

Drought Legacies Can Extend to Nutrient Stoichiometry: Relative Potassium Enrichment in Sugar Maple Foliage Outlasts Hydrological Recovery

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**DROUGHT LEGACIES CAN EXTEND TO NUTRIENT STOICHIOMETRY:
RELATIVE POTASSIUM ENRICHMENT IN SUGAR MAPLE FOLIAGE
OUTLASTS HYDROLOGICAL RECOVERY**

Running title: Drought nutrient legacy in sugar maple

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14 **KEYWORDS:**

15 Drought legacy; foliar nutrient stoichiometry; potassium; osmotic adjustment; *Acer saccharum*;

16 ontogenetic variation

17 **ABSTRACT**

18 **Background and Aims:** Drought legacies are well documented for growth, carbon allocation and
19 carbohydrate reserves, but whether they extend to mineral nutrition is largely untested. We asked
20 whether a stoichiometric imprint persists in sugar maple foliage once soil moisture has recovered,
21 and whether it can be traced to soil nutrient supply or to wood composition.

22 **Methods:** In a sugar maple (*Acer saccharum* Marsh.) forest in Quebec, Canada, throughfall was
23 reduced by about 75% over four growing seasons in three paired plots. The following growing
24 season, when moisture no longer differed from controls, we sampled foliage and fine-branch wood
25 of mature trees and saplings, along with soil pH and ion supply. Six nutrients (N, P, K, Ca, Mg,
26 Mn) were expressed as five isometric log-ratio (ilr) balances, [NPK|CaMgMn], [NP|K], [N|P],
27 [CaMg|Mn] and [Ca|Mg], analysed with linear mixed and structural equation models.

28 **Results:** Of the five balances, only [NP|K] retained a treatment signal, at both stages: the
29 geometric mean of N and P relative to K was 17.2% lower in exclusion plots, while [N|P] was
30 unchanged, indicating a relative shift toward potassium. No indirect route to the foliage was
31 supported for [NP|K], through either soil supply or wood composition.

32 **Conclusion:** A nutrient imbalance persisted after hydrological recovery, without a supported
33 source in either soil or wood, pointing to tree regulation as a plausible explanation. Transfer
34 between wood and foliage did not follow the conventional division between mobile and immobile
35 elements. Nutritional constraints may outlast the hydrological signature of drought.

36

37 **ABBREVIATIONS**

- 38 **BCa**: bias-corrected and accelerated bootstrap
- 39 **CFI**: comparative fit index
- 40 **CND**: compositional nutrient diagnosis
- 41 **DBH**: diameter at breast height
- 42 **DRIS**: diagnosis and recommendation integrated system
- 43 **Ilr**: isometric log-ratio
- 44 **PC1**: first principal component
- 45 **PRS**: plant root simulator
- 46 **REW**: relative extractable water
- 47 **RMSEA**: root-mean-square error of approximation
- 48 **SEM**: structural equation model

1 INTRODUCTION

Warming is intensifying drought worldwide, increasing both its severity and associated soil moisture deficits (Gebrechorkos et al. 2025). In temperate forests, the ecological effects of such events increasingly persist after the drought itself has ended (Müller and Bahn 2022). Trees that survive a drought often carry its signature for years, a phenomenon that is known as a drought legacy: reduced radial growth, altered carbon allocation, depleted non-structural carbohydrates and elevated mortality risk persist long after soil moisture levels have recovered (Anderegg et al. 2015; Kannenberg et al. 2019; Müller and Bahn 2022; Bose et al. 2024; Liu et al. 2025). Moreover, repeated droughts can compound into stand-level mortality (Sánchez-Pinillos et al. 2022).

Drought legacies were first characterized through altered carbon and growth. A growing body of work now documents their signature in soil microbial communities as well (Kaisermann et al. 2017; Oram et al. 2025). Whether drought leaves a persistent imprint on tree mineral nutrition and upon the nutrient cycling that underpins this functioning has yet to receive greater attention. Moreover, most studies of tree nutrition have focused upon the drought period itself; whether an altered nutrient balance persists once soil moisture has recovered remains largely unknown, even though repeated summer drought has already been shown to shift sugar maple foliar nutrition during the treatment period at our site (Parsons et al. 2025). A persistent shift in nutrient balance after hydrological recovery could therefore represent an overlooked mechanism affecting tree resilience.

Such an effect is expected because water and nutrients are tightly coupled: soil water deficit constrains the mass-flow and diffusion of nutrients to the roots, alters uptake and resorption, and reshapes the internal remobilization of elements among tissues (Bréda et al. 2006; Sardans and Peñuelas 2015). Concretely, water stress commonly raises foliar potassium, which is mobilized for osmotic adjustment and stomatal control, whereas the mass-flow-driven delivery of calcium

and magnesium declines and the balance between nitrogen and phosphorus shifts (Sardans and Peñuelas 2015; Bhardwaj et al. 2025). Foliar nutrient stoichiometry, i.e., the relative balance among functionally distinct elements supporting growth, osmotic regulation, structure or photosynthesis, integrates these processes much better than does any single concentration. It therefore offers an ecologically interpretable read-out of a drought legacy, potentially distinguishing adaptive physiological adjustment from a pathological imbalance. Indeed, persistent imbalances have been linked to drought-induced forest decline (Elser et al. 2000; Hevia et al. 2019).

The persistence and cost of such a legacy are likely to depend on ontogenetic stage. Saplings and mature trees differ in rooting depth, water access and storage capacity. Moreover, these differences shape their response to drought for both water and nutrients: mature trees can potentially buffer stress through deeper water uptake and larger internal reserves, whereas saplings are exposed to greater stress, given their shallower roots and reduced storage capacity (Perron et al. 2026). A drought-induced nutrient imbalance may therefore arise through different physiological pathways across ontogeny, ranging from reduced uptake of soil nutrients to increased remobilization of stem reserves. Given that a nutritional legacy that is concentrated in saplings could disproportionately affect sapling recruitment and long-term stand persistence, resolving these pathways and their stage-dependence is important to understanding how drought reshapes forest nutrition.

Sugar maple (*Acer saccharum* Marsh.) provides a particularly relevant model for investigating drought-induced nutritional legacies. It is a dominant, iconic and economically important species of the temperate hardwood forests of eastern North America (Burns 1990), and its sapling recruitment has become increasingly limited in parts of its range, raising concerns about future stand persistence (Gravel et al. 2011). Sugar maple is also particularly sensitive to nutritional stress: its decline has been repeatedly associated with foliar imbalances in the base cations

calcium and magnesium, together with disturbed potassium and manganese status (Ouimet and Camiré 1995; St.Clair et al. 2008; Bal et al. 2015). These imbalances can be driven in part by soil acidification and decades of atmospheric pollutant deposition (Duchesne et al. 2025). Sapling establishment is further constrained by competition from American beech (*Fagus grandifolia* Ehrh.) (Gravel et al. 2011). Because drought tends to exacerbate such pre-existing imbalances rather than act in isolation, a drought legacy that has accumulated in saplings would compound these pressures and could shape the trajectory of maple-dominated stands under intensifying drought.

Here, we used a four-year-long, consecutive growing-season throughfall-exclusion experiment in sugar maple stands, sampling soil, foliage and fine-branch wood during the growing season following the last treatment, once soil moisture had recovered. We asked whether repeated growing-season soil moisture deficits leave a legacy on foliar nutrient stoichiometry that would carry into the subsequent growing season and, if so, through which physiological pathways. Furthermore, we asked whether drought legacies differed between ontogenetic stages. We first hypothesized that repeated growing-season drought would leave a persistent nutritional legacy into the following growing season, which is expressed through altered element ratios, particularly those involving potassium, given its central role in osmotic adjustment under water stress. Second, we hypothesized that the magnitude and pathways of this legacy would differ between ontogenetic stages, with saplings exhibiting stronger nutritional disruption than would mature trees because of their lower capacity to buffer drought-induced resource limitations. Beyond these two hypotheses, we characterized the response of the full set of nutrient ratios and the pathways transmitting them as an exploratory analysis, without prescribing their direction a priori. By extending the drought-legacy framework beyond carbon allocation and tree growth to nutrient stoichiometry, and by examining the physiological pathways that may carry it, this study aims to clarify how repeated drought may reshape the nutrition and long-term persistence of temperate

hardwood forests. More broadly, we ask which nutrients retain a drought imprint and by which route is it transmitted, pointing to nutrient stoichiometry as an overlooked dimension of drought legacy that could constrain forest recovery under intensifying drought.

2 MATERIALS AND METHODS

2.1 Study site

The study was conducted in the Kenauk Nature Reserve (45.75° N, 74.94° W), which is a 265 km² private forest in southern Quebec, Canada. The climate is humid continental, with mean monthly air temperatures ranging from −12.5 °C in January to 18.9 °C in July, with a mean annual temperature of 5.3 °C. Mean annual precipitation is approximately 1204 mm, of which about 20% falls as snow (1981–2010 normals, station 7035110; Environment and Climate Change Canada, 2025). Soils are classified as Dystric Brunisols (Canadian System of Soil Classification) or Typic Dystrochrepts (USDA Soil Taxonomy; Soil Classification Working Group 1998). They have a moder humus form and an organomineral horizon of about 2 cm, which has developed on glacial till that is composed mainly of gneiss, quartz and granite and reaching a depth of up to 110 cm (Lajoie 1967). The canopy is a sugar maple–yellow birch (*Betula alleghaniensis*) stand dominated by sugar maple (*Acer saccharum* Marsh.), and the absence of major anthropogenic disturbance over several decades has allowed this structure to persist. Growing-season water availability varied among years, as shown by the control plots, where relative extractable water was lowest in 2022 and increased thereafter (Fig. 2).

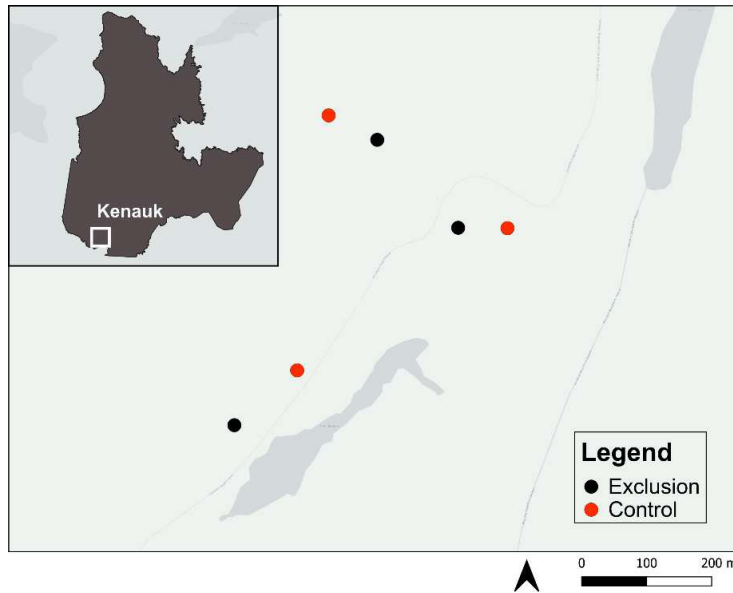
2.2 Experimental design and tree selection

A throughfall reduction system was established on six 400 m² plots (20 × 20 m; Fig. S1-S2), each of which was equipped with 42 waterproof tarps installed approximately at 1.5 m above the ground, excluding about 75% of incoming precipitation. Tarps were deployed each summer (June to early September) from 2021 to 2024 to simulate summer drought and were removed for the

rest of the year, allowing precipitation to recharge soil moisture outside the treatment window. No throughfall reduction was applied in 2025. The measurements that are reported here (taken during summer 2025) therefore characterize the legacy of the imposed soil moisture deficits in the first growing season following the end of the exclusion treatment. Three sites were monitored, each comprising paired exclusion and control plots (Fig. 1). Sites were about 500 m apart, whereas the treatment and control plots within each site were less than 150 m apart. Selection criteria included similar plant communities among sites, flat topography, and the absence of major disturbance. Basal area ranged from 30.6 to 45.1 m² ha⁻¹ and was dominated by sugar maple (74–99% of plot basal area), accompanied mainly by eastern hophornbeam (*Ostrya virginiana*) saplings in the understory.

In total, 18 sugar maple saplings and 18 sugar maple trees were sampled, which were evenly distributed across plots and treatments (3 individuals per ontogenetic stage, site and treatment). Individuals were selected on the basis of diameter at breast height (DBH), averaging ($\pm$ SD) 6.7

160 ± 1.0 cm for saplings and 28.6 ± 5.0 cm for trees, with suppressed and co-dominant crowns,
161 respectively. All selected individuals were free of dieback, cankers, and other visible pathologies.



162

163 **Figure 1.** Location of the study site within the Kenauk Nature Reserve (Outaouais, Quebec,
164 Canada) and spatial arrangement of the six experimental plots. Inset: location within the Province
165 of Quebec.

166 2.3 Pedologic measurements

167 Surface volumetric soil water content (0–11 cm) was measured with a time-domain
168 reflectometry probe (FieldScout TDR 350, Spectrum Technologies, Inc., Aurora, IL).
169 Measurements were taken systematically at 3 m intervals (42 per plot) every three weeks from
170 mid-June to August of each year from 2022 to 2025. No measurements were taken in 2021; in
171 2025, only those readings that were collected before tree sampling (before mid-July) were
172 considered. At each point, three readings were taken and averaged. Values were converted to
173 relative extractable water (REW), a dimensionless index that is commonly used in forest

ecophysiology because it relates more directly to water that is available for vegetation than to raw volumetric water content (Vicca et al. 2012). REW was computed as:

$$REW = \frac{\theta - \theta_{WP}}{\theta_{fc} - \theta_{WP}} \quad (1)$$

where θ is the measured volumetric water content ($\text{m}^3 \text{m}^{-3}$), θ_{fc} is the volumetric water content at field capacity ($\text{m}^3 \text{m}^{-3}$) and θ_{WP} is the volumetric water content at the wilting point ($\text{m}^3 \text{m}^{-3}$). Water contents at field capacity (θ_{fc}) and at the wilting point (θ_{WP}) were derived from the van Genuchten water retention curves (van Genuchten 1980), where parameters were estimated with the ROSETTA v3 pedo-transfer function (model H2; Zhang and Schaap, 2017) from the particle-size fractions (sand, silt, clay) that were measured for each site $\times$ treatment combination. θ_{fc} and θ_{WP} correspond to the volumetric water content at matric potentials of -33 kPa and -1500 kPa , respectively. $REW < 0.4$ is commonly associated with the onset of water stress in temperate forest species (Granier et al. 1999).

Soil nutrient availability was assessed with PRS probes (Plant Root Simulator, Western Ag Innovations, Saskatoon, SK). These plastic probes ($15 \times 3 \text{ cm}$) support an ion-exchange membrane of 17.5 cm^2 , which is charged either negatively (for cation adsorption) or positively (for anion adsorption). One kit of four anion and four cation probes was installed in each plot and incubated for one month (July 2025, coinciding with the plant sampling period). After retrieval, probes were rinsed with deionized water and sent to Western Ag Innovations for analysis of available NO_3^- , NH_4^+ , P, K, Ca, Mg and Mn using ICP-OES and segmented flow analysis. Results were expressed as ion supply rates, in micrograms per 10 cm^2 of membrane over the one-month incubation period. Soil pH was measured in each plot from three random samples, separately for the organic horizon (FH) and the mineral horizon (A, 0-20 cm), by suspending the soil in water

(ratio 1:2), agitating the suspension, and measuring pH with a combination electrode (SevenCompact S220, Mettler Toledo).

2.4 Tree nutrition samples

Maple nutritional status was characterized using two complementary compartments: leaves, which reflect integrated nutritional status at sampling; and fine-branch wood, which provides an indicator of mineral reserves (Muhammad et al. 2020; Dalling et al. 2024). Sampling was conducted in July 2025. This period corresponds to the stabilization of foliar mineral concentrations and is recommended for mineral-status analysis (van den Driessche 1974). For each individual, a healthy mid-canopy branch was collected by a professional arborist, and ten fully developed leaves were sampled per branch to form a representative composite. Wood segments (about 5 cm long, < 2 cm diameter) were taken from the same branches, proximal to the annual shoot and including bark. Fine branches (diameter < 2 cm) concentrate a higher proportion of mineral elements than do coarse branches and the stem (Royer-Tardif et al. 2017), and represent a functionally relevant storage compartment, particularly for strongly remobilized elements (N, P, K), for which the redistribution to leaves under water stress is well documented (Dalling et al. 2024; Hart et al. 2024; Millard and Grelet 2010). All foliar and wood samples were oven-dried, ground and sieved to 500 µm. Potassium, P, Ca, Mg and Mn concentrations were determined by ICP-OES after HNO₃-H₂O₂ acid digestion (IRDA method 322), and total N was determined by dry combustion using a LECO analyzer.

2.5 Isometric log-ratio transformation and Compositional Nutrient Diagnosis indices

The six mineral nutrients that were considered (N, P, K, Ca, Mg, Mn) are those commonly used in the assessment of sugar maple nutrition and decline (Ouimet and Camiré 1995; St.Clair et al. 2008). Because mineral concentrations are compositional data, the six concentrations sum to a constant or near-constant value, so that they are confined to a simplex of D = 6 parts and

221 occupy a $D - 1$ rather than a D -dimensional Euclidean space, and this constant-sum constraint
 222 induces spurious correlations among elements. They were therefore subjected to the closure
 223 operation and transformed into isometric log-ratio (ilr) balances, each representing the scaled log-
 224 ratio of the geometric means of two groups of elements (Aitchison 1982; Egozcue et al. 2003).
 225 The sequential binary partitions defining the five log-ratios were formed as orthogonal contrasts
 226 of 1, 0 and -1, and fixed a priori on biological grounds, following Parent et al. (2013), with
 227 manganese added as an antagonist of magnesium. The latter is an element that is frequently
 228 imbalanced in sugar maple (St.Clair et al. 2008; Bal et al. 2015) (Table S1). Each ratio was
 229 therefore chosen to carry ecological, rather than merely statistical meaning. The first split,
 230 [NPK|CaMgMn], separates the remobilizable, metabolically active elements from those the foliar
 231 status of which depends more upon continued root uptake, and expresses the allocation between
 232 the physiologically mobile pool and the largely uptake-dependent pool. Phloem mobility is,
 233 however, a gradient rather than a dichotomy: N, P and K are readily re-translocated and held in
 234 substantial internal reserves, Ca and Mn are poorly mobile in the phloem, and Mg occupies an
 235 intermediate position, being phloem-mobile and re-translocated from older to growing tissues,
 236 particularly during senescence or deficiency (Marschner 2011). Mg is therefore placed with Ca
 237 and Mn on the basis of its association with the base cations in sugar maple nutrition and decline.
 238 Within the mobile group, [NP|K] contrasts the elements involved in the growth process, i.e.,
 239 nitrogen in proteins and phosphorus in nucleic acids, with potassium, which is the main
 240 osmoticum and regulator of turgor and stomata, so that a shift toward K is consistent with greater
 241 relative investment in osmotic regulation than growth. The dual element ratio [N|P] is the classical
 242 nitrogen-to-phosphorus ratio, indexing the relative investment in N-rich proteins versus P-rich
 243 ribosomes. Within the uptake-dependent group, [Ca|Mg] opposes structural calcium with
 244 metabolic magnesium. The former is involved in cell walls, membrane stability and signaling, while
 245 the latter is at the core of chlorophyll and a cofactor of many enzymes. The ratio of the two
 246 captures the balance between structural integrity and photosynthetic function. The amalgamated

element ratio [CaMg|Mn] contrasts the base cations with manganese, a balance the decline of which (low calcium and magnesium with elevated manganese) is a recognized signature of soil acidification and manganese toxicity in declining sugar maple (Ouimet and Camiré 1995; St.Clair et al. 2008). Transformations used the *acom*p and *ilr* functions of the *compositions* package (van den Boogaart and Tolosana-Delgado 2008) in R, and this Euclidean representation allows the application of linear mixed and structural equation models.

The ilr ratios were then centered and scaled using the mean and standard deviation of a reference population, yielding foliar CND indices for each tree and ratio: the further the absolute value of an index is from 0, the further the composition lies from the optimum (Parent & Dafir, 1992). Reference values were those obtained from DELFES 1.3 software and were established from foliar concentrations in stands with optimal growth and vigour (Ouimet & Camiré, 1995). They cannot be considered strictly optimal but provide comparability with studies based on the Diagnosis and Recommendation Integrated System (DRIS) and give an order of magnitude of imbalance.

2.6 Statistical analysis

2.6.1 Linear mixed-effects models

REW was modeled with a robust linear mixed model (Huber-type M-estimation; Koller, 2016) with treatment, year, their interaction and site as fixed effects and plot as a random effect. Significance was assessed with 95% bootstrap confidence intervals (*confintROB*).

Foliar and wood ilr ratios were analyzed with Gaussian linear mixed models that were fitted with the *lmer* function of the *lme4* package (Bates et al. 2015) in R. The ilr coordinates, which are continuous and unbounded, were compatible with the normality and homoscedasticity assumptions of linear models, which were confirmed by residual diagnostics. For each balance, we fitted a linear mixed-effects model with the ilr coordinate as the response variable. Stage

(sapling or mature tree), treatment (exclusion or control), and their interaction (stage × treatment) were included as fixed effects, with plot as a random intercept. Because the plot was the unit of treatment randomization (n = 3 plots per treatment), the plot-level random intercept accounts for the non-independence of individuals that were sampled within the same plot and provides the appropriate error term for testing the treatment effect, thereby preventing pseudoreplication. The degrees-of-freedom for the treatment test are thus determined primarily by the number of plots, rather than by the number of individuals. The stage × treatment interaction was retained in all models, regardless of whether it was significant or not, given that it embodies the central hypothesis of a stage-dependent nutritional response. Random slopes were not considered because the limited number of sites (3) was insufficient to reliably estimate their variance. Fixed and random effects correspond to the full factorial design and the sampling design, respectively; no model-selection procedure was applied. Treatment effects are reported in the text as percentage changes in the corresponding ratio of geometric means, obtained by back-transforming the model coefficient as $\exp(\beta / \sqrt{(rs/(r + s))}) - 1$, where r and s are the numbers of parts in the numerator and denominator groups of the balance.

Model validation used the *DHARMA* package (Hartig 2024), i.e., checking the uniform distribution of simulated residuals (QQ-plot), the absence of over-dispersion, and the absence of patterns in residuals against fitted values. These diagnostics confirmed satisfactory model adequacy.

Departure of each foliar CND index from the nutritional optimum (theoretical value of 0) was tested with a one-sample Wilcoxon signed-rank test against $\mu_0 = 0$, two-sided and using the exact distribution, separately for each ratio, ontogenetic stage and treatment group (n = 9 per group). A

non-parametric test was used because sample sizes per group were too small to rely on normality. No group was compared with another; each was compared with the optimum.

2.6.2 Structural equation models

Structural equation models served two aims that a comparison of foliar means cannot address: whether changes were mediated by soil nutrient availability or wood nutrient composition, and whether opposing pathways masked net effects on foliar nutrient balances. A model was fitted for each of the five ilr ratios, separately by stage (sapling and mature tree) and employing an identical causal structure. Estimation used maximum likelihood (ML) in lavaan package (Rosseel 2012), which was preferred over local estimation (piecewiseSEM) because adding a plot random effect to each equation was not estimable at $n = 18$ per stage. Residual non-independence at the plot level is therefore acknowledged as a limitation. Fit was assessed with the global χ^2 test of model fit, that is the likelihood-ratio test of the specified model against the saturated model under maximum likelihood, together with CFI and RMSEA (Table S2). CFI is the Comparative Fit Index where values closer to 1 than to 0 indicate better fits. RMSEA is the Root-Mean-Square Error of Approximation, where values that are closer to 0 than to 1 indicate better fits. The ilr transformation produces continuous, approximately Gaussian variables, supporting the use of the ML estimator.

The *a priori* causal structure was described as follows: Treatment, the single exogenous variable, coded 2 for control and 1 for exclusion, influences the mean pH of the organic and mineral horizons, as well as soil mineral nutrient availability, which in turn influences wood and foliar nutrient composition. Wood is a potential mediator between soil and leaves, thereby representing a potential pathway for the remobilization of internal reserves. A wood-to-foliage path was specified for every balance, including the base-cation balances, so that any contrast between balances in the strength of this route is a result rather than a modeling choice. A direct treatment effect on the plant compartments was also allowed. The general path structure can be

described by the following: Treatment → pH → PC1 → wood → leaves; Treatment → PC1 → wood → leaves; Treatment → PC1 → leaves; Treatment → wood → leaves; Treatment → leaves. The four endogenous variables were soil pH, soil mineral availability, wood composition and foliar composition. Because soil mineral availability cannot be represented directly by the PRS ion fluxes (non-compositional data), a principal component analysis was performed on the ion fluxes, log-transformed as $\log(x + 1)$, then centered and scaled to unit variance, so that each analysis was run on the correlation matrix. Fluxes were grouped according to the subcomposition underlying each balance, giving five separate analyses (Table S3). No rotation was applied, and the unrotated first component (PC1) of each analysis (Table S3) was retained as the variable summarizing soil nutrient availability in the structural equation models (Lê et al. 2008). PRS-derived fluxes were measured once per plot and assigned to every individual in that plot.

Indirect and total treatment effects were obtained as products and sums of path coefficients and tested with 95% bias-corrected and accelerated bootstrap confidence intervals (*BCa*, 5000 resamples; MacKinnon et al. 2002). An effect was considered as being supported when its interval excluded zero. This approach was preferred over the delta method, which approximates the standard error of a product of coefficients by a first-order Taylor expansion and treats the resulting statistic as normally distributed. The product of two estimated coefficients is skewed, particularly at small sample sizes, so that approximation misstates the coverage of the resulting intervals. Indirect and total effects are reported in unstandardized form, given that their standardized intervals are unstable at small sample size; direct path coefficients are reported as standardized values and tested with Wald tests at $\alpha = 0.05$. All data and R code supporting these analyses are archived in Zenodo (Simoneau et al. 2026).

3 RESULTS

3.1 Treatment effects on soil water availability at the plot scale

During the three exclusion years for which REW was measured (2022-2024), REW in exclusion plots was significantly lower than in controls, by 0.59 on the REW scale (Fig. 2; 95% CI [0.52, 0.66]), and remained mostly below the critical threshold of 0.4 (Granier et al. 1999). REW also varied across the study period, being higher in 2023 ($\beta = 0.25$, 95% CI [0.19, 0.31]) and 2024 ($\beta = 0.55$, 95% CI [0.50, 0.61]) compared to 2022, and it varied among sites (Site 2: $\beta = 0.35$, 95% CI [0.32, 0.38]). In 2025, when no exclusion was applied, REW no longer differed between plot types ($\beta = -0.08$, CI [-0.29, 0.19]) and remained above 0.4 in both treatment and control plots.

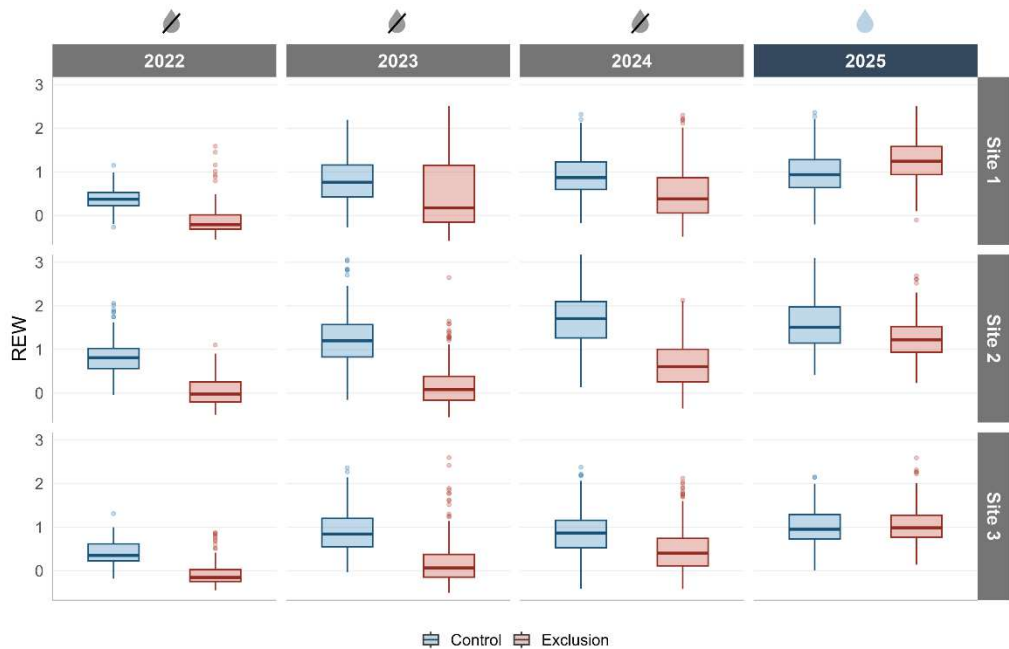


Figure 2. Relative extractable water (REW, unitless) in exclusion and control plots across three sites and four measurement years (2022–2025) at Kenauk Nature Reserve. Gray strip headers indicate years during which the precipitation exclusion treatment was applied (June–August

2022–2024); the blue-gray strip header indicates the post-exclusion year (2025). Box plots display the median (central line), first and third quartiles (box limits), and values within 1.5 times the interquartile range (whiskers); data points beyond the whiskers are shown individually as outliers.

3.2 Legacy effects of throughfall exclusion on foliar nutrient stoichiometry

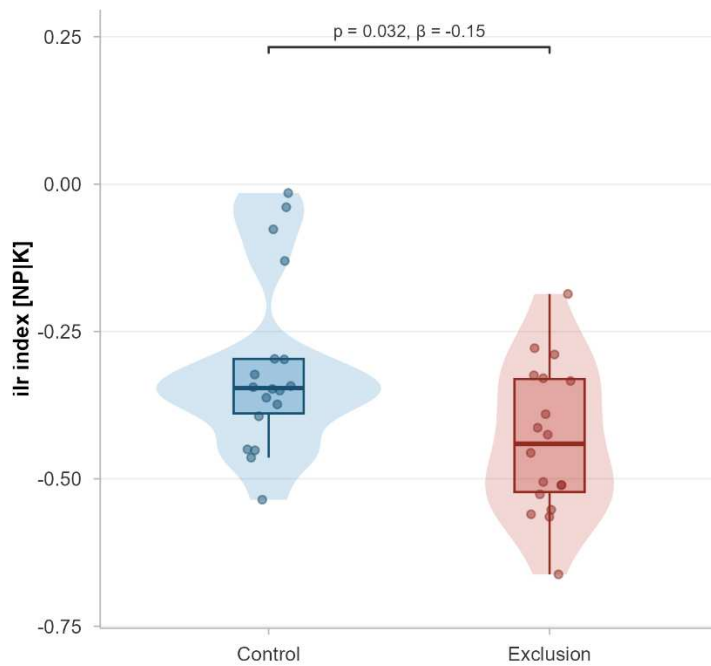
The nutritional imprint of the exclusion treatment was largely confined to a single balance. One year after the last exclusion, once soil moisture no longer differed between treatment and control plots, only the foliar [NP|K] ratio showed a main effect of the treatment: it was 17.2% lower in previously excluded plots (Fig. 3), indicating a relative enrichment in potassium compared with nitrogen and phosphorus. The response was consistent across ontogenetic stages: neither stage nor its interaction with the treatment affected this ratio (Table 1). Expressed as CND indices, this shift moved individuals in excluded plots away from the nutritional optimum, in saplings ($W = 3$, $p = 0.020$) and, marginally, in mature trees ($W = 6$, $p = 0.055$; one-sample Wilcoxon signed-rank test against $\mu_0 = 0$, exact, $n = 9$ per group), whereas individuals in control plots did not depart from it (saplings $W = 18$, $p = 0.65$; mature trees $W = 19$, $p = 0.73$). Each group was tested against the optimum and no group was tested against another, so the contrast between stages is not itself a test of a stage effect.

In the wood compartment, variation was driven by ontogeny rather than the exclusion treatment. Of the five wood ratios, only [NP|K] differed between stages, with sapling branches exhibiting an [NP|K] ratio that was 26.2% higher than that of the mature trees (Fig. S3); no exclusion signal was detected in any ratio at either stage (Table 1). Thus, [NP|K] responded in both compartments, but to different drivers: past drought in foliage and ontogenetic stage in wood.

Beyond this, the only other ratio to show evidence of a drought response was foliar [Ca|Mg], and the response was confined to saplings. It exhibited a marginal treatment $\times$ stage interaction,

378 with saplings in exclusion plots tending toward lower values (Fig. S4); consistently, their CND
 379 index fell below the optimum (one-sample Wilcoxon signed-rank test against $\mu_0 = 0$, exact, $n = 9$:
 380 $W = 1$, $p = 0.008$), whereas that of control saplings did not depart from it ($W = 11$, $p = 0.20$); in
 381 mature trees neither group departed from the optimum (exclusion $W = 13$, $p = 0.30$; control $W =$
 382 12 , $p = 0.25$). The [CaMg|Mn] ratio varied marginally with stage alone, with saplings showing
 383 higher values irrespective of treatment (Table 1).

384 Overall, ontogenetic stage accounted for few of the differences observed across the five ilr
 385 balances in both compartments. Apart from the higher wood [NP|K] ratios in saplings, stage-
 386 related differences were absent in the foliage and marginal for [CaMg|Mn]. The legacy in foliar
 387 [NP|K] was stage-independent, with a similar response in saplings and mature trees.



388

389 **Figure 3.** Foliar ilr balance [NP|K] of sugar maple in response to precipitation exclusion treatment.
 390 Violin plots show the kernel density estimate of the data distribution.

391 Across models, the variance that was explained by fixed effects alone was generally low (R^2_m
 392 $= 3-24\%$), but increased substantially with the inclusion of the plot random effect ($R^2_c = 19-83\%$).

For the [NP|K] ratio, however, the random effect could not be estimated in either compartment (singular fit), limiting the interpretation of the associated R^2_c values (Table 1). A plot-level variance of zero is consistent with the layout of the experiment, in which the exclusion and control plots of a site lay less than 150 m apart on flat topography and in similar plant communities, so that the treatment effect on this balance is tested against the residual variance.

Table 1. Summary of linear mixed model results for foliar and wood ilr ratios in response to past precipitation exclusion, ontogenetic stage and their interaction.

ilr index	Model fit		Fixed effects (estimates & p-values)		
	R^2_m	R^2_c	Stage	Treatment	Stage:Treatment
Compartment: foliar (F)					
NPK CaMgMn	0.032	0.631	−0.002 (0.98)	−0.038 (0.88)	0.162 (0.26)
NP K	0.172	NA	−0.012 (0.85)	−0.15* (0.032)	0.052 (0.58)
N P	0.070	0.723	0.042 (0.25)	−0.051 (0.64)	−0.034 (0.51)
Ca Mg	0.221	0.404	0 (1)	−0.008 (0.9)	−0.124 (0.059)
CaMg Mn	0.109	0.759	0.278 (0.084)	−0.057 (0.91)	0.258 (0.25)
Compartment: wood (B)					
NPK CaMgMn	0.055	0.702	−0.119 (0.17)	0.023 (0.92)	0.189 (0.13)
NP K	0.236	NA	0.19* (0.012)	−0.023 (0.75)	−0.132 (0.2)
N P	0.072	0.695	0.077 (0.065)	−0.028 (0.81)	−0.062 (0.29)
Ca Mg	0.191	0.191	−0.038 (0.71)	−0.019 (0.85)	−0.195 (0.18)
CaMg Mn	0.051	0.830	0.138 (0.18)	0.042 (0.92)	0.118 (0.42)

Note: R^2_m : variance explained by fixed effects only. R^2_c : variance explained by the full model including random effects (plot). NA: random effect variance estimated at zero (singular fit), R^2_c is therefore not interpretable. All models had 28 residual degrees of freedom for Stage and the Stage x Treatment interaction and 4 for Treatment. Fixed effect estimates are unstandardized coefficients from linear mixed models (*lmer*) with plot as random effect. Reference levels: mature

trees (Stage) and Control (Treatment). Positive Stage estimates indicate higher values in saplings relative to mature trees; positive Treatment estimates indicate higher values in exclusion plots relative to control plots. Measurements were taken in summer 2025, the first growing season following cessation of the precipitation exclusion treatment (active exclusion: June to August 2021 to 2024, Kenauk Nature Reserve, Québec).

Significance: * $p < 0.05$; . $p < 0.10$; bold = $p < 0.05$.

3.2.1 Pathways linking soil, wood and foliar nutrient composition

Three patterns emerged from the structural equation models (Table S4 – S5, Fig. 4). These models carry no plot-level random effect, so paths involving the treatment are tested against individual rather than plot-level variance; they describe the covariance structure linking soil, wood and foliage rather than providing a second test of the treatment. Read on those terms, a treatment path to wood composition appeared for four of the five balances, mostly in saplings, whereas the mixed models of Table 1 detected none. Second, the most consistently supported route to the foliage was not the wood alone, but the sequence running from soil nutrient availability through wood composition. This pathway was supported for [NPK|CaMgMn] in mature trees, for [N|P] at both stages, and for [CaMg|Mn] in saplings. Third, only one balance showed opposing soil- and wood-mediated pathways that offset each other: for [CaMg|Mn] in saplings, both pathways were supported, resulting in no net effect on the foliage balance.

For the balances involving N, P and K, wood and foliar composition were closely related, although the mixed models detected no treatment effect in the wood itself. For [NPK|CaMgMn], the ratio contrasting the strongly remobilized elements (N, P, K) with those that were more dependent on root uptake (Ca, Mg, Mn), the only supported pathway was from soil availability through wood composition in mature trees ($-0.087 [-0.323, -0.003]$), yet the total treatment effect on foliar nutrient composition was not supported at either ontogenetic stage. For [N|P], the total treatment effect was supported only in saplings ($-0.145 [-0.251, -0.045]$). This was the only balance for which both wood-mediated pathways showed a supported effect ($-0.059 [-0.145, -0.018]$), acting in the same direction as the total effect rather than opposing it. The [NP|K] ratio was the exception: in mature trees, the total treatment effect on the foliar ratio was supported

(-0.150 [-0.281, -0.015]), yet no path from the treatment or the soil to the foliage attained significance. Furthermore, the treatment covaried with soil availability at both stages without that availability reaching the leaves.

Soil pH was associated with soil mineral availability for both [Ca|Mg] and [CaMg|Mn], but not for the N- and P-dominated ratios, consistent with the stronger influence of pH on base-cation availability than on N or P supply. For [Ca|Mg], treatment effects were confined to saplings. The exclusion treatment was directly associated with lower ratios in both the wood and the foliage, and its total effect on the foliage, i.e., the sum of the direct and indirect contributions, was significant (-0.14 [-0.25, -0.05]). No pathway was supported in mature trees. For [CaMg|Mn], soil availability was associated with wood composition at both stages (-0.88 and -0.82), and wood composition with foliar composition (1.04 and 0.97). Wood composition and soil availability are strongly colinear in this model, which inflates the standardized wood-to-foliage coefficient beyond unity and makes its magnitude non-comparable across balances. Two wood-mediated routes of opposite sign were supported, one going from the treatment through the wood (0.32 [0.01, 0.73] in mature trees, 0.50 [0.17, 0.90] in saplings) and one going from soil availability through the wood (-0.28 [-0.70, -0.06] in saplings), and the total effect was null at both stages.

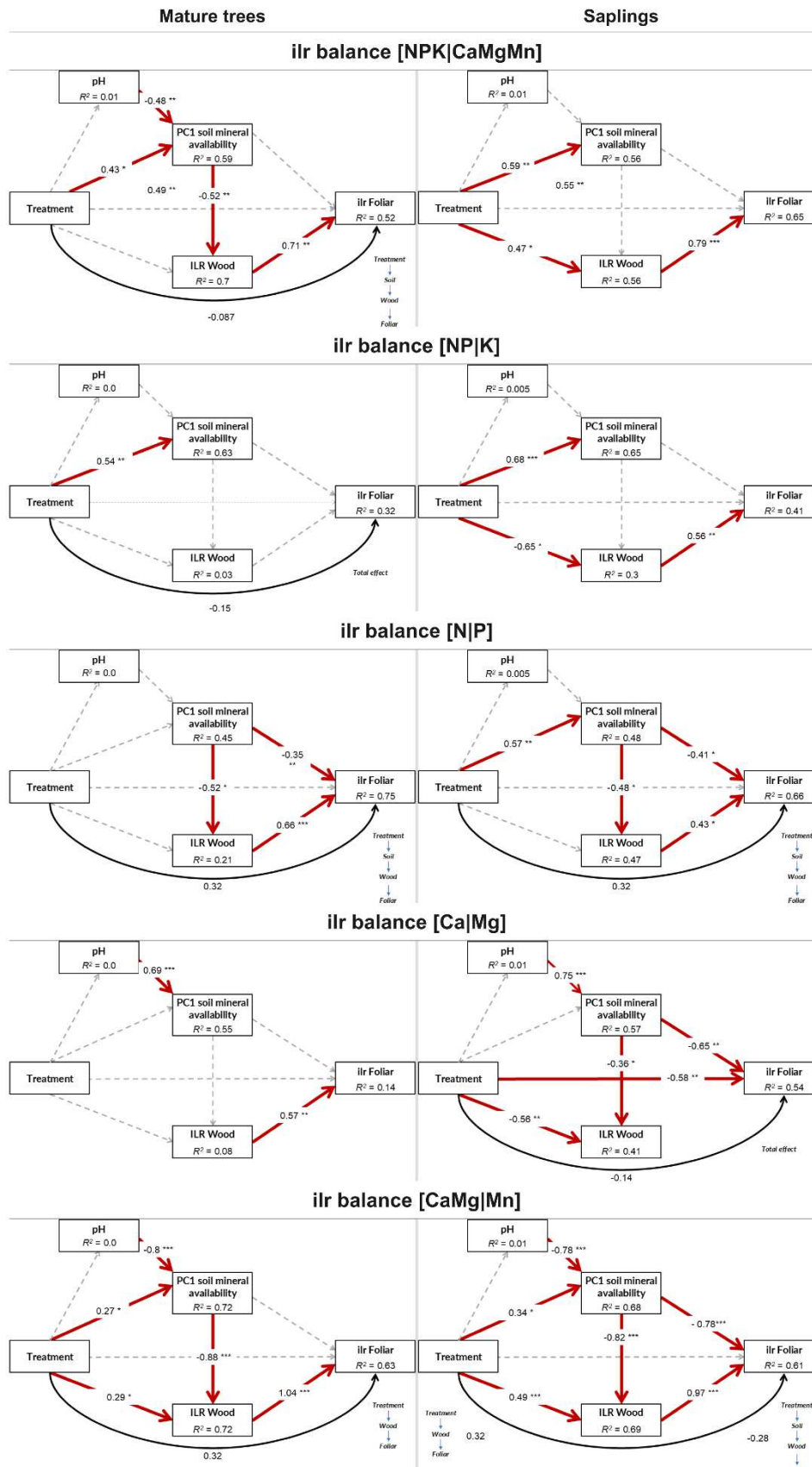


Figure 4. Structural equation models of the direct and indirect effects of throughfall exclusion on the five foliar ilr balances in sugar maple. Each row shows one balance, with mature trees on the left and saplings on the right ($n = 18$ per model). Boxes are observed variables: PC1 is the first principal component of soil ion supply for the elements of the balance shown, and ilr is the isometric log-ratio balance for the same elements, measured in fine-branch wood or in the foliage. Red solid arrows are direct paths supported at $p < 0.05$, grey dashed arrows are paths that were specified but not supported ($p \geq 0.05$), and the numbers beside the arrows are standardized coefficients, with asterisks giving the Wald test: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Black curved arrows are indirect effects of the throughfall exclusion on the foliar balance whose bootstrap confidence interval excluded zero: the route is named beside each arrow, and arrows labelled “Total effect” give the sum of all routes. R^2 is the proportion of variance explained for each endogenous variable. Treatment is coded with the control plots as reference, so a negative coefficient indicates lower values under exclusion. Coefficients are given in Table S4 for the direct paths and in Table S5 for the indirect and total effects; model fit statistics are given in Table S2.

Model fit was good for both stages (Table S2). Among mature trees, only the [NPK|CaMgMn] and [Ca|Mg] models returned elevated RMSEA and marginally low CFI. Because RMSEA is strongly inflated at $df = 1$ and small n (Kenny et al. 2015), inference was based primarily upon the χ^2 test, which did not reject any model, and upon bootstrap confidence intervals for the estimated effects.

4 DISCUSSION

4.1 A drought legacy on foliar nutrient stoichiometry

One year after the last growing season exclusion, when soil moisture in exclusion plots had returned to control levels, the foliar stoichiometry of sugar maple still differed from that of control trees. These results indicate that drought legacies can extend beyond radial growth and carbon allocation (Anderegg et al. 2015; Kannenberg et al. 2019; Rehschuh et al. 2022) to foliar nutrient stoichiometry, and persist after hydrological recovery. The exclusion treatment had imposed a marked edaphic moisture deficit: REW in exclusion plots was below that of controls and fell below the critical threshold of 0.4 (Granier et al. 1999) at least once during the exclusion period. This suggests that water availability was reduced in the exclusion plots, although the absence of direct physiological measurements prevents us from confirming water stress. Persistent nutrient imbalances had been reported in stands that are already declining under drought (Hevia et al. 2019). Repeated summer drought was shown to shift sugar maple nutrition during the exclusion at our study site (Parsons et al. 2025); by sampling after soil moisture had recovered, our design provides evidence of a legacy under restored soil moisture conditions.

Consistent with our first hypothesis, this legacy took the form of a single specific shift, i.e., a relative enrichment in K compared with N and P, which was expressed in leaves of saplings and mature trees alike. The foliar [NP|K] ratio decreased under exclusion while [N|P] remained stable (Table 1), which was a dissociation suggesting that the response primarily involved K relative to N and P. The N:P ratio reflects the allocation between nitrogen-rich proteins and phosphorus-rich nucleic acids (Elser et al. 2000); its stability suggests that the relative balance between N and P was maintained, while their balance with K shifted. Potassium governs cellular osmotic potential, turgor maintenance and stomatal regulation, thereby allowing individuals to adjust their internal water status under reduced water availability (Bhardwaj et al. 2025). A relative rise in foliar K compared with N and P is therefore consistent with widespread osmotic acclimation

of woody species to water stress rather than necessarily indicating a detrimental nutrient imbalance. The departure from CND reference values could reflect a physiological adjustment; even so, osmotic acclimation cannot be established from stoichiometry alone, and other mechanisms could contribute to the observed shift. Three pathways could account for the persistence of this adjustment, i.e., mobilization of wood reserves, a lasting shift in soil mineral availability, or direct regulation within the leaf, which we disentangle below.

4.2 Neither wood nutrient reserves nor soil nutrient supply explain the legacy effects

Our second hypothesis was not supported. The foliar response was of similar magnitude at both stages, and although the paths that reached support differed between saplings and mature trees, the coefficients were not compared formally across stages, so that difference cannot be read as a stage effect. The shift in foliar [NP|K] was of similar magnitude in saplings and mature trees. Saplings were more affected only for the base cations, whose foliar status depends on soil supply, and only marginally so. Ontogenetic stage thus shaped the pathway of legacy effects, but not the magnitude of the observed foliar nutrient response. Potassium is highly phloem-mobile (Marschner 2011), so a likely explanation would be a drawdown of branch reserves. That mechanism predicts the opposite of what we observed: exporting K from the branches should raise wood [NP|K], against the direction of the foliar shift. The mixed models detected no wood response at either stage (Table 1), so nothing is demonstrated in that compartment; the only discernible change, a decrease in saplings (Table S4), nonetheless runs with the foliar shift rather than against it. In mature trees, the same foliar effect persisted with no detectable change in wood composition or soil nutrient availability. A treatment effect on foliar [NP|K] was found overall, but no individual pathway reached significance, potentially reflecting limited statistical power. The persistence of the same imbalance across both stages, including in mature trees where it was not

associated with wood or soil conditions, suggests that the response may involve mechanisms beyond a passive legacy of the past deficit.

A second pattern emerged for [NPK|CaMgMn]. The exclusion treatment had no net effect on this foliar ratio (Table 1), yet a negative pathway going from soil availability through wood composition was supported in mature trees (Table S5) while the pathway from the exclusion treatment through wood remained positive but marginal (0.108 [-0.005, 0.465]). Consequently, the combined wood-mediated pathways did not differ from zero. The same opposition, more strongly expressed, appears for [CaMg|Mn], where a positive pathway through the wood (0.32 [0.01, 0.73] in mature trees, 0.50 [0.17, 0.90] in saplings) and a negative pathway going from soil availability through the wood was supported in saplings (-0.28 [-0.70, -0.06]), with the two offsetting one another resulting in no total effect at both stages.

Both stages preserved their foliar balance between N, P and K versus Ca, Mg and Mn, but potentially through different pathways. The only wood-mediated pathway that was supported for [NPK|CaMgMn] went from soil availability through wood, so that its maintenance cannot be attributed to a draw on reserves, which would be independent of the current soil supply. Where wood-mediated effects were supported, for [N|P] at both stages, they acted in the same direction as the total effect rather than opposing it, so the wood amplified the treatment signal rather than buffering it. Increased reliance on reserves that repeated drought could have depleted faster than they can be replenished is not supported here: where supported, the wood signal was opposite to the pattern expected from reserve mobilization. In mature trees, the net effect was null despite support for that pathway, suggesting that other pathways offset its contribution. This echoes the classical distinction between individuals that maintain tissue composition and those that develop persistent nutrient imbalances (Sardans et al. 2008). Sugar maple appears to acclimate at both stages, but saplings do so while also developing a base-cation imbalance that mature trees avoid. What sustains this adjustment in the absence of ongoing water stress and without detectable

changes in reserves or soil supply remains unresolved. Epigenetic regulation of K-transporter expression or persistent shifts in mycorrhizal association are plausible but untested mechanisms (Kambona et al. 2023).

4.3 Foliar base-cation responses reflect soil supply, mediated by wood

For Ca, Mg and Mn, foliar status was associated with the supply that was available to each tree rather than with remobilization from wood reserves. Soil pH was associated with their availability across both base-cation balances, consistent with the established control of pH over base-cation solubility (Marschner 2011; Neina 2019), although this relationship rests on evidence that is derived from six plots and is therefore weakly resolved.

For [CaMg|Mn], soil availability was the dominant predictor of wood composition at both stages, and the foliage was more closely associated with wood than with soil availability directly. The exclusion treatment covaried with foliage composition through two pathways of opposite sign, both of which were individually supported: one positive pathway through wood and one negative pathway from soil availability through wood. Their combined effect was not supported at either stage, and the total treatment effect was null. Thus, a balance can involve two opposing active pathways while showing no net response, a pattern that would not be apparent from a comparison of foliar means alone.

The [Ca|Mg] balance revealed a sensitivity that was specific to saplings. Neither soil availability nor the wood mediated this effect: the foliar ratio of saplings did covary with soil availability, but the treatment had not shifted soil availability at either stage, so the route by which it reached the foliage cannot be identified. Given that calcium reaches the roots largely through mass flow and is not re-translocated once deposited in tissues (Marschner, 2011), reduced soil moisture during the treatment years could constrain its acquisition, with limited possibility of internal compensation. In contrast, magnesium is phloem-mobile and can be supplied from older

tissues; thus, a decline in the calcium-to-magnesium balance would be expected under reduced calcium acquisition. The fact that this response was detected only in saplings is consistent with their potentially greater dependence on shallower horizons, the depth at which we documented the water deficit (0–11 cm), although rooting depth was not measured and this remains an inference.

Together, these responses do not support a partitioning of pathways according to element mobility. The wood-to-foilage pathway was tested for all five balances so that any contrast in support could emerge from the data, and it was supported in every balance in at least one ontogenetic stage, including [Ca|Mg] and [CaMg|Mn], which comprise elements conventionally treated as immobile. However, these associations were partial and, for [CaMg|Mn], entangled with soil availability, so they cannot be interpreted as evidence of remobilization. Instead, in the base-cation balances, wood appears to track soil supplies rather than acting as an independent nutrient store. The distinction our data support is therefore not one of mobility but one of supply: the potassium signal persisted without an identifiable source in either compartment, whereas the base-cation balances remained linked to pH and soil availability.

4.4 Implications of persistent nutritional drought legacies

The persistence of the [NP|K] shift one year after treatment provides evidence of a nutritional drought legacy, and its occurrence at both ontogenetic stages makes it consequential at the stand level. Neither larger reserves nor deeper rooting protected mature trees, suggesting that the legacy is not buffered by tree size and is not restricted to a single cohort. Soil moisture had recovered while the element imbalance had not, indicating that hydrological recovery is not sufficient for nutritional recovery. Under the increasingly shortened intervals between droughts that are projected for North America (Cook et al. 2020), successive nutritional imbalances could accumulate rather than be reset between events, although this possibility cannot be tested with the single post-treatment year analyzed in this study. A marginal exception concerns the base

cations: only saplings showed a [Ca|Mg] response, consistent with a greater reliance on surface soil horizons that were more affected by exclusion for elements supplied primarily by mass flow. This may add to the constraints already limiting sapling recruitment.

4.5 Limitations

Three limitations constrain these conclusions. First, with three plots per treatment, the random-effect variance could not always be estimated, resulting in a singular fit for [NP|K] and limiting the power of individual pathway tests. As a result, several pathways could not be confirmed. Second, the structural equation models do not include a plot-level random effect, so that paths involving the treatment are tested against individual rather than plot-level variance. Every supported indirect effect that is reported here begins either with the treatment acting on soil availability or with the treatment acting on wood composition, and neither of these first pathways retains support when tested at the scale at which the treatment was applied. The linear mixed models of Table 1 therefore provide the conservative test of the treatment effect, and the structural models are best read as descriptions of the covariance structure linking soil, wood and foliage. Third, water stress was inferred from soil moisture rather than being measured physiologically, and rooting depth, which was invoked to explain the sapling sensitivity to base cations, was not measured.

5 CONCLUSION

We show that a relative enrichment in foliar potassium persists one year after four summers of throughfall exclusion, when soil water no longer differed from controls, and that neither soil nutrient supply nor wood nutrient composition was supported as an explanation for this legacy. Wood composition was nonetheless coupled to foliar composition in all five balances, in at least one ontogenetic stage, including the calcium, magnesium and manganese balances, indicating that coupling between the two compartments does not

614 follow the conventional division based on phloem mobility. Drought legacies therefore extend
615 beyond carbon allocation and tree growth to mineral nutrition, and hydrological recovery
616 does not necessarily imply nutritional recovery.

617 We hypothesize that drought legacies in foliar stoichiometry are most likely to persist for
618 elements whose internal regulation contributes directly to drought response, with potassium
619 a prime candidate because of its osmotic role. By contrast, we expect weaker legacies where
620 foliar composition primarily reflects current soil nutrient supply. This hypothesis could be
621 tested using foliar chemistry from long-term monitoring networks combined with documented
622 drought histories to establish how widespread and durable such legacies are. The distinction
623 matters for diagnosis. Our CND indices placed excluded individuals away from the reference
624 optimum, which a routine diagnosis would report as an imbalance to correct, whereas the
625 shift may instead partly reflect a legacy of physiological adjustment to drought. Foliar
626 composition sampled after a drought should therefore be interpreted in light of the water
627 history of the stand, rather than against reference values alone. If such legacies prove
628 widespread across successive droughts, they may represent an overlooked constraint on
629 forest recovery.

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Figures:

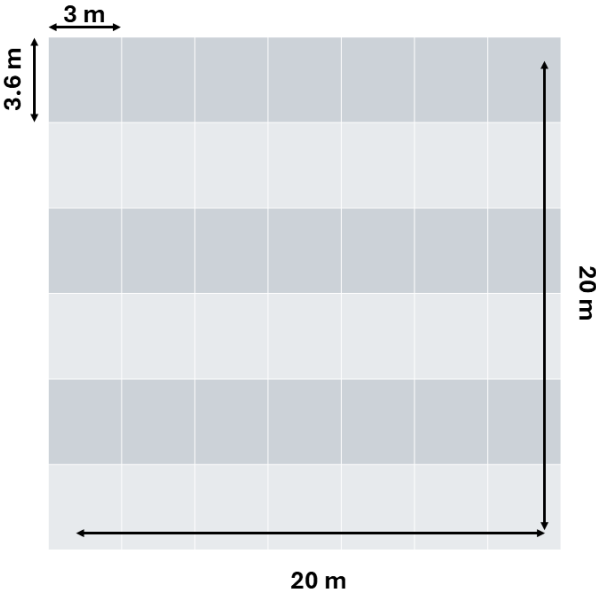


Figure S1. Schematic of the precipitation exclusion setup. Each 20 × 20 m experimental plot is covered by 42 impermeable tarps (3.6 × 3 m each) arranged in 7 columns and 6 rows and installed approximately 1.5 m above the ground. The resulting cover (21 × 21.6 m, ≈ 454 m²) extends beyond the plot boundaries to limit edge effects.

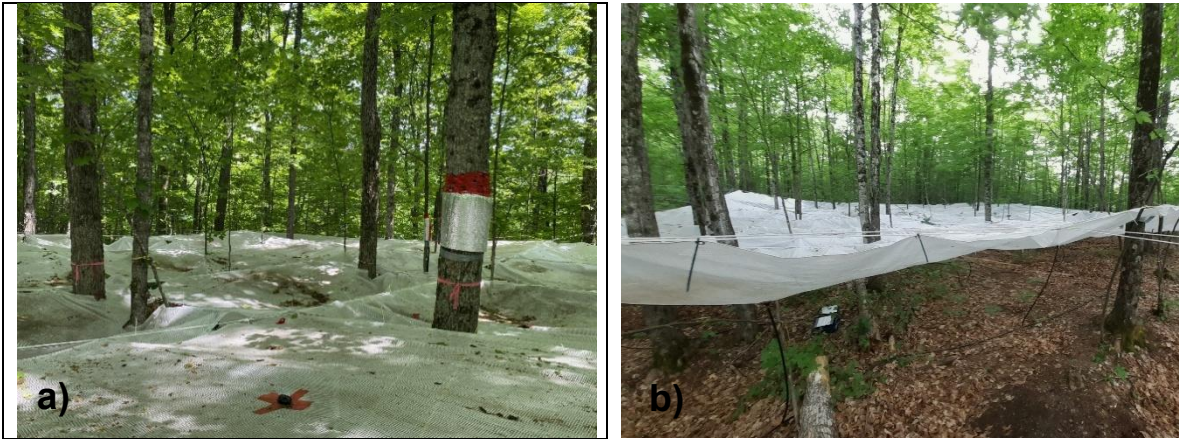
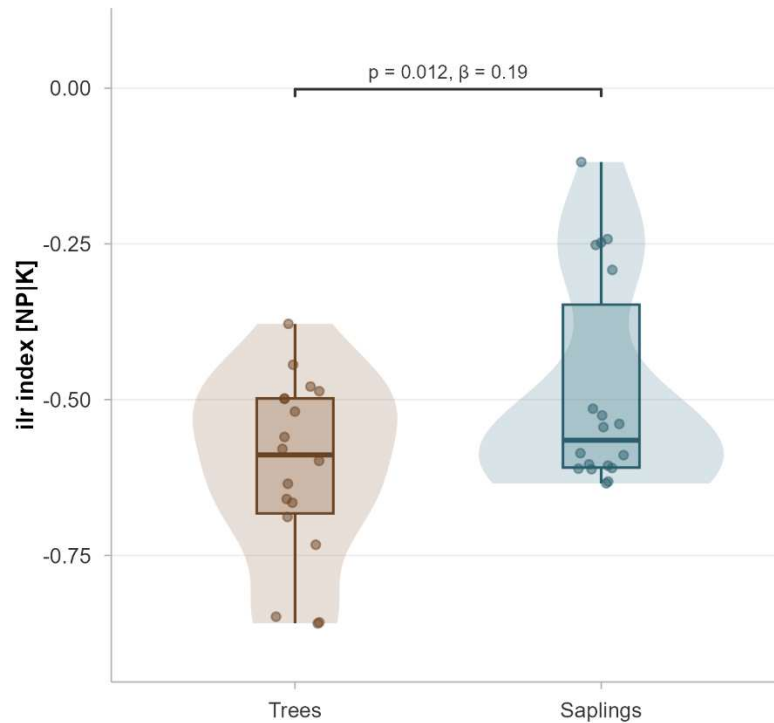
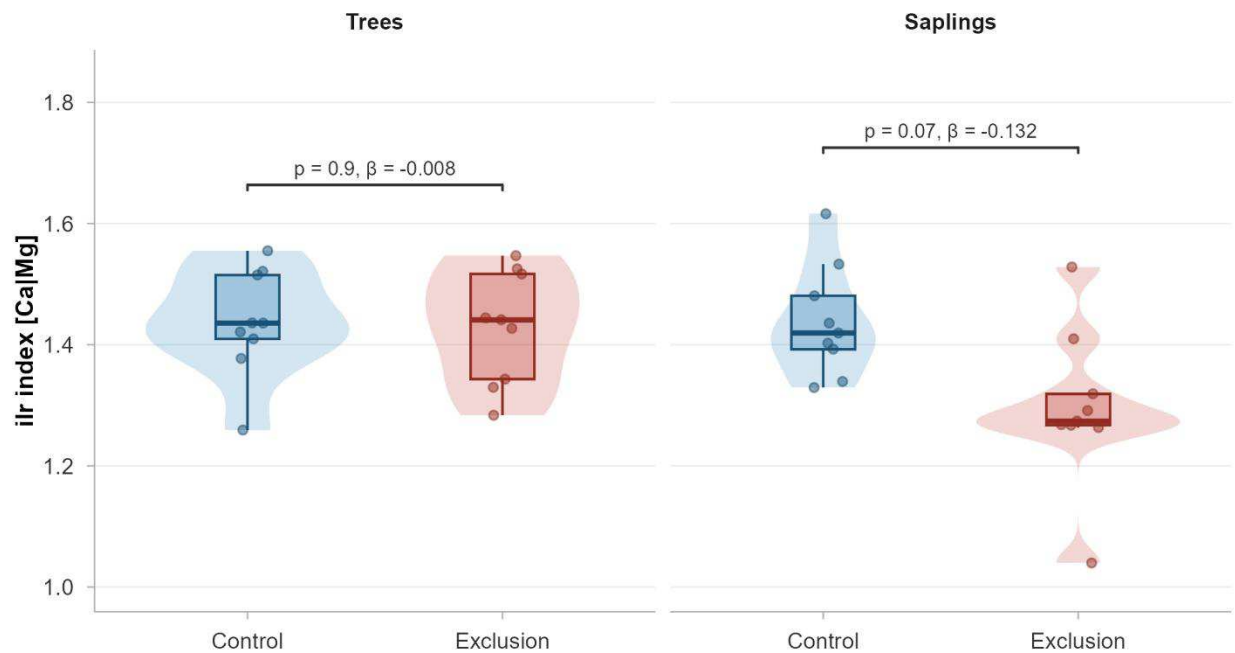


Figure S2. Photographs of the precipitation exclusion device: (a) overhead view showing the tarp arrangement; (b) ground-level view showing the tarp underside at approximately 1.5 m above the forest floor. Photos: A. Maheu, 2023.



649

650 **Figure S3.** Wood ILR balance [NP|K] of sugar maple in response to developmental stage.



651

652 **Figure S4.** Foliar ILR balance [Ca|Mg] of sugar maple in response to precipitation exclusion
653 treatment, by developmental stage.

654 **Tables:**

655 **Table S1.** Sequential binary partitioning (SBP) matrix defining the five ILR balances used in this
656 study.

ILR balance	Element contrasts (+1 / -1 / 0)						Group size	
	N	P	K	Ca	Mg	Mn	r	s
[NPK CaMgMn]	+1	+1	+1	-1	-1	-1	3	3
[NP K]	+1	+1	-1	0	0	0	2	1
[N P]	+1	-1	0	0	0	0	1	1
[CaMg Mn]	0	0	0	+1	+1	-1	2	1
[Ca Mg]	0	0	0	+1	-1	0	1	1

657 **Note:** The sequential binary partition (SBP) defines how elements are grouped to compute each isometric log-ratio
658 (ILR) balance. Elements coded +1 form the numerator group and elements coded -1 form the denominator group;
659 elements coded 0 are excluded from the balance. Each balance contrasts the geometric mean concentration of the
660 numerator group against that of the denominator, expressed on a log scale. r and s indicate the number of elements in
661 the numerator and denominator groups respectively, and are used to compute the orthonormal coefficient ensuring the
662 balances are isometric. The five balances collectively account for all compositional variation among the six elements
663 (N, P, K, Ca, Mg, Mn).

664

665 **Table S2.** Goodness-of-fit indices of structural equation models for foliar ILR balances by
666 developmental stage.

ILR balance	Stage	χ^2	df	p-value	CFI	RMSEA
[NPK CaMgMn]	<i>Trees</i>	3.07	1	0.08.	0.944	0.339
	<i>Saplings</i>	0.19	1	0.67	1.000	0.000
[NP K]	<i>Trees</i>	1.17	1	0.28	0.975	0.097
	<i>Saplings</i>	0.56	1	0.46	1.000	0.000
[N P]	<i>Trees</i>	0.48	1	0.49	1.000	0.000
	<i>Saplings</i>	0.40	1	0.53	1.000	0.000

ILR balance	Stage	χ^2	df	p-value	CFI	RMSEA
[Ca Mg]	Trees	2.38	1	0.12	0.932	0.277
	Saplings	0.03	1	0.87	1.000	0.000
[CaMg Mn]	Trees	1.07	2	0.59	1.000	0.000
	Saplings	1.63	2	0.44	1.000	0.000

Note: χ^2 , degrees of freedom and p-value are from the likelihood-ratio test of each model against the saturated model. Conventional thresholds for CFI and RMSEA are not applied here, because both indices are unreliable at one to two degrees of freedom and n = 18 per stage (Kenny et al. 2015); they are reported for completeness. Inference is based on the χ^2 test and on the bootstrap confidence intervals given in Tables S4 and S5. Significance: . $p < 0.10$

Table S3. PCA of soil nutrient stoichiometry across elemental subsets (N, P, K, Ca, Mg, Mn): variance explained by the first two principal components.

Subcomposition	PC1 (%)	PC2 (%)
NPK	75.07	22.16
NP	94.19	5.81
CaMg	59.68	40.32
CaMgMn	58.98	38.67
NPKCaMgMn	58.45	28.33

Note: Each PCA was run on the soil ion fluxes of the sub-composition underlying each ILR balance. The first component (PC1) was retained to summarize soil mineral availability in the structural equation models.

Table S4. Standardized direct path coefficients (β , with Wald p-values in parentheses) of the structural equation models for each foliar ILR balance of sugar maple, by developmental stage (saplings, trees).

Path	Mature trees	Saplings
[NPK CaMgMn]		
Treatment → pH	-0.01 (0.973)	0.07 (0.758)
Treatment → Soil availability	0.43* (0.018)	0.59** (0.001)
Treatment → Wood	0.27 (0.065)	0.47* (0.020)
Treatment → Foliage	-0.10 (0.619)	0.02 (0.929)
pH → Soil availability	-0.48** (0.008)	-0.32 (0.076)
Soil availability → Wood	-0.52** (0.002)	-0.16 (0.457)
Soil availability → Foliage	0.00 (0.988)	-0.08 (0.657)
Wood → Foliage	0.71** (0.003)	0.79*** (< 0.001)
[NP K]		
Treatment → pH	-0.01 (0.973)	0.07 (0.758)
Treatment → Soil availability	0.54** (0.004)	0.68*** (< 0.001)
Treatment → Wood	-0.16 (0.553)	-0.65* (0.018)
Treatment → Foliage	-0.38 (0.112)	-0.19 (0.494)
pH → Soil availability	-0.29 (0.113)	-0.13 (0.433)
Soil availability → Wood	0.15 (0.586)	0.27 (0.329)
Soil availability → Foliage	-0.16 (0.518)	0.14 (0.592)
Wood → Foliage	-0.03 (0.876)	0.56** (0.007)
[N P]		
Treatment → pH	-0.01 (0.973)	0.07 (0.758)
Treatment → Soil availability	0.36 (0.096)	0.57** (0.004)
Treatment → Wood	0.07 (0.736)	-0.23 (0.269)
Treatment → Foliage	-0.01 (0.961)	-0.09 (0.589)
pH → Soil availability	-0.22 (0.297)	-0.04 (0.830)
Soil availability → Wood	-0.52* (0.020)	-0.48* (0.018)
Soil availability → Foliage	-0.35** (0.009)	-0.41* (0.029)
Wood → Foliage	0.66*** (< 0.001)	0.43* (0.016)
[Ca Mg]		
Treatment → pH	-0.01 (0.973)	0.07 (0.758)
Treatment → Soil availability	-0.25 (0.112)	-0.13 (0.407)
Treatment → Wood	0.03 (0.889)	-0.56** (0.002)
Treatment → Foliage	-0.06 (0.757)	-0.58** (0.003)
pH → Soil availability	0.69*** (< 0.001)	0.75*** (< 0.001)
Soil availability → Wood	0.29 (0.217)	-0.36* (0.047)
Soil availability → Foliage	-0.14 (0.598)	-0.65** (0.009)
Wood → Foliage	0.57** (0.002)	0.14 (0.482)
[CaMg Mn]		
Treatment → pH	-0.01 (0.973)	0.07 (0.758)
Treatment → Soil availability	0.27* (0.032)	0.34* (0.012)
Treatment → Wood	0.29* (0.025)	0.49*** (< 0.001)
Treatment → Foliage	-0.13 (0.064)	-0.03 (0.735)
pH → Soil availability	-0.80*** (< 0.001)	-0.78*** (< 0.001)
Soil availability → Wood	-0.88*** (< 0.001)	-0.82*** (< 0.001)
Soil availability → Foliage	0.10 (0.423)	0.02 (0.875)
Wood → Foliage	1.04*** (< 0.001)	0.97*** (< 0.001)

Note: Standardized direct path coefficients (β) of the structural equation models, with Wald p-values in parentheses.

Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; bold indicates $p < 0.05$.

Table S5. Unstandardized indirect and total effects of precipitation exclusion on foliar ILR balances of sugar maple, with 95% bias-corrected accelerated (BCa) bootstrap confidence intervals, by developmental stage.

Route	Mature trees	Saplings
[NPK CaMgMn]		
via soil availability (foliar)	0.001 [-0.207, 0.172]	-0.029 [-0.333, 0.212]
via pH and soil availability (foliar)	0.000 [-0.035, 0.045]	0.001 [-0.016, 0.050]
via wood	0.108 [-0.005, 0.465]	0.227 [-0.009, 1.016]
via soil availability and wood	-0.087 [-0.323, -0.003]	-0.044 [-1.069, 0.077]
via pH, soil availability and wood	-0.001 [-0.060, 0.047]	0.002 [-0.016, 0.049]
<i>All wood-mediated routes (subtotal)</i>	<i>0.018 [-0.156, 0.283]</i>	<i>0.204 [-0.007, 0.416]</i>
Total effect	-0.038 [-0.302, 0.218]	0.187 [-0.123, 0.442]
[NP K]		
via soil availability (foliar)	-0.028 [-0.202, 0.078]	0.025 [-0.073, 0.332]
via pH and soil availability (foliar)	0.000 [-0.050, 0.017]	0.000 [-0.039, 0.005]
via wood	0.002 [-0.092, 0.151]	-0.097 [-0.290, 0.022]
via soil availability and wood	-0.001 [-0.112, 0.045]	0.027 [-0.009, 0.241]
via pH, soil availability and wood	0.000 [-0.014, 0.006]	0.000 [-0.038, 0.003]
<i>All wood-mediated routes (subtotal)</i>	<i>0.001 [-0.048, 0.063]</i>	<i>-0.070 [-0.212, 0.007]</i>
Total effect	-0.150 [-0.281, -0.015]	-0.097 [-0.219, 0.017]
[N P]		
via soil availability (foliar)	-0.031 [-0.131, 0.002]	-0.061 [-0.195, 0.016]
via pH and soil availability (foliar)	0.000 [-0.022, 0.012]	0.000 [-0.014, 0.038]
via wood	0.012 [-0.091, 0.137]	-0.026 [-0.154, 0.076]
via soil availability and wood	-0.031 [-0.148, -0.001]	-0.031 [-0.357, -0.001]
via pH, soil availability and wood	0.000 [-0.056, 0.013]	0.000 [-0.007, 0.030]
<i>All wood-mediated routes (subtotal)</i>	<i>-0.018 [-0.114, 0.050]</i>	<i>-0.059 [-0.145, -0.018]</i>
Total effect	-0.051 [-0.172, 0.057]	-0.145 [-0.251, -0.045]
[Ca Mg]		
via soil availability (foliar)	0.006 [-0.016, 0.115]	0.022 [-0.016, 0.101]
via pH and soil availability (foliar)	0.000 [-0.019, 0.089]	-0.009 [-0.100, 0.079]
via wood	0.003 [-0.044, 0.092]	-0.021 [-0.165, 0.065]
via soil availability and wood	-0.007 [-0.128, 0.001]	0.002 [-0.003, 0.048]
via pH, soil availability and wood	0.000 [-0.023, 0.013]	-0.001 [-0.022, 0.009]
<i>All wood-mediated routes (subtotal)</i>	<i>-0.004 [-0.060, 0.049]</i>	<i>-0.020 [-0.162, 0.052]</i>
Total effect	-0.008 [-0.088, 0.076]	-0.143 [-0.250, -0.048]
[CaMg Mn]		
via soil availability (foliar)	0.027 [-0.025, 0.262]	0.007 [-0.103, 0.134]
via pH and soil availability (foliar)	0.001 [-0.047, 0.080]	-0.001 [-0.054, 0.051]
via wood	0.320 [0.010, 0.730]	0.496 [0.175, 0.904]
via soil availability and wood	-0.258 [-0.728, 0.014]	-0.282 [-0.696, -0.058]
via pH, soil availability and wood	-0.006 [-0.424, 0.272]	0.047 [-0.324, 0.267]
<i>All wood-mediated routes (subtotal)</i>	<i>0.056 [-0.509, 0.539]</i>	<i>0.260 [-0.252, 0.769]</i>
Total effect	-0.057 [-0.543, 0.453]	0.231 [-0.298, 0.698]

Note: Unstandardized indirect and total effects with 95% bias-corrected accelerated (BCa) bootstrap confidence intervals (5000 resamples); estimates in bold have a confidence interval excluding zero. Effects are reported unstandardized because standardized bootstrap intervals are unstable at this sample size. Each route is a product of path coefficients along the named sequence; wood refers to the ilr balance in fine-branch wood and soil availability to the first principal component of the PRS ion fluxes. The subtotal row, in italics, sums the wood-mediated routes listed above it and is not an additional effect. The total effect is the sum of the direct effect and of all indirect routes, excluding

the subtotal. Routes in which pH reaches a plant compartment without passing through soil availability are not tabulated;
all were negligible ($|\text{estimate}| \leq 0.02$) and none differed from zero.

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STATEMENTS AND DECLARATIONS

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Competing Interests

The authors declare no competing interests.

Author Contributions

Martin Simoneau: conceptualization; methodology; investigation; formal analysis; data curation; visualization; writing – original draft. **Audrey Maheu**: conceptualization; methodology; funding acquisition; writing – review and editing. **David Rivest**: conceptualization; methodology; supervision; writing – review and editing. **Annie Desrochers**: conceptualization; methodology; supervision; writing – review and editing. **Philippe Nolet**: conceptualization; methodology; supervision; writing – review and editing. All authors read and approved the submitted version.

Data Availability

The data and R code supporting the results of this study are archived in Zenodo at <https://doi.org/10.5281/zenodo.22311230>. The files are openly accessible.