In our particular case, a meteorological station located approximately 5 km from the studied site ensure high correlations between interpolated and observed climatic variables.

2.5. Fluxes calculation

Annual (water year: October to September) fluxes in precipitation, soil leaching, and stream water were calculated for H, NO_3 , NH_4 , SO_4 , K, Ca and Mg. Precipitation input were calculated by combining ion concentrations with the cumulative weekly water input. For the soil rooting zone (50 cm), monthly average soil solution concentrations (30 cm) were combined with simulated monthly water exports obtained from the FORHYM II hydrological model, which was previously calibrated for the LLW site (Arp and Yin, 1992). The bias of this estimation (30 cm concentrations instead of 50 cm) is of small importance for base cation fluxes, which vary slightly with depth (Duchesne and Houle, 2008). Watershed exports were calculated by combining ion concentrations with the cumulative weekly water export. Exports and concentrations during the spruce budworm outbreak (1981–1984) and after (1999–2003) were compared with a Wilcoxon signed-rank test (Wilcoxon, 1945).

3. RESULTS

3.1. Tree growth and spruce budworm outbreak observations

Most of the watershed was harvested in 1941. Pre-established regeneration reached breast height around 1948 (Fig. 1). Since then, tree growth has ranged from 1.9 to $4.4 \text{ cm}^2 \text{ tree}^{-1}$ (mean = $2.6 \text{ cm}^2 \text{ tree}^{-1}$) except for three distinct periods (1967, 1977–1979 and 1981–1984). During those periods, tree growth averaged 38% lower ($1.6 \text{ cm}^2 \text{ tree}^{-1}$) than the mean growth observed over the entire chronology. The relative defoliation, as observed by aerial survey, ranged from 20 to 100% from 1976 to 1984, with the exception of 1979, where no defoliation occurred (Gray et al., 2000). Since 1986, tree growth has been generally higher as compared to the beginning of the chronology.

3.2. Soil water concentrations and nutrient fluxes

Forest floor and soil water sample concentrations are presented in Figure 2. Most element concentrations in the forest floor and soil solution were generally higher during the spruce budworm outbreak and declined thereafter. Although the spruce budworm abundance was dramatically reduced in 1985, K and inorganic N species remained high for a few years afterwards, as compared to the unperturbed period.

Water deposition and water fluxes below the rooting zone and at the stream outlet do not differ significantly during the

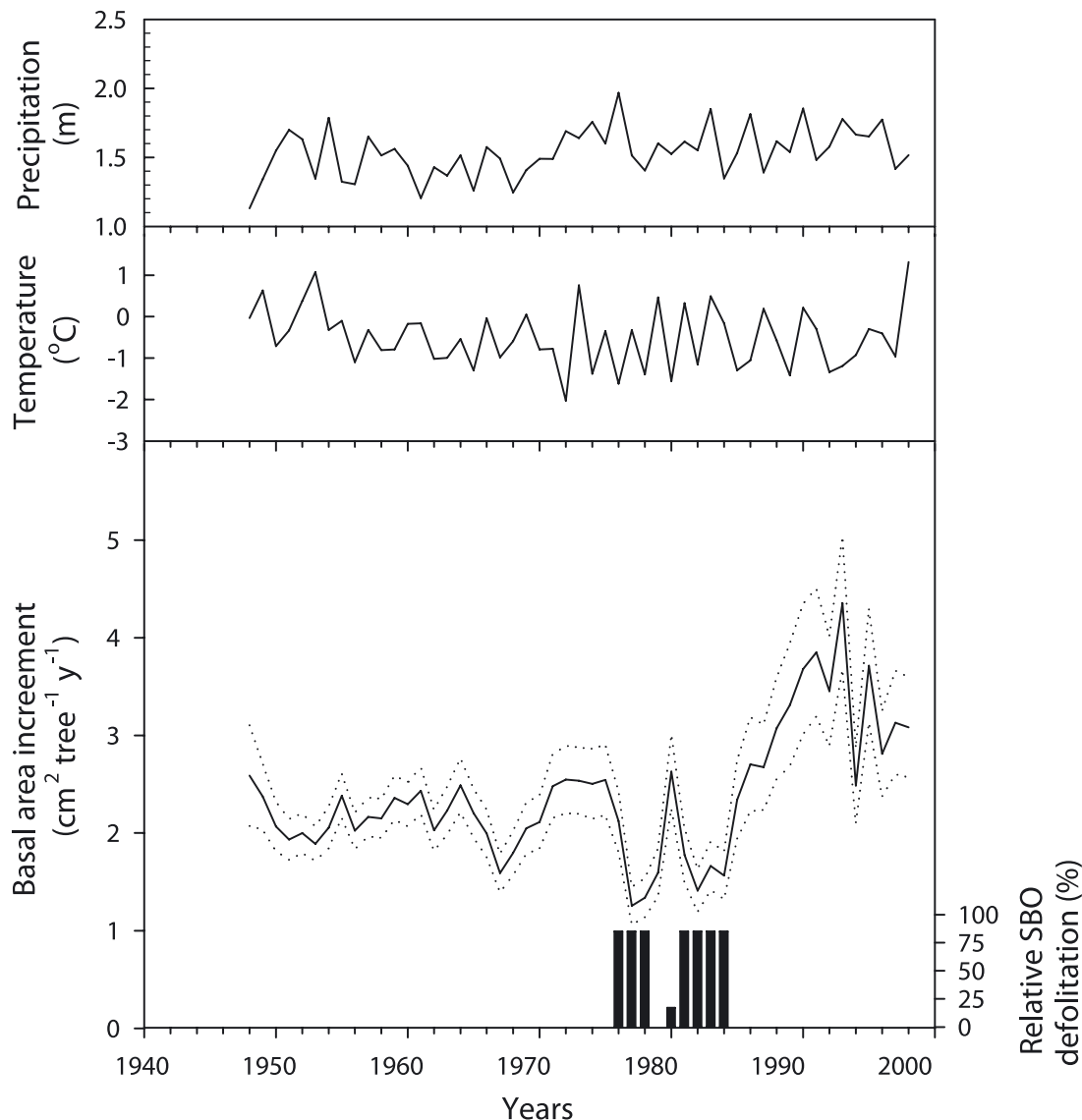


Figure 1. Annual precipitation, mean temperature, basal area increment of dominant and co-dominant balsam fir and relative damage (bottom right axis) caused by the 1976–1984 spruce budworm outbreak. Dotted lines represent ± 1 standard error.

spruce budworm outbreak and the post-outbreak period ($p \geq 0.24$). Comparison of precipitation, soil leaching and stream fluxes for the spruce budworm outbreak (1981–1984) period and the post outbreak are presented for each element in Figure 3. Atmospheric wet deposition of SO_4 was 1.6 times higher during the spruce budworm outbreak as compared to the post outbreak period ($p = 0.043$). Marginally insignificant differences were also observed for atmospheric deposition of H that was 1.5-fold higher ($p = 0.083$). Soil leaching of H, K, Ca, Mg, N- NH_4 , N- NO_3 and SO_4 were 2.3, 8.3, 2.4, 2.7, 6.2, 30.1 and 2.2 times higher, respectively, during the spruce budworm outbreak as compared to post outbreak values ($p \leq 0.043$). Stream flow exports of Mg were relatively similar, while H, Ca and N- NO_3 stream exports were lost in greater amounts during the spruce budworm outbreak ($p \leq 0.043$).

4. DISCUSSION

4.1. The effect of the spruce budworm outbreak on tree growth

The growth reduction during the 1977–1979 and 1981–1984 periods are not related to any particular climatic episodes but are synchronized with the defoliation caused by the spruce budworm as observed by aerial surveys (Fig. 1). Mean annual basal area increment during the spruce budworm outbreak is 38% lower than the average growth since 1948. Such an effect of spruce budworm outbreak on growth is typical for coniferous sites (Morin et al., 2007). The short burst of higher growth rate in 1980 was likely due to a strong decrease in spruce budworm abundance. This pattern of strongly reduced budworm

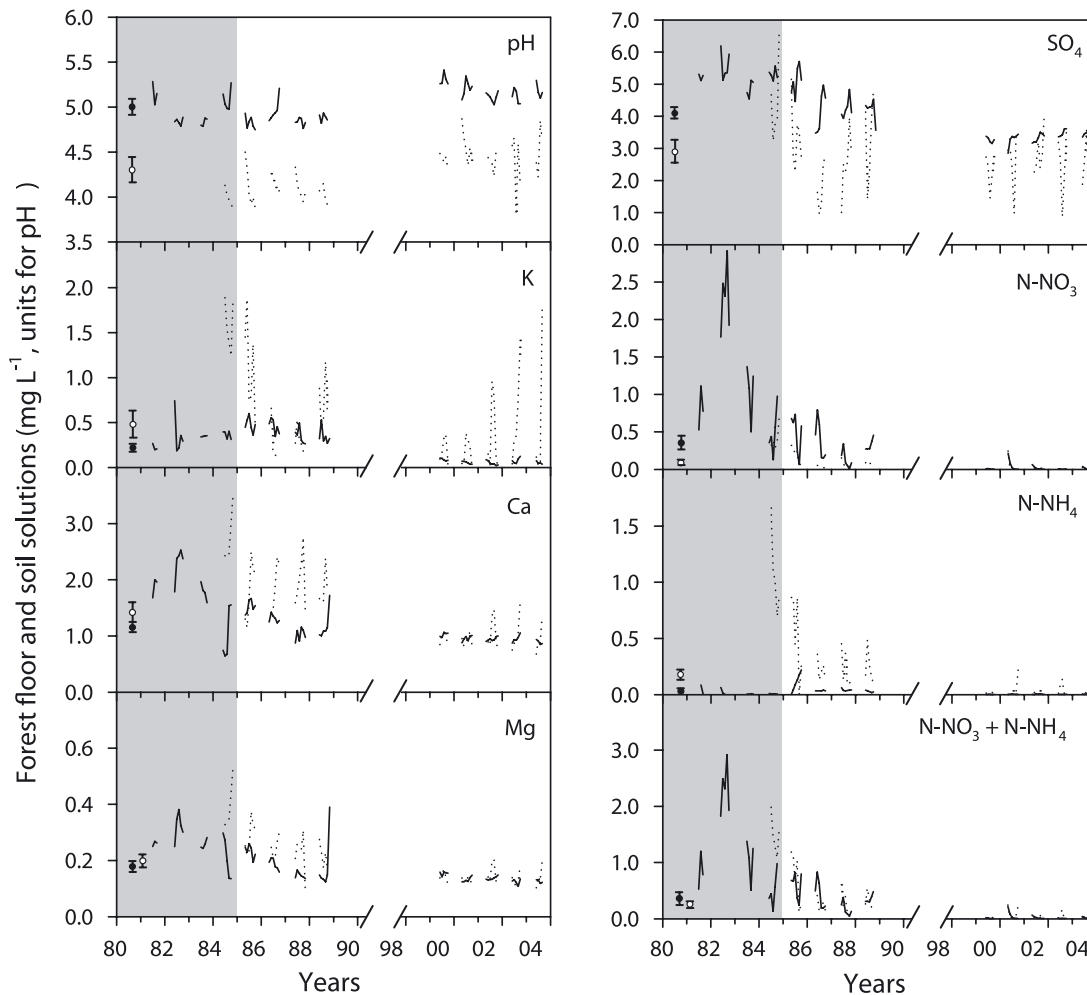


Figure 2. Temporal variations of major ions in the forest floor (dotted line) and the mineral soil (straight line) percolates. The shaded areas represent the spruce budworm outbreak period. Error bars on the left indicate average standard error of monthly concentrations.

abundance within the middle of an outbreak has been observed for large portions of the landscape in the provinces of Québec (Gray et al., 2000; Jardon and Morin, 2003) and Nova Scotia (Ostaf and MacLean, 1995).

Tree growth is generally higher following spruce budworm outbreak as compared to the beginning of the chronology. We suggest that remnant trees that were not killed during the spruce budworm outbreak benefited from space created by the mortality of some individuals, and consequently exhibit higher growth. Tree growth was also considerably reduced in 1967. However, that year does not correspond to any report of spruce budworm outbreak in the province (Gray et al., 2000; Jardon and Morin, 2003). Climate records from the Québec City airport indicated that 1967 was the coldest spring (March–May; 0.1 °C, normal = 3.3 °C) and the wettest summer (June–August; 496 mm, normal = 359 mm) recorded since 1943 (CRIACC, 2008). Such extreme climate conditions may have had considerable effects on tree growth (Fritts, 1976). Consequently, we suggest that the 1967 growth reduction was related to climate.

4.2. The effect of spruce budworm outbreak on soil leaching exports

Very important differences in soil leaching exports (and to a lesser extent in streams) were observed when the spruce budworm outbreak and the unperturbed period were compared. The differences were particularly important for inorganic N ($\text{NO}_3 + \text{NH}_4$) and K, two elements known to be actively recycled through biotic reactions in forest soils (Aber and Driscoll, 1997; Likens et al., 1994; Johnson et al., 2008). The higher inorganic N and K exports during the spruce budworm outbreak cannot be attributed to higher atmospheric fluxes of these elements, because there were no significant differences in wet deposition of these elements between the time of the spruce budworm outbreak and the unperturbed period. Other factors known to affect N cycling, such as climate fluctuations (Mitchell et al., 1996) cannot be supported because temperature and precipitation during the growing season (June–September) were not different between the two periods (12.7 ± 1.5 vs. 13.6 ± 0.9 °C and 352 ± 122 mm vs. 362 ± 103 mm

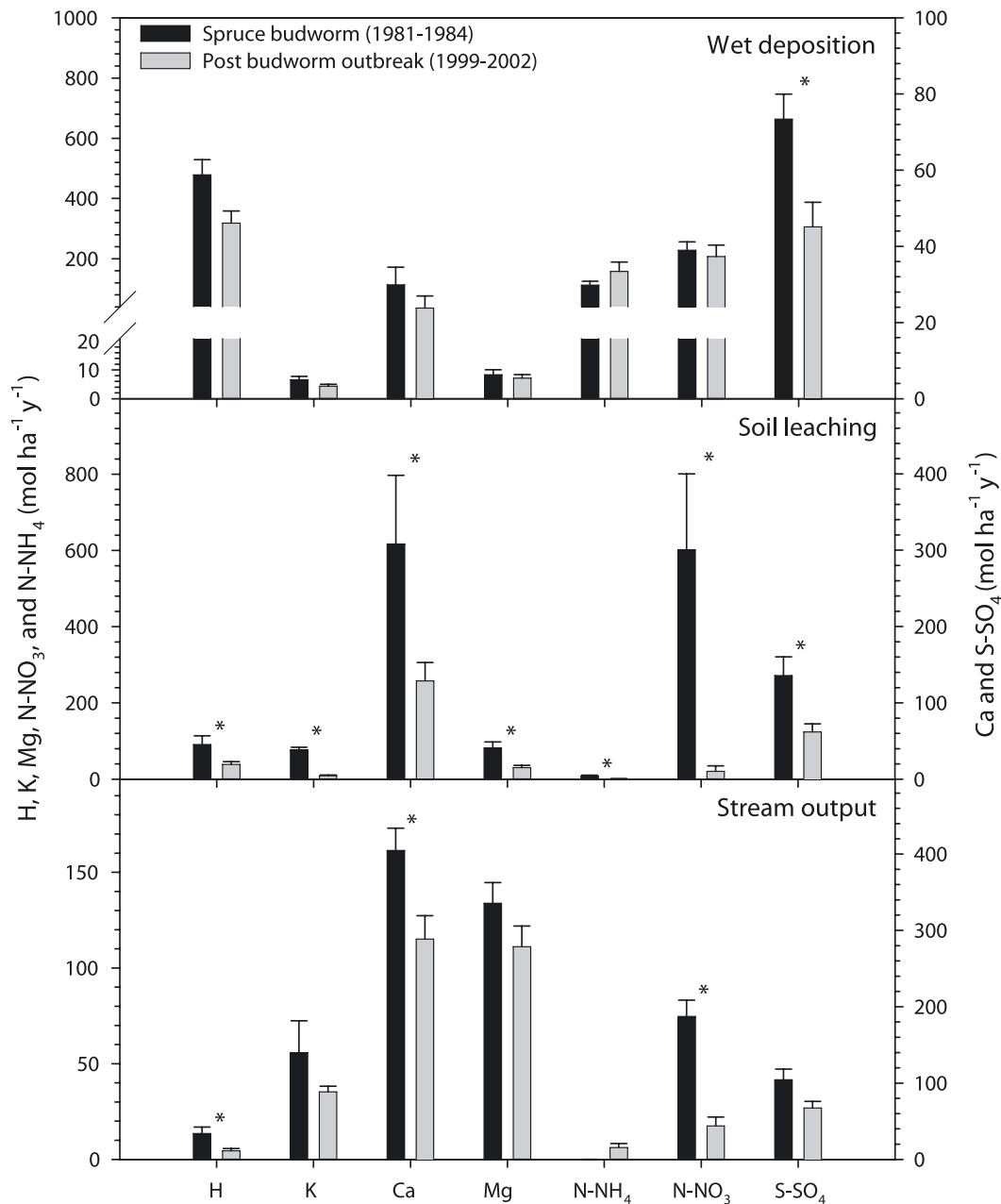


Figure 3. Atmospheric depositions and soil and stream major ion fluxes during the spruce budworm outbreak period and the post outbreak period. Error bars show the Standard Error. Test significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

for the spruce budworm outbreak and unperturbed period respectively; $p \geq 0.15$). In fact, annual NO₃ concentration and export, both in the soil solution below the rooting zone and at the stream watershed output, were not correlated to annual N depositions or to annual precipitation and temperature. However, strong correlations were found between the percent of defoliation attributable to the spruce budworm outbreak and NO₃ concentrations in the soil solution ($r = 0.84$) and the stream ($r = 0.96$). We thus considered that the high soil leaching losses of elements during the spruce budworm outbreak was a direct consequence of the spruce budworm outbreak it-

self. Although such a potential impact of spruce budworm outbreak could have been expected, the leaching losses caused by such a perturbation have never been quantified before.

4.3. Inorganic N species

Some studies have shown similar strong effects on NO₃ leaching for different degrees of defoliation caused by different species of insect outbreaks in the northeastern USA (Eshleman et al., 1998; Lewis, 1998; Reynolds et al., 2000;

Swank et al., 1981; Webb et al., 1995). The reduction (up to 38%) in annual balsam fir growth (Fig. 1), and therefore in nutrient uptake, could explain a part of the higher N (and K) leaching losses during the spruce budworm outbreak. For example, if we assume that the reduction in total N uptake ($900 \text{ mol ha}^{-1} \text{ y}^{-1}$, unpublished data) was nearly proportional to the reduction in growth, then, a difference of $343 \text{ mol ha}^{-1} \text{ y}^{-1}$ in tree uptake could be potentially available for leaching, which would represent 55% of total soil N leaching losses. Defoliation may have had indirect effects, such as decreasing the above-ground biomass water uptake and increasing light transmission to the forest floor, thus increasing soil moisture and soil temperature. This situation is likely favourable to increased microorganism activity, and hence increased soil organic matter (and organic N) decomposition rates.

Decomposition of budworm excreta and cadavers may also contribute to N leaching, since insects can convert an important part of the N sequestered in the needle canopy, which amounts to $12\,500 \text{ mol ha}^{-1}$ at our site (unpublished data) to readily available organic N and NH_4 (Hollinger, 1986). The soil rooting zone inorganic N exports during the spruce budworm outbreak were $610 \text{ mol ha}^{-1} \text{ y}^{-1}$, as compared to $341 \text{ mol ha}^{-1} \text{ y}^{-1}$ for atmospheric wet deposition, clearly showing that internal sources contributed to the soil leaching export. This situation is in contrast with the unperturbed period during which inorganic N is strongly retained within the soil. In fact, the inorganic N exports below the rooting zone were 30 times higher during the spruce budworm outbreak than during the undisturbed 1999–2002 period, with NO_3 comprising 67% of the total inorganic N exports.

Most of the high NO_3 exports following insect outbreaks were reported for deciduous forests (Lewis, 1998; Webb et al., 1995). The high N- NO_3 exports below the rooting zone for the LLW is surprising, given the inhibiting effect of the high phenolic content of balsam fir litter (Baldwin et al., 1983; Olson and Reiners, 1983; Thibault et al., 1982). In addition, nitrification rarely occurs under pH 4.5 (Rudebeck and Persson, 2000; Ste-Marie and Paré, 1999), while the humus layer pH during the spruce budworm outbreak was 4.3. To examine more closely the inorganic N fluxes within the soil profile, we used data from 1985 for which LFH fluxes were available. Although the spruce budworm outbreak was nearly over by 1985, the effect clearly persisted for a few years afterwards, as shown by the high K and inorganic N concentrations in the soil lysimeters (Fig. 2) that remained high as compared to the unperturbed period. This is probably due to tree mortality, which may reach 20 to 25% following intense spruce budworm outbreak, while foliage reconstitution and growth of living trees may need 5 to 7 years before totally recovering (Ostaf and MacLean, 1995). As a result, openings in the canopy may persist for a few years after the end of the outbreak, enhancing light and rain penetration to the forest floor and potentially favouring higher organic matter decomposition rates. Moreover, the dead tree organic matter, particularly within the needles and the small branches, may constitute readily available sources of K and N that may continue to be lost for a few years following the outbreak. Although, mortality data were not available for the

Lake Laflamme site, Houle and Carignan (1992) reported that freshly fallen dead balsam fir on the ground represented up to 25% of the total tree biomass at the LLW site in 1988, suggesting that balsam fir mortality was important.

The examination of the 1985 data suggests that N transformation processes were profoundly disturbed within the soil profile as a result of the spruce budworm outbreak. Important amounts of N- NH_4 ($376 \text{ mol ha}^{-1} \text{ y}^{-1}$) were exported below the forest floor, contributing to nearly 90% of the total inorganic N fluxes ($418 \text{ mol ha}^{-1} \text{ y}^{-1}$) as compared to insignificant N- NH_4 fluxes during the unperturbed period. Although the amount of inorganic N exported from the mineral soil was nearly similar ($201 \text{ mol ha}^{-1} \text{ y}^{-1}$) to the amount exported below the humus layer, 67% of it was composed of N- NO_3 , demonstrating that incoming NH_4 from the humus layer was almost totally nitrified within the mineral soil. The higher pH (average 4.9, Fig. 2) and lower dissolved organic carbon (DOC) (average 4.6 mg L^{-1} , unpublished data) concentrations (and presumably phenolic compounds) found in the mineral soil solution, as compared to the low pH (average 4.3) and the high DOC (average 22.4 mg L^{-1} , unpublished data) of the forest floor solution was probably a factor explaining the intense nitrification within the mineral soil.

Although the N- NO_3 export at the catchment scale was 4.2 times higher during the spruce budworm outbreak ($75 \text{ mol ha}^{-1} \text{ y}^{-1}$) than during the unperturbed period ($18 \text{ mol ha}^{-1} \text{ y}^{-1}$), it was clearly lower than the spruce budworm outbreak soil leaching losses ($602 \text{ mol ha}^{-1} \text{ y}^{-1}$) (Fig. 3). One possibility to explain this difference is that the NO_3 exported from mid-slope sites may have been taken up by trees and/or soil microorganisms lower on the watershed slope before reaching the lake. There is a small abundance of cedar trees surrounding the lake perimeter that may have sequestered a part of the incoming NO_3 . It seems doubtful, however, that they could uptake such an important proportion of the NO_3 lost upslope. Important in-lake losses may also have occurred via (1) denitrification in the riparian zone and within the oxygen-free, organic-rich sediment belting the lake, (2) uptake by the important macrophyte community at the lake littoral, and finally (3) phytoplankton uptake followed by sedimentation.

4.4. Cation losses

The loss of K through soil leaching (Fig. 3) was particularly high ($76.4 \text{ mol ha}^{-1} \text{ y}^{-1}$) during the spruce budworm outbreak as compared to 1999–2002 values ($9.4 \text{ mol ha}^{-1} \text{ y}^{-1}$). For example, soil exports of K during the spruce budworm outbreak were 8.3 times higher than 1999–2002 values, as compared to 2.4- and 2.7-fold for Ca and Mg, respectively. The K concentration in soil solution remained high until 1988, while other cations showed earlier signs of recovery (Fig. 2). Potassium is a highly mobile element whose tight retention in the rooting zone of forest ecosystems is ensured almost exclusively by biotic processes. The large K losses during the spruce budworm outbreak were thus indicative of a breakdown of biological retention mechanisms as also evidenced by the high NO_3 exports discussed above. Several studies of insect outbreaks

have also demonstrated increased basic cation export following intense defoliation (Eshleman et al., 1998; Reynolds et al., 2000; Swank et al., 1981; Webb et al., 1995). Many of the reasons used above to explain the higher N fluxes also hold for K losses, including lower tree uptake and increased organic matter decomposition rates.

Catchment losses of K during the spruce budworm outbreak were lower than the soil leaching losses, but the differences were not as important as for NO₃. The biotic uptake that may potentially occur (trees and macrophytes) at the lake littoral vicinity as described above may also explain the difference in K fluxes. In addition, a substantial portion of the catchment K exports originates from weathering of the till located below the rooting zone (Duchesne and Houle, 2008). Consequently, the signal of an important biotic source of K during the spruce budworm outbreak is somehow diluted in the K provided by weathering, which is not the case for NO₃ for which the weathering contribution is negligible.

The relatively low losses of Ca and Mg as compared to K during the spruce budworm outbreak may be explained by the fact that Ca and Mg both have a high capacity to adsorb within the soil exchangeable complex, contrary to K. They are thus less sensitive to losses than elements that cycle almost entirely through biotic reactions, such as K and inorganic N species. Soil solution leached from reconstructed soil columns from LLW revealed a similar pattern of cation leaching with endogenous nitrate production (Boutin and Robitaille, 1989). In addition, Ca and Mg losses are often associated with soil leaching losses of SO₄ (Reus and Johnson, 1985). Regulations to control air pollution in the United States and Canada were significantly strengthened and expanded in 1990, with the ratification of the Clean Air Act Amendment (CAAA) in the USA. Consequently, in Canada and the USA, total SO₂ emissions have declined by approximately 50% and 40%, respectively, between 1980 and 2000 and are predicted to continue to decline between 2000 and 2020 (Niemi, 2004). The fact that both SO₄ wet deposition and leaching were significantly higher during the spruce budworm outbreak may explain in part the higher Ca and Mg losses during this period.

5. CONCLUSION

For the first time, the nutrient losses associated with spruce budworm outbreak have been quantified. During the spruce budworm outbreak, the soil leaching losses of N-NO₃, N-NH₄ and K were increased by 30.1-, 6.2- and 8.3-fold, respectively, as compared to the unperturbed period. The disruption of tree uptake as well as an increased rate of organic matter decomposition are likely responsible for the high exports observed during the spruce budworm outbreak. When the recurrence of spruce budworm outbreak (33 y) and a plausible average length of such events (5 y) are taken into consideration, it is estimated that in the long term, 5.6 times more NO₃, 1.5 times more K and 1.2 times more NH₄ are leached from the soil profile during outbreaks. The important leaching losses during spruce budworm outbreak, when added to the losses caused by tree harvesting and fire (and acid deposition for K)

may have considerable effects on soil fertility and ecosystem sustainability.

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