Geoderma 460 (2025) 117443

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Windthrow modifies soil solution chemistry and nutrient leaching in the Canadian black spruce boreal forest

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ARTICLE INFO

Handling Editor: Alberto Agnelli

Keywords:
Boreal forest
Forest disturbance
Forest soil
Soil solution
Nitrogen cycle
Windthrow

ABSTRACT

Soil solution chemistry is directly related to vegetation nutrition and growth in forest ecosystems. However, the impacts of natural disturbances on boreal forest soil solution composition and nutrient fluxes remain unclear. In this study, we explore the effects of a windthrow on soil solution chemistry collected weekly between 2012 and 2018 during the snow-free period at a Canadian black spruce boreal forest site. We show that the windthrow had an important effect on soil solution chemistry within only a few days, inducing much higher NO_3^- and NH_4^+ concentrations and a strong pH drop, persisting up to six years after the disturbance. Following the windthrow, soil solution major ion concentrations (i.e., K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, SO_4^{2-}) similarly increased but with various intensities and recovery times. This windthrow also occurred on a site receiving a chronic ammonium nitrate treatment as part of a N deposition simulation experiment, which showed that two decades of N treatment had nearly no impacts on soil solution NO_3^- and NH_4^+ concentrations. Therefore, our results indicate that windthrows could potentially alter the North American boreal forest soil chemistry much more than elevated N deposition corresponding to 200 years of accelerated ambient N deposition. While this finding needs to be supported by larger studies, it clearly highlights the significance of wind disturbances' impacts on nutrient cycling and calls for more research as windthrow frequency is predicted to increase with global change.

1. Introduction

The black spruce–moss forest is the largest bioclimatic zone of the boreal forest and covers ~2 million km^2 in North America (Canada's National Forest Inventory, 2025). This large ecosystem plays crucial environmental roles such as sheltering biodiversity and storing substantial amounts of carbon (C), mostly in its soils (Pan et al., 2011).

Fires, insect outbreaks, and windthrows are the main natural disturbances experienced by boreal forests. By strongly modifying vegetation composition, tree stands density, and soil chemistry, they constitute the starting point of boreal forest ecosystems regeneration. The duration of a forest regeneration cycle depends on tree stands composition, geographic location, and environmental conditions (Taeroe et al., 2019). However, climate change is inducing more severe and frequent natural disturbances and can ultimately reduce forest regeneration cycle time (Kautz et al., 2017; Westerling, 2016).

Windthrows are much less studied than other major disturbances like fires. However, they can still significantly impact forest ecosystems by increasing tree mortality and facilitating insect outbreaks (Seidl et al., 2017). Windthrows consist of partial or total tree stands being uprooted and/or broken by strong winds, usually during storms. Windthrow vulnerability is mainly driven by tree stand characteristics (e.g., species, age, root anchorage), soil properties, and exposition to wind (Anyomi et al., 2017; Elie and Ruel, 2005; Meunier et al., 2002; Waldron et al., 2013). However, climate is a determining factor in windthrow frequency, and warmer and wetter conditions were shown to favorize windthrow occurrence worldwide as it impacts tree anchorage and growth (Seidl et al., 2017). Because average temperature and precipitation are predicted to globally increase in the Canadian boreal zone (Price et al., 2013), most of the North American boreal forest will likely experience more wind disturbances in the future. More specifically, in eastern Canada, prediction models indicate a future higher risk of windthrow in boreal forests due to an increase of the length of unfrozen soil conditions (Saad et al., 2017).

In addition to potential wood loss for the forestry sector, windthrows can profoundly affect soil nutrient concentrations and fluxes. In Europe,

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https://doi.org/10.1016/j.geoderma.2025.117443
Received 26 February 2025; Received in revised form 22 May 2025; Accepted 10 July 2025
Available online 16 July 2025

windthrows were shown to modify forest soil nitrogen (N) content and C stocks (Crișan et al., 2021; Mayer et al., 2023). In a coniferous forest of central Europe, a 12,000-ha windthrow induced major cation (NH_4^+, K^+, Ca^{2+}, Mg^{2+}) and anion (NO_3^-) leaching (Bischoff et al., 2008). Similarly, a study regrouping 33 sites in the Swedish boreal forest showed that NO_3^- concentration significantly increased in soil solution for ~5 years following a windthrow (Hellsten et al., 2015).

Despite their frequency and their important consequences on forest ecosystems, the exact impacts of windthrows on soil solution nutrient concentrations in the North American boreal forest are still uncertain, as no study investigated these so far. The objective of the present study was to assess the long-term impacts of a naturally formed windthrow on North American boreal forest soil solution chemistry. In 2012, a windthrow occurred on an experimental site located in the eastern Canadian black spruce boreal forest. For 7 years following the disturbance, we measured ion concentrations and pH in soil solution collected in lysimeters placed at 60 cm depth. This windthrow also happened on a site receiving a chronic ammonium nitrate treatment as part of an N deposition simulation experiment (see Houle et al., 2025) which allowed us to compare the effects of 18 years of N addition and windthrow on soil solution chemistry and nutrient leaching. Based on previous studies, we predicted that the windthrow would significantly modify soil solution chemistry and induce higher ion leaching for at least a few years. As N treatment had only minor impacts on soil solution (Houle et al., 2025), we also predicted that the windthrow would represent a much greater disturbance than higher N deposition to soil solution composition and nutrient cycling.

2. Methods

2.1. Site description

The site involved in this study belongs to a network of forest watershed experimental sites monitored by the government of Quebec since the 2000s, and is located in the boreal forest of Quebec, Canada, within the black spruce – moss bioclimatic domain. At this site, black spruce (*Picea mariana* [Mill.] B.S.P) is the dominating tree species, with a basal area of ~28.5 $m^2 \cdot ha^{-1}$ (Houle et al., 2015), and the understory vegetation mainly comprises feather mosses (e.g., *Pleurozium schreberi* [Willd. ex Brid.] Mitt., *Ptilium crista-castrensis* [Hedw.] De Not.) and ericaceous shrubs (e.g., *Rhododendron* groenlandicum [Oeder] Kron & Judd). Soil and humus are respectively classified as Orthic Humo-Ferric Podzol and Mor type (Soil Classification Working Group, 1998) and organic F-H horizons are acid with pH ranging from 2.8 to 3 (Ste-Marie and Houle, 2006). Mean annual temperature is 0̊C whereas mean annual precipitation is 823 mm. Ambient N deposition is considered very low and is estimated to 3 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Ste-Marie and Houle, 2006). Additional information about the environmental characteristics of the study site is presented in Table S1.

2.2. Fertilization experimental design

The study site is part of an N fertilization experiment set up in 2000 and described in detail in Houle et al. (2024a). This site consists of 9 experimental units measuring 10 × 10 m, separated by at least 10 m and all located approximately 100 m away from the road, receiving low N treatment (LN), high N treatment (HN), or no treatment (control, C). LN and HN treatments corresponded to applications of 9 $kg \cdot N \cdot ha^{-1} \cdot yr^{-1}$ and 30 $kg \cdot N \cdot ha^{-1} \cdot yr^{-1}$ respectively (i.e., 3-fold and 10-fold increase of ambient N deposition measured at the beginning of the experiment), and consisted of applications of a NH_4NO_3 solution supplied as four passes using a backpack sprayer (Solo, Newport News, VA, USA). Treatment application started in June 2001 and was performed once a month between June and October every year.

2.3. Soil solution sampling and chemical analyses

In October 2000, two tension lysimeters (Soil moisture Equipment Corp., Model 1911) per experimental unit were placed at 30 and 60 cm depths. For 17 years (2002–2018), soil solution was collected weekly from May to November and stored at 4̊C until analysis.

After collection, samples were filtered at 0.45 μm (Nucleopore) and pH was measured with a probe. Soil solution NO_3^- and NH_4^+ concentrations were respectively measured by ion chromatography and colorimetry (Technicon AA2), while other ion concentrations (i.e., Na^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, SO_4^{2-}) were measured by plasma emission spectrometry. All elemental concentrations and pH data are summarized in Table S2.

2.4. Windthrow

On August 30th 2012, strong winds recorded at a maximum of 82 $km \cdot h^{-1}$ at the on-site meteorological station created an important total windthrow on the experimental forest site. It is worth precising that the meteorological station is located ~300 m away from the zone affected by the windthrow and that winds could have thus reached higher speeds than the value recorded.

The windthrow greatly disturbed tree stands on one experimental unit that was receiving HN treatment. On this unit and as of 2025, only one black spruce tree was still alive and there were 6 standing dead trees. One broken tree was located about 1 m away from the soil lysimeter and there was no living or standing dead trees within a 3 m radius of the lysimeter. The regeneration status of the experimental unit currently includes ~20 balsam fir trees with an average height of 1 m and 5 white birch trees with an average height of 2 m.

After the windthrow occurred, the site was left as is and no alterations were made. Soil solution continued to be collected as described in Section 2.3, but N treatment was suspended indefinitely due to safety issues.

After the windthrow, the lysimeter located at 30 cm depth received lower amounts of soil solution, probably because of its proximity with the soil surface disturbed by the windthrow, which resulted in obtaining less frequent observations as collected solution volumes were often too low. Therefore, we only show the 60 cm-depth lysimeters data in this study. Since the latter is out of the black spruce rooting zone and that nutrients cannot be taken back by roots, the collected soil solution can be entirely considered as leaching losses from the forest plot.

2.5. Statistical analyses

All statistical analyses were performed on data collected from 2002 to 2018 with R Studio v.4.3.1. (R Core Team, 2023). Figures were built with *ggplot2* (Wickham, 2016) and *ggbiplot* packages (Vu and Friendly, 2024).

To visualize and compare soil solution analyses inside and outside of the windthrow area, we used data from lysimeters placed at 60 cm depth on the unit affected by the windthrow and on the two other units receiving HN treatment but undisturbed by the windthrow (Figs. 1 and 2). In the experimental unit affected by the windthrow, linear models were used to estimate the effects of time (i.e., assessed with the collection date) and the occurrence of windthrow on soil solution pH and log-transformed ion concentrations (NO_3^-, NH_4^+, Na^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, SO_4^{2-}). Additionally, Principal Component Analysis (PCA) was performed to further assess the relationship between windthrow and soil solution pH and ion concentrations. All variables were shifted to be zero-centered and subsequently scaled to have unit variance using the prcomp function prior to perform the PCA.

3. Results

On August 30th, 2012, strong winds measured at 82 $km \cdot h^{-1}$ are

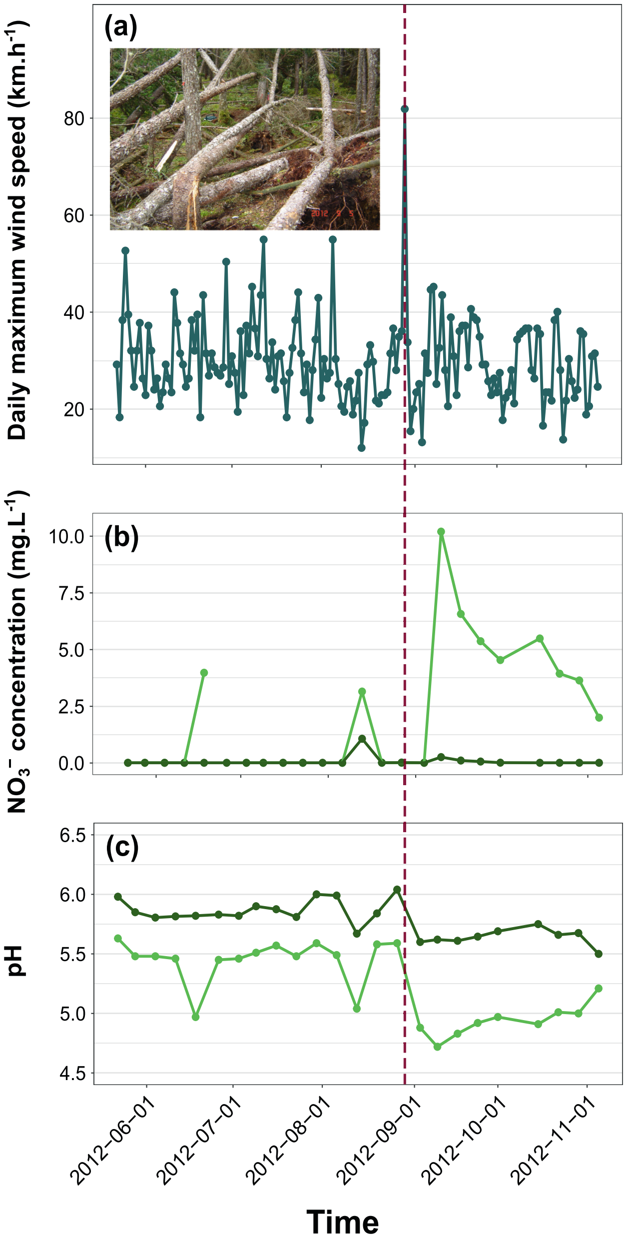

Fig. 1. Daily maximum wind speed (a), and soil solution NO_3^- concentration (b) and pH (c) measured across 2012 at an experimental boreal forest site. The photo (a) was taken on September 5th, 2012, and shows the windthrow that occurred a few days prior on one of the experimental units. The dashed red line corresponds to the creation date of the windthrow. Light green points correspond to observations from the experimental unit affected by the windthrow and dark green points correspond to the means of observations from the two undisturbed units.

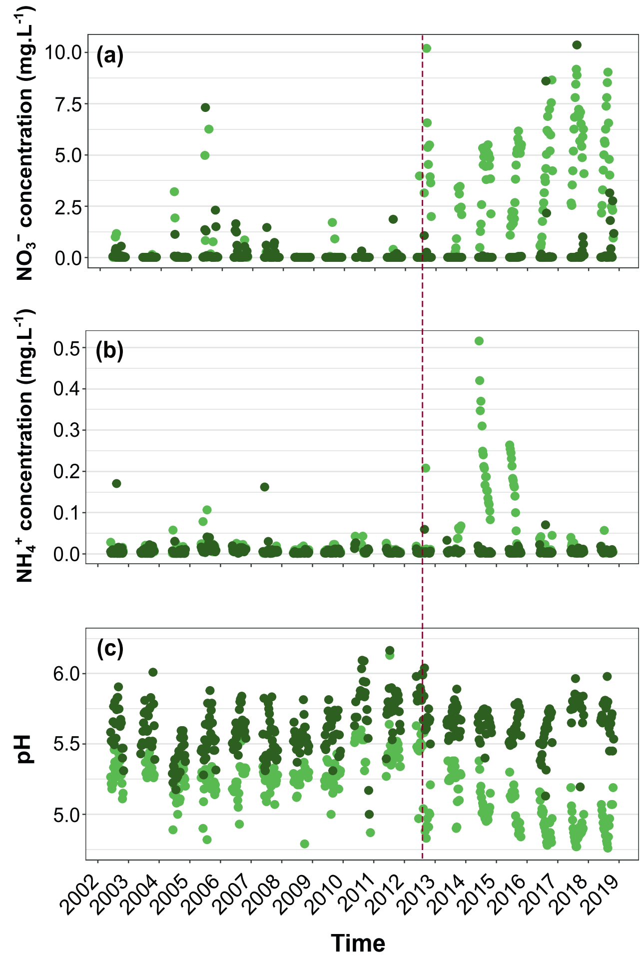

Fig. 2. Soil solution NO_3^- concentration (a), NH_4^+ concentration (b), and pH (c) measured at an experimental boreal forest site from 2002 to 2018. The dashed red line corresponds to the creation date of the windthrow. Light green points correspond to observations from the experimental unit affected by the windthrow and dark green points correspond to the means of observations from the two undisturbed units.

thought to be the cause of the windthrow discovered less than a week later on an experimental unit (Fig. 1a). These winds displayed the highest daily maximum speed recorded in 2012 and the second highest daily maximum speed recorded between 2001 and 2020 (Fig. S1). After the estimated date of the windthrow (i.e., 2012-08-30), soil solution NO_3^- concentration and pH were drastically impacted, with changes noticeable as soon as 11 and 5 post-disturbance days respectively (Fig. 1b and c). NO_3^- and pH displayed opposite shifts that followed two successive phases after the windthrow. The first phase consisted of a massive short-term increase of NO_3^- concentration from 0.01 $mg{\cdot}L^{-1}$ (measured the week before the windthrow) to 5.22 $mg{\cdot}L^{-1}$ (averaged concentration between 2012-09-10 and 2012-11-05), and less severely, a decrease of pH from 5.59 (measured the week before the windthrow) to 4.94 (averaged value between 2012-09-04 and 2012-11-05). The second phase was longer and consisted of a more progressive increase of NO_3^- from 0.09 to 9.18 $mg{\cdot}L^{-1}$ between 2013-08-12 and 2017-08-07, and a decrease of pH from 4.9 to 4.76 between 2013-09-09 and 2018-08-20 (Fig. 2a and c). NO_3^- concentration reached its maximum in August 2017 whereas pH reached its minimum in August 2018, 5 and 6 years after the disturbance respectively. These observations were supported by linear model results indicating that the windthrow had a positive effect on soil solution NO_3^- and a negative effect on pH (Table S3).

The influence of the windthrow on NH_4^+ concentration was also significant (Table S3) but differed from its effect on NO_3^- and pH, as the two successive response phases were less clear and the duration of the impact was much shorter. Following the disturbance, NH_4^+ concentration slightly increased between 2012-09-04 and 2012-09-17, which respectively correspond to 5- and 18-days post-windthrow. Then, NH_4^+ increased more drastically between June 2014 and September 2015 (+6400 %) and reached a peak at 0.52 $mg{\cdot}L^{-1}$ on 2014-06-09. Mid-September 2015, 3 years after the windthrow, NH_4^+ concentrations shifted back to pre-disturbance values (Fig. 2b).

Seasonal variations of soil solution NO_3^- and pH were also altered by the windthrow (Figs. 2a, c and S2). On both windthrow-affected and undisturbed experimental units, post-disturbance NO_3^- concentration increased to reach a peak in mid-August/early September and subsequently decreased. However, the regression line peak was ~5 times higher for the unit impacted by the windthrow compared to the two other HN treatment plots (Fig. S2). Pre-windthrow pH varied similarly on all experimental units, but post-windthrow pH displayed opposite seasonal variation patterns between disturbed and undisturbed units. pH peaked at the same time as NO_3^- concentration (i.e., mid-August/early September) but showed a downward peak on the windthrow unit (reaching a minimum of 4.72) and an upward peak on undisturbed units (reaching a maximum of 6.03). The PCA biplot indicated that NO_3^- was one of the elements most impacted by the windthrow as it appears out of the pre-windthrow ellipse and in the post-windthrow ellipse (Fig. 3). In good agreement with temporal variations shown in Figs. 1 and 2, the PCA also clearly indicates that NO_3^- was negatively correlated with pH. The other anions (SO_4^{2-}, Cl^-) and cations (Na^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}) formed two distinct groups that seemed to be positively related and similarly impacted by the windthrow. For the two latter groups, linear models showed that sampling date and windthrow occurrence had significant effects for all ions (K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, and SO_4^{2-}), except for Na^+ (Table S3). Alike NO_3^- and NH_4^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, and SO_4^{2-} concentrations all increased shortly after the windthrow but with contrasted intensities and recovery times (Fig. S3). Among these ions, K^+ displayed the highest peak of concentration following the windthrow (increase of +26,000 %) while Mg^{2+} showed the weakest responses to disturbance (+375 %). Cl^- and SO_4^{2-} recovered a year later, in 2016, but K^+, Ca^{2+}, Mg^{2+}, and Mn^{2+} did not seem to recover before the end of the study in 2018.

4. Discussion

As we predicted, the total windthrow created in 2012 on an HN treatment experimental unit had important and visible impacts on soil solution chemistry. Shortly after the windthrow, ion concentrations (i.e., NO_3^-, NH_4^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, and SO_4^{2-}) significantly increased in soil solution (Fig. 2; Fig. S2), indicating higher nutrient

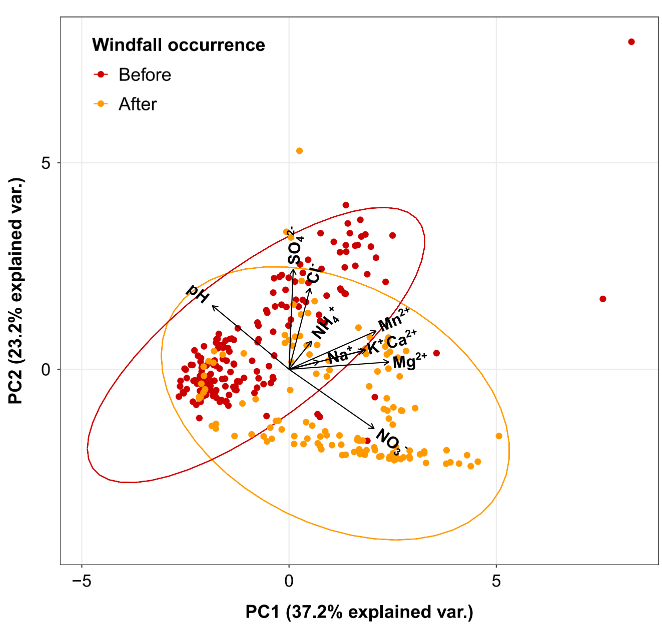

Fig. 3. Principal Component Analysis (PCA) biplot of elemental concentrations and pH measured in soil solution collected from 2002 to 2018 at an experimental boreal forest site, before (red) and after (orange) the windthrow. The PCA regroups 310 observations. Points represent samples and ellipses represent 95 % confidence intervals.

leaching. The most striking shift was NO_3^- concentrations that raised up to ~10 times average pre-windthrow values, only a few days after the disturbance. Post-windthrow elemental concentrations fluctuated with various intensities and recovery times, potentially because of ions' specific mobility and properties in soil. For example, because of its soil diffusion coefficient, NO_3^- is more mobile and prone to leaching via soil solution compared to NH_4^+ (Owen and Jones, 2001), which probably explained the higher concentration of NO_3^- compared to NH_4^+ in soil solution (Fig. 2).

To our knowledge, this is the first report of long-term windthrow effects on soil solution chemistry in the North American boreal forest. Windthrow studies are scarce most likely because forest natural wind disturbances happen randomly and are often not accessible, especially in the boreal forest where the road network is limited. However, a few studies in European temperate and boreal forests showed similar results of increased cation (NH_4^+, K^+, Ca^{2+}, Mg^{2+}) and anion (NO_3^-) leaching for 1 to 5 years following windthrow (Bischoff et al., 2008; Hellsten et al., 2015; Yu et al., 2016). Other major forest disturbances such as insect outbreaks, fire, drought, and harvesting were also shown to induce ion leaching in temperate and boreal forests (Futter et al., 2010; Houle et al., 2016, 2009; Lamontagne et al., 2000).

The observed increased leaching following windthrow could be caused by higher inputs of water from precipitation due to broken and dead trees (which implies less canopy interception and transpiration) and increased mineralization by soil microbes due to warmer and wetter soil conditions (as more precipitation and sunlight can reach the forest floor because of a more open canopy) (Vodde et al., 2011). Previous work showed that net nitrification is low but present in the organic FH horizon at our study site (Ste-Marie and Houle, 2006) with reported values being typical of boreal forests soils (Sponseller et al., 2016). Therefore, the observed peak of NO_3^- concentration right after the windthrow could be partially explained by an increase of net nitrification promoted by more favorable soil conditions (Cheng et al., 2012; Li et al., 2020). On the other hand, tree mortality and soil disruption could impact the soil microbiome and cause a loss of bacterial and fungal diversity and biomass (especially symbiotic ectomycorrhizal fungi colonizing tree roots). This could lead to lower microbial activity such as respiration but also to reduce microbial nutrient uptake and transport which can ultimately impact forest biogeochemical cycles.

Moreover, tree damage and mortality most likely prevented or reduced tree nutrient uptake and caused forest floor physical disturbance such as feather moss (i.e., main understory vegetation at the experimental site) layer uplifts. Feather mosses are known to retain important amounts of nutrients, especially N, preventing them to reach deeper soil horizons and controlling tightly soil solution chemistry in boreal forests (Gornall et al., 2007; Koranda and Michelsen, 2021). Therefore, change in the homogeneity of the moss cover induced by windthrow, as well as reduced tree nutrient uptake, can affect soil solution elemental concentrations and leaching rates, as demonstrated by previous work in European forests (Mellert et al., 1998; Ritter et al., 2005).

In our study, Na^+ was the only element that was not significantly affected by the windthrow (Table S3). Compared to other measured cations, Na^+ is not considered an essential nutrient for plant growth and generally has a conservative behaviour in forest ecosystems (Houle et al., 1999). Therefore, the processes involved in higher nutrient leaching could have not impacted Na^+.

At the study site, soil solution elemental alterations led to concomitant pH drops, up to ~1.2 times average pre-windthrow values, showing lasting soil acidification. The negative relationships between major base ion concentrations (especially NO_3^-) and pH are also visible on the PCA biplot where the variables are located at the opposite of each other (Fig. 3). The observed lower soil pH is most likely due to higher NO_3^- leaching due to reduced vegetation uptake which simultaneously produced protons and caused soil net acidification (Gundersen et al., 2006). Forest soil acidification induced by base cations leaching is a well documented process that has been extensively showed in N fertilization experiments worldwide (Moldan et al., 2018; Tian and Niu, 2015) but was less studied in natural wind disturbance settings. The observed soil acidification at the study site echoes findings from Yu et al. (2016) showing that storm-induced windthrows caused soil base cations leaching and concomitant pH drop, potentially affecting acidification recovery in a Swedish spruce forest.

Interestingly, both soil solution NO_3^- and pH displayed a strong and opposite seasonal pattern after the windthrow, which did not exist before the disturbance (Fig. S2). This indicates that not only absolute NO_3^- and pH values were impacted by the windthrow but also the seasonality of N cycling and soil processes during the snow-free and growing periods. These changes could impact vegetation and tree regrowth after windthrows, but further research is needed to evaluate how soil solution chemistry alterations could influence boreal forests' regeneration and productivity.

Recently, we showed that two decades of N addition (i.e., HN treatment), corresponding to 200 years of accelerated ambient N deposition, did not significantly affect soil solution NO_3^-, NH_4^+, Ca^{2+} concentrations and pH at the same experimental site (Houle et al., 2025). This, along with results from other N fertilization studies (Houle and Moore, 2019; Houle et al., 2024a,b), indicates that the eastern Canadian boreal forest soil solution chemistry and N cycle are highly resilient to N deposition, potentially because of its strong and widespread N limitation (Du et al., 2020). Therefore, our work shows that windthrows can alter the North American boreal forest soil solution and nutrient fluxes much more drastically than two decades of elevated N deposition. This finding highlights the probably underestimated significance of wind disturbances' impacts on forest soils and nutrient cycling.

5. Conclusion

In this work, we show that a total windthrow at a Canadian black spruce boreal forest site induced significant higher leaching of NO_3^-, NH_4^+, K^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Cl^-, and SO_4^{2-}, lasting between 1 and 6 years after the disturbance. This study is the first to report that wind disturbance can have much stronger impacts on forest soil solution chemistry than N addition corresponding to 200 years of accelerated ambient N deposition. The particularly intense response of NO_3^- to the windthrow illustrates an unexpectedly fast and strong effect of wind disturbance on the N cycling of a forest ecosystem that is highly resilient to N deposition. However, it is worth precising that, even if the windthrow occurred naturally, our results originate from soil solution collected on an experimental site receiving chronic artificial N addition and more work is needed to validate our conclusions in natural settings and at a larger scale. More generally, additional studies are necessary to further assess the effects of wind disturbances on forest soil chemistry as windthrow frequency is predicted to increase in the North American boreal forest (Saad et al., 2017).

CRediT authorship contribution statement

Marie Renaudin: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation. **Daniel Houle:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jean-David Moore:** Writing – review & editing, Resources, Methodology, Conceptualization. **Louis Duchesne:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the Ministère des Ressources naturelles et des Forêts du Québec (project no. 112332063) and by the Climate Change and Atmospheric Pollutants program of Environment and Climate Change Canada, Science and Technology branch. We would like to thank S. Desalliers, P. Desjardins, J. Gagné, J. Martineau, J.-P. Mottard, M. St-Germain, and B. Toussaint for field assistance, and the staff of the Laboratoire de chimie organique et inorganique (Direction de la Recherche Forestière, QC) for chemical analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117443.

Data availability

Data will be made available on request.

References

Anyomi, K.A., Mitchell, S.J., Perera, A.H., Ruel, J.C., 2017. Windthrow dynamics in Boreal Ontario: a simulation of the vulnerability of several stand types across a range of wind speeds. Forests 8 (7). https://doi.org/10.3390/f8070233.

Bischoff, W.A., Mayer, S., Schrumpf, M., Freibauer, A., 2008. Nutrient leaching from soils affected by windthrow in the High Tatra. Windstorm Res. 8–12.

Canada's National Forest Inventory, 2025. Table 14.2. Area (1000 ha) of forest land by species group, age class and boreal zone in Canada. Combined remeasured (2007-2017) and projected (2006-2017 with NFI projection system) data (Version 3, November 2023). https://nfi.nfis.org/resources/general/summaries/t1/en/BORE/html/bore_t14_lsage20_area_en.html (accessed 24 February 2025).

Cheng, Y., Cai, Z.c., Zhang, J.b., Lang, M., Mary, B., Chang, S.X., 2012. Soil moisture effects on gross nitrification differ between adjacent grassland and forested soils in central Alberta, Canada. Plant Soil 352 (1–2), 289–301. https://doi.org/10.1007/s11104-011-0997-2.

Crişan, V.E., Dincă, L.C., Oneţ, A., Enescu, R.E., Cristian Teuşdea, A., Oneţ, C., 2021. Impact of windthrows disturbance on chemical and biological properties of the forest soils from Romania. Environ. Eng. Manag. J. 20.

Du, E., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., et al., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13 (3), 221–226. https://doi.org/10.1038/s41561-019-0530-4.

Elie, J.G., Ruel, J.C., 2005. Windthrow hazard modelling in boreal forests of black spruce and jack pine. Can. J. For. Res. 35 (11), 2655–2663. https://doi.org/10.1139/x05-189.

Futter, M.N., Ring, E., Högbom, L., Entenmann, S., Bishop, K.H., 2010. Consequences of nitrate leaching following stem-only harvesting of Swedish forests are dependent on spatial scale. Environ. Pollut. 158 (12), 3552–3559. https://doi.org/10.1016/j.envpol.2010.08.016.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J., Van Der Wal, R., 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153 (4), 931–941. https://doi.org/10.1007/s00442-007-0785-0.

Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests effects of air pollution and forest management. Environ. Rev. 14 (1), 1–57. https://doi.org/10.1139/a05-015.

Hellsten, S., Stadmark, J., Pihl Karlsson, G., Karlsson, P.E., Akselsson, C., 2015. Increased concentrations of nitrate in forest soil water after windthrow in southern Sweden. For. Ecol. Manage. 356, 234–242. https://doi.org/10.1016/j.foreco.2015.07.009.

Houle, D., Lajoie, G., Duchesne, L., 2016. Major losses of nutrients following a severe drought in a boreal forest. Nat. Plants 2 (12), 1–5.

Houle, D., Marty, C., Duchesne, L., 2015. Response of canopy nitrogen uptake to a rapid decrease in bulk nitrate deposition in two eastern Canadian boreal forests. Oecologia 177 (1), 29–37. https://doi.org/10.1007/s00442-014-3118-0.

Houle, D., Moore, J.D., 2019. Soil solution, foliar concentrations and tree growth response to 8 years of ammonium-nitrate additions in two boreal forests of Quebec, Canada. For. Ecol. Manage. 437, 263–271. https://doi.org/10.1016/j.foreco.2019.01.024.

Houle, D., Ouimet, R., Paquin, R., Laflamme, J.-G., 1999. Interactions of atmospheric deposition with a mixed hardwood and a coniferous forest canopy at the Lake Clair Watershed (Duchesnay, Quebec). Can. J. For. Res. 29 (12), 1944–1957.

Houle, D., Duchesne, L., Boutin, R., 2009. Effects of a spruce budworm outbreak on element export below the rooting zone: a case study for a balsam fir forest. Ann. For. Sci. 66 (7), 707. https://doi.org/10.1051/forest/2009057.

Houle, D., Moore, J.D., Renaudin, M., 2024a. Eastern Canadian boreal forest soil and foliar chemistry show evidence of resilience to long-term nitrogen addition. Ecol. Appl. 34 (3). https://doi.org/10.1002/eap.2958.

Houle, D., Renaudin, M., Duchesne, L., Moore, J.D., Benoist, A., 2024b. Soil solution chemistry weak response to long-term N addition points towards a strong resilience of northeastern American forests to past and future N deposition. Sci. Total Environ. 946, 174387.

Houle, D., Renaudin, M., Moore, J.D., Duchesne, L., 2025. Black spruce boreal forest soil solution inorganic nitrogen is highly resilient to 20 years of elevated nitrogen deposition. Biogeochemistry 168 (1), 1–11.

Kautz, M., Meddens, A.J.H., Hall, R.J., Arneth, A., 2017. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Glob. Ecol. Biogeogr. 26 (5), 533–552. https://doi.org/10.1111/geb.12558.

Koranda, M., Michelsen, A., 2021. Mosses reduce soil nitrogen availability in a subarctic birch forest via effects on soil thermal regime and sequestration of deposited nitrogen. J. Ecol. 109 (3), 1424–1438. https://doi.org/10.1111/1365-2745.13567.

Lamontagne, S., Carignan, R., D'arcy, P., Prairie, Y.T., Paré, D., 2000. Element export in runoff from eastern Canadian Boreal Shield drainage basins following forest harvesting and wildfires. Can. J. Fish. Aquat. Sci. 57 (S2), 118–128.

Li, Z., Zeng, Z., Tian, D., Wang, J., Fu, Z., Zhang, F., et al., 2020. Global patterns and controlling factors of soil nitrification rate. Glob. Chang. Biol. 26 (7), 4147–4157. https://doi.org/10.1111/gcb.15119.

Mayer, M., Rusch, S., Didion, M., Baltensweiler, A., Walthert, L., Ranft, F., et al., 2023. Elevation dependent response of soil organic carbon stocks to forest windthrow. Sci. Total Environ. 857. https://doi.org/10.1016/j.scitotenv.2022.159694.

Mellert, K.H., Kölling, C., Rehfuess, K.E., 1998. Vegetation development and nitrate leaching in 13 windthrown forest ecosystems in Bavaria. Forstarchiv 69 (1), 3–11.

Meunier, S., Ruel, J.C., Laflamme, G., Achim, A., 2002. Résistance comparée de l'épinette blanche et du sapin baumier au renversement. Can. J. For. Res. 32 (4), 642–652. https://doi.org/10.1139/x01-212.

Moldan, F., Jutterström, S.E.A.K., Hruška, J., Wright, R.F., 2018. Experimental addition of nitrogen to a whole forest ecosystem at Gårdsjön, Sweden (NITREX): nitrate leaching during 26 years of treatment. Environ. Pollut. 242, 367–374. https://doi.org/10.1016/j.envpol.2018.06.093.

Owen, A.G., Jones, D.L., 2001. Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. Soil Biol. Biochem. 33 (4–5), 651–657.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Philipps, O.L., et al., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., et al., 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ. Rev. 21 (4), 322–365. https://doi.org/10.1139/er-2013-0042.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ritter, E., Dalsgaard, L., Einhorn, K.S., 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. For. Ecol. Manage. 206 (1–3), 15–33. https://doi.org/10.1016/j.foreco.2004.08.011.

Saad, C., Boulanger, Y., Beaudet, M., Gachon, P., Ruel, J.C., Gauthier, S., 2017. Potential impact of climate change on the risk of windthrow in eastern Canada's forests. Clim. Change 143 (3–4), 487–501. https://doi.org/10.1007/s10584-017-1995-z.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., et al., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7 (6), 395–402. https://doi.org/10.1038/nclimate3303.

Soil Classification Working Group, 1998. In: The Canadian System of Soil Classification, third ed. Agriculture and Agri-Food Canada Publication, Ottawa, p. 187.

Sponseller, R.A., Gundale, M.J., Futter, M., Ring, E., Nordin, A., Näsholm, T., Laudon, H., 2016. Nitrogen dynamics in managed boreal forests: recent advances and future research directions. Ambio 45, 175–187. https://doi.org/10.1007/s13280-015-0755-4.

Ste-Marie, C., Houle, D., 2006. Forest floor gross and net nitrogen mineralization in three forest types in Quebec, Canada. Soil Biology Biochem. 38 (8), 2135–2143. https://doi.org/10.1016/j.soilbio.2006.01.017.

Taeroe, A., de Koning, J.H., Löf, M., Tolvanen, A., Heiðarsson, L., Raulund-Rasmussen, K., 2019. Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative review. For. Ecol. Manage. 446, 304–316.

Tian, D., Niu, S., 2015. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10 (2). https://doi.org/10.1088/1748-9326/10/2/024019.

Vodde, F., Jõgiste, K., Kubota, Y., et al., 2011. The influence of storm-induced microsites to tree regeneration patterns in boreal and hemiboreal forest. J. For. Res. 16, 155–167. https://doi.org/10.1007/s10310-011-0273-6.

Vu, V.Q., Friendly, M., 2024. ggbiplot: a grammar of graphics implementation of biplots. R package version 0.6.2.

Waldron, K., Ruel, J.C., Gauthier, S., 2013. Forest structural attributes after windthrow and consequences of salvage logging. For. Ecol. Manage. 289, 28–37. https://doi.org/10.1016/j.foreco.2012.10.006.

Westerling, A.L.R., 2016. Increasing western U.S. forest wildfire activity: sensitivity to changes in the timing of spring. Philos. Trans. R. Soc. B 371 (1696). https://doi.org/10.1098/rstb.2015.0178.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis, vol. 35. Springer, New York.

Yu, L., Belyazid, S., Akselsson, C., Van Der Heijden, G., Zanchi, G., 2016. Storm disturbances in a Swedish forest – a case study comparing monitoring and modelling. Ecol. Model. 320, 102–113.