Biogeochemistry
https://doi.org/10.1007/s10533-023-01039-6

Nitrogen-bedrock interactions regulate multi-element nutrient limitation and sustainability in forests

Kaveh G. Siah · **Steven S. Perakis** ·
Julie C. Pett-Ridge · **Gregory van der Heijden**

Received: 12 December 2022 / Accepted: 12 April 2023

Abstract Nutrient limitation of tree growth can intensify when nutrients are lost to forest harvest, creating challenges for forest growth and sustainability. Forest harvest accelerates nutrient loss by removing nutrient-containing biomass and by increasing nutrient leaching, shaping patterns of nutrient depletion that cause long-term shifts in nutrient limitation. Nitrogen most frequently limits tree growth, but where nitrogen is abundant, nutrient limitation often shifts to phosphorus and base cations, depending on soil mineralogy. We used the process-based biogeochemical model NutsFor to evaluate how multiple elements can limit long-term forest growth via interactions between soil nitrogen (low vs. high nitrogen) and soil mineralogy (sedimentary vs. basaltic bedrock). Simulations were run for 525 years with 40-year harvest intervals for managed Douglas-fir forests of the Oregon Coast Range. In low nitrogen sites, nutrient limitation switched after several centuries from nitrogen to phosphorus, as cycles of forest growth and harvest depleted soil organic phosphorus pools. In contrast, high nitrogen sites displayed severe base cation depletion and reduced tree growth within only one to two rotations, with sedimentary bedrock sites limited by calcium and basaltic sites by both calcium and potassium. Harvesting stimulated the largest fractional losses of nitrogen and potassium across all simulations, and additionally of calcium in high nitrogen sites. These multi-element simulations of interactions among harvesting, soil nitrogen, and bedrock type provide a set of testable predictions to guide monitoring and changes in management aimed at sustaining long-term forest productivity across a wide range of soil biogeochemical conditions.

Keywords Biogeochemistry · Nitrogen · Calcium · Potassium · Phosphorus · Mineral weathering · Forest harvest · Logging · Nutrient · Model

One Sentence Summary: This study shows that logged conifer forests growing on high nitrogen soils

Responsible Editor: Steven J. Hall.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10533-023-01039-6.

K. G. Siah
Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

K. G. Siah (✉) · J. C. Pett-Ridge
Department of Crop and Soil Science, Oregon State University, Corvallis, OR, USA
e-mail: kavehsiah@gmail.com

S. S. Perakis
Forest and Rangeland Ecosystem Science Center, US Geological Survey, OR, Corvallis, USA

G. van der Heijden
Biogéochimie des Ecosystèmes Forestiers, INRAe, Champenoux, France

are likely to experience base cation limitation within short (40–80 year) time frames.

Introduction

Nitrogen (N) is the most common limiting nutrient of forest growth globally, in part because it accumulates slowly in soil compared to more common rock-derived nutrients (LeBauer and Treseder 2008). Other key nutrients including phosphorus (P) and base cations (calcium (Ca), magnesium (Mg), or potassium (K)) that are regularly abundant in soil-forming bedrock are less likely to limit tree growth, though emerging evidence suggests such non-N limitations may be geographically widespread (Mika and Moore 1990; Likens et al. 1998; Nykvist 2000; Vadeboncoeur 2010; Perakis et al. 2013; Mainwaring et al. 2014; Bauters et al. 2022). Several factors can lead to growth limitation by nutrients other than N. For instance, highly weathered soils enriched in iron (Fe) and aluminum (Al) minerals can fix P into unavailable forms (Vitousek et al. 2010), and soil acidification and base cation deficient bedrock can predispose forests to base cation limitation (Likens et al. 1994; Nykvist 2000). Soil acidification caused by high inputs of N and/or sulfur (S) compounds may induce base cation limitation within relatively short time frames (i.e., decades to centuries), particularly when mineral weathering and atmospheric resupply of nutrients are low (Bockheim and Langley-Turnbaugh 1997; Perakis et al. 2006; Bigelow and Canham 2007; Leys et al. 2016). In addition, high N inputs may overcome N scarcity, leading to co-limitation or serial limitation by other nutrients (Berendse et al. 1992; Goswami et al. 2017). Differences in nutrient limitation patterns shape many phenomena of widespread importance, including rates of tree growth (Vicca et al. 2012), response to disturbance (Kranabetter et al. 2016), climate (St.Clair et al. 2008), and elevated CO_2 (Terrer et al. 2019), and the sustainability of forest harvest (Ranger and Turpault 1999; Vadeboncoeur et al. 2014).

Nutrient limitation and depletion are issues of enduring importance to sustainable forestry. However, because forests are dominated by relatively long-lived species, the emergence and diagnosis of changing nutrient limitation patterns and their impact on tree growth can be difficult to discern (Sullivan et al. 2014). Long intervals between forest harvests (i.e., compared to annual crops) allow forests to accumulate nutrients from atmospheric deposition and mineral weathering, and redistribute them internally to meet tree growth (Vadeboncoeur et al. 2014). In addition, aggrading forests often retain limiting nutrients tightly, while less limiting nutrients may be lost without reducing short-term growth (Vitousek and Reiners 1975). However, forest harvest can accelerate nutrient loss substantially by the removal of nutrients in harvested biomass and by accelerating nutrient leaching (Ranger and Turpault 1999). The relative importance of these two major nutrient loss pathways is not well constrained across gradients in soil fertility shaped by variation in soil N and bedrock type. Because N (and to a lesser degree P) are most often limiting nutrients, most studies focus on N (and P) depletion in forests (Hume et al. 2018). Yet, mass-balance calculations of nutrient input and removal also often identify Ca as susceptible to long-term nutrient depletion (Mann et al. 1988; Federer et al. 1989; Thiffault et al. 2011; Vadeboncoeur et al. 2014; Vanguelova et al. 2022). Understanding how high N supply interacts with other elements is essential for capturing shifts in nutrient limitation from N to other non-N nutrients.

Temperate forests of the Oregon Coast Range provide a diverse biogeochemical template for examining how soil N, bedrock type, and forest harvest influence soil nutrient depletion and limitation. These forests occupy broad gradients of soil N, P and base cation supply that span contrasting basaltic and sedimentary bedrock. Soil N cycles vary naturally from N-limited to N-saturated due to legacies of symbiotic N fixation by red alder trees (Perakis et al. 2011). Increases in soil N accumulation promote soil organic P accumulation, whereas soil base cations (particularly Ca) are depleted at high N sites by millennia of soil acidification and coupled nitrate and base cation leaching (Perakis et al. 2013, 2017; Hynicka et al. 2016). These diverse soil conditions create a wide range of observed nutrient limitation of tree growth by N, Ca, and P (Mainwaring et al. 2014). This soil diversity also challenges simple prediction of how nutrient limitation may intensify and shift with multiple harvest removals. For example, soils derived from basaltic and sedimentary bedrock both exhibit sharp declines in exchangeable base cations at high N sites, yet basaltic sites display a higher reserve capacity of weatherable minerals than sedimentary sites, creating potential bedrock-dependent differences in nutrient sustainability (Hynicka et al. 2016). Nutrient depletion by repeated forest harvest could thus lead to both N and rock-dependent shifts in nutrient limitation patterns in these forests. However, quantitative multi-element comparisons of nutrient depletion and limitation are generally lacking across such biogeochemically diverse forests.

Due to the long time frames necessary to measure changes in forest nutrient limitation, dynamic modeling approaches can be important and useful tools. Simulation models that evaluate ecosystem-level nutrient inputs, transformations, and losses, and their modification by climate and tree growth, can capture long-term dynamics of forest element balances that are not possible with simple nutrient budgets (Homann et al. 2000; Valipour et al. 2018). Most biogeochemical simulation models focus on N due to its common role as a limiting nutrient, yet an early simulation analysis of repeat forest harvest effects on high N sites of the Oregon Coast Range suggested only small declines in long-term productivity (Sachs and Sollins 1986). Accordingly, subsequent experimental fertilization studies have suggested that P and base cations (not N) are more likely to limit tree growth on high N sites (Mainwaring et al. 2014). Mass balance nutrient budget calculations can be used to estimate rates of nutrient depletion for multiple elements in forests (Mann et al. 1988; Ranger and Turpault 1999; Vadeboncoeur et al. 2014), but are less able to examine biogeochemical interactions among nutrients as nutrient pools and availability change over time (van der Heijden et al. 2017a; van der Heijden et al. 2017b). Dynamic simulation models that simultaneously examine N, P, and base cation biogeochemistry are very rare (Homann et al. 2000). One such model is the Nutrient Cycling in Forest Ecosystems model (NutsFor), a coupled biogeochemical, mineral weathering, hydrologic, and plant growth model, which mechanistically links soil N, P, and base cation inputs, cycling, and losses in the plant-soil system (van der Heijden et al. 2017a; van der Heijden et al. 2017b). Such multi-element dynamic simulation models can be particularly well suited for evaluating nutrient sustainability across sites that differ widely in underlying biogeochemical characteristics due to interactions between N and mineral weathering supplies of P and base cations from bedrock.

We used a dynamic biogeochemical simulation model (NutsFor) to evaluate how differences in soil N and bedrock type interact to influence long-term nutrient supply and limitation in temperate conifer forests of the Pacific Northwest. We modeled a recurring 40-year bole-only harvest regime for Douglas-fir forests, as this is representative of large areas of highly productive forest in the Oregon Coast Range. The NutsFor model was used to answer the following questions: (1) How do differences in site N affect nutrient limitation and long-term forest growth?, (2) How do differences in bedrock nutrient supply interact with N to influence nutrient limitation and growth?, and (3) What are the relative importance of leaching vs. biomass removal as nutrient loss pathways for sites that differ in N and bedrock? Our overarching focus is to examine biogeochemical interactions caused by differences in site N and bedrock, to gain insight into how different biogeochemical site factors drive nutrient depletion and limitation.

Methods

Site description

The Oregon Coast Range (OCR) is in the temperate coniferous forest biome of western North America, with a climate of cool wet winters and warm dry summers (Table 1). Soils of the area escaped the last major glaciation, and are derived principally from either sedimentary or basaltic bedrock. Sedimentary soils develop from late Eocene to Early Miocene marine sandstone and siltstone deposits, whereas basaltic soils develop from Eocene basaltic pillow lavas originally derived from submarine volcanoes. Soil N content varies from low to high N on both rock types (Perakis et al. 2006; Hynicka et al. 2016). This variation reflects legacies of symbiotic N-fixation by red alder, because N inputs via atmospheric deposition and asymbiotic fixation are relatively low (Perakis et al. 2011). Holocene wildfires and more recent logging can facilitate red alder, which fixes up to ~150 kg N ha^{-1} yr^{-1} in pure upland stands (Binkley et al. 1994), even when soil N is abundant (Menge et al. 2023). The large historic N inputs have created wide differences in soil N on both basaltic and sedimentary sites that persist to the present managed conifer forests (Perakis and Sinkhorn 2011; Perakis et al. 2011).

We selected four sites, from a broad range of previously studied sites in the Oregon Coast Range

Table 1 Observed site characteristics

Site	Location ID*	Taxonomic Classification (USDA)	MAP (mm)	MAT (°C)
LNS	7	Andic Humudept/Andic Dystrudept	2217	11.3
LNB	19	Typic Fulvudand	2804	10.5
HNS	39	Andic Dystrudept	2000	10.7
HNB	RR1	Typic Fulvudand	3171	8.7

LNS is Low N Sedimentary, LNB is Low N Basalt, HNS is High N Sedimentary, HNB is High N Basalt

*Location ID indicates the code used for these sites in previous publications. Sedimentary site data is reported in Perakis and Sinkhorn 2011, and basalt site data is reported in Hynicka et al. 2016

(Perakis et al. 2006; Perakis and Sinkhorn 2011; Hynicka et al. 2016) to serve as representative examples for model calibration and simulation. The sites span both low N and high N soil conditions on both sedimentary and basaltic bedrock. This 2 × 2 matrix of 4 sites thus includes a low N sedimentary site (LNS), a low N basaltic site (LNB), a high N sedimentary site (HNS) and a high N basaltic site (HNB) (Tables 1 and 2, and Fig. S1). Previous work determined aboveground net primary productivity for the sedimentary sites was 8.91 Mg ha^{-1} yr^{-1} at the low N site, and 13.63 Mg ha^{-1} yr^{-1} at the high N site (Perakis and Sinkhorn 2011).

The NutsFor model

The Nutrient Cycling in Forest Ecosystems model (NutsFor) is a stand-level biogeochemical cycling model developed by van der Heijden et al. (2017a, b), describing the speciation, cycling, and vertical transport of 18 chemical components: Ca^{2+}, Mg^{2+}, K^+, Na^+, Cl^-, R^-, HR (where "R" refers to an organic anion), PO_4^{3-}, NO_3^-, NH_4^+, SO_4^{2-}, DOC, SiO_2, H^+, DON, DOP, ANC, Al species (Al^{3+}, $Al(OH)^{2+}$, $Al(OH)_2^+$, $Al(OH)_3$, $Al(OH)_4^-$) and carbonic acid species (H_2CO_3, HCO_3^-, CO_3^{2-}). Each of these species is tracked within each layer in the soil profile. For this study, the total soil profile from 0 to 100 cm depth was divided into 8 layers (Tables S1 through S4). As a hybrid of several models, NutsFor incorporates all major nutrient cycling processes inherited from the Nutrient Cycling Model (NuCM) (uptake, translocation, leaching, mineral weathering, organic matter dynamics, deposition fluxes) (Munson et al. 1992, Fig. 1) as well as additional components from the ForSAFE, WatFor (van der Heijden et al. 2019), and PROFILE models (Sverdrup and Warfvinge 1993; Wallman et al. 2005; van der Heijden et al. 2019).

Table 2 Site nutrient content: observed versus simulated

Site		C	N	P	S†	Ca	Mg	K
		Mg ha^{-1}		kg ha^{-1}				
LNS	Simulated	176	9.5	1653	2298	6149	2676	1388
	Observed	176	9.5	1672	2280	6151	2678	1388
LNB	Simulated	109	5.9	1602	2298	1772	1737	468
	Observed*	109	5.9	1602	2280	1792	1460	406
HNS	Simulated	387	21	3717	2301	243	172	500
	Observed	387	21	3716	2280	171	155	484
HNB	Simulated	295	14.1	3676	2301	164	80	112
	Observed*	294	14.1	3676	2280	160	73	107

Site nutrient content represents the sum of the exchangeable, litter, and SOM pools, to 100 cm depth

*Observed values are calculated based on measured values at 5, 15, 25, 35 and 45 cm depths (Hynicka et al. 2016), without litter contribution. Content was extrapolated to 100 cm depth using linear regression

†Calculated from DF-1 Site Dataset (Johnson and Lindberg 1992)

NutsFor simulates tree biomass accrual via user-entered optimal increment (See Appendix). The optimal biomass increments are set for every biomass compartment (bole, bark, branch, foliage). Nutrient uptake is assumed to occur via roots, but roots are not explicitly modeled as a unique biomass pool. The full potential growth is achieved for each site in each year if the required uptake of nutrients (determined by the target nutrient concentrations of each biomass compartment and the growth increment) is available from the simulated fluxes. Modeled sites were assumed to be pure Douglas-fir tree plantations, which are common across the study area. We did not include any other vegetation in the model, for simplification and because herbicide use in managed forests greatly limits shrub and herbaceous biomass at stand establishment, and this is largely maintained by shading as forests reach canopy closure (Stokely et al. 2018). We do not consider the effects of fire in the model, and wildfires are rare and aggressively suppressed in our study region, and because broadcast burning to control slash is increasingly rare, with slash control generally limited to localized burn piles. Potential tree biomass (Mg/ha) targets were based on Bruce's Site Index of tree height (feet) at 80 years age, as estimated from the CIPSANON growth and yield model for this region (Joo et al. 2020). The model was initialized for 20-year-old stands based on the availability of representative plant and soil chemical data for this age class (Supplementary Tables S1–S5).

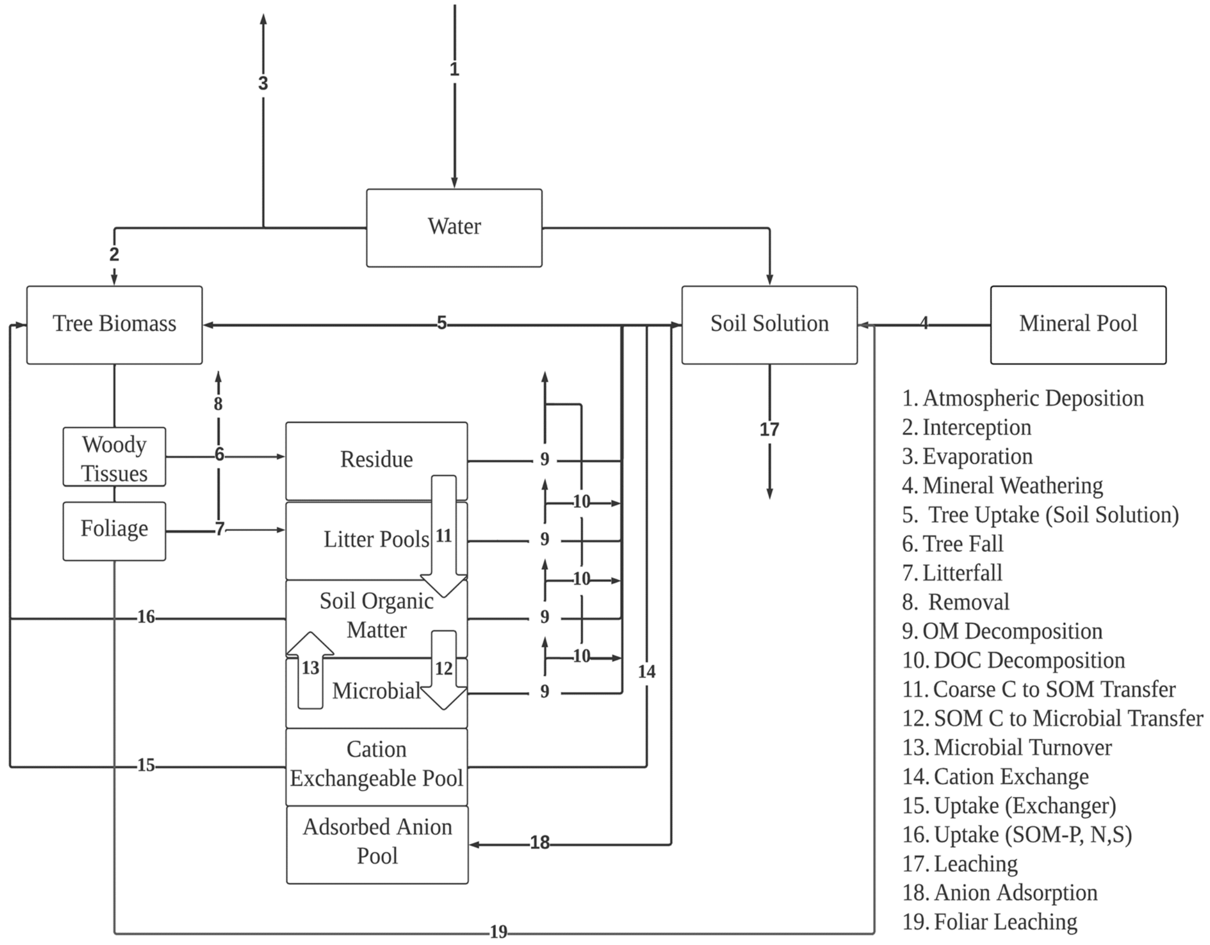

Fig. 1 NutsFor process design chart, arrows show interactions between pools (processes). Additional model information is available in van der Heijden et al. (2017a, b)

Nutrient mineralization in NutsFor is determined by organic matter decomposition rates and nutrient release factors. Decomposition rates determine the decomposition flux of organic matter, and additional parameters dictate the fraction of C incorporated into soil C or released as DOC to soil solution and as CO_2 to the atmosphere. Nutrient release from decomposed organic matter fraction is determined by a "nutrient release factor" that ranges from zero to one, where a value of one indicates nutrient release at C:nutrient stoichiometry identical to the source organic matter. Both nutrient uptake and release occur from a soil microbial pool. We updated the model to also include direct tree access to N, P, and S in soil organic matter (hereby represented as SOM-P, N, and S parameters) (See Appendix). The model simulates cation exchange reactions for Na^+, K^+, ${NH_4}^+$, Ca^{2+}, Mg^{2+}, ${Al_3}^+$, and H^+ following the Gapon formulation (Sposito 1977). It simulates anion adsorption and desorption through either Langmuir (${SO_4}^{2-}$ and Cl^-) or Freundlich (${PO_4}^{3-}$) isotherms. All anion sorption is non-competitive and insensitive to pH change.

Elemental transport through soil layers is simulated through the NutsFor hydrological sub-module, WatFor (van der Heijden et al. 2019). The hydrological model uses daily potential evapotranspiration, average air temperature, and rainfall volume to determine water fluxes. Soil water metrics such as soil water volumetric content at field capacity, wilting point and saturation, root fraction, as well as stoniness are used to calculate water yield fluxes in each layer of the soil profile. In the model, topography was simplified to no slope to allow one-dimensional water fluxes, similar to assuming that lateral water inputs equal lateral water outputs.

Elemental losses in the NutsFor model occur through either soil porewater leaching from the deepest layer or from forest biomass removal by harvest. The model does not include gaseous N loss, but both field measurements and stable isotope mass balances suggest only limited N loss via gaseous pathways in these forests (Erickson and Perakis 2014; Perakis et al. 2015). The model also does not include biological N fixation, which occurs at only low rates (<1 kg N ha^{-1} yr^{-1}) in Douglas-fir forests where symbiotic N-fixing red alder is absent (Perakis et al. 2011).

The NutsFor mineral weathering engine is inherited from the PROFILE model (Sverdrup and Warfvinge 1988). PROFILE is a soil mineral weathering model designed to dynamically compute mineral weathering fluxes based on soil chemistry. It simulates mineral weathering by linking the exposed mineral surface area to a series of rate coefficients describing kinetic and chemical controls on mineral dissolution (Sverdrup and Warfvinge 1988).

For this study, all NutsFor model simulations included a 40-year bole-only harvest regime, where 97% of bole biomass and 90% of bark biomass were removed from the site, and 100% of foliage and branch biomass were left on the site. During each simulated harvest event, 99% of the standing crop was cut down, leaving 1% of trees standing (the model has a mathematical limitation and cannot represent 100% harvest removal). To represent accrual of leaf area of evergreen needles on the growing tree canopy early in stand development, all sites had zero litterfall rates until 11 years of age. At 11 years, litterfall was set to 1000 kg·$ha^{-1}yr^{-1}$, and in subsequent years was allowed to vary dynamically from 1000 to 2300 kg·$ha^{-1}yr^{-1}$. The litterfall amounts are dynamic in response to nutrient limitation, with litterfall reduced in proportion to foliage growth for stands that cannot obtain the required nutrient uptake of any nutrient. Additional details of model parameterization are in the Appendix.

Model inputs

We modeled a constant 2500 mm of annual rainfall to provide consistent hydrological characteristics across all four sites used in model simulations. Rainfall chemistry was taken directly National Atmospheric Deposition Program measurements at the Alsea Ranger Guard Station in the Oregon Coast Range (OR02 dataset, NADP, 2022). Soil water metrics (field capacity, wilting point, and saturation point) were derived from Oregon Coast Range soils in the National Cooperative Soil Survey Soil Characterization Database (NCSS-SCD 2022).

Mineralogy and mineral abundance for basalt-derived soils were based on mineral data from nearby sites in the National Cooperative Soil Survey—Soil Characterization Database (NCSS-SCD) of soils of similar basaltic geologic origin, and from data in Franklin (1971) (Table S1–S4). Basaltic minerals consisted of augite, labradorite, hornblende, olivine, chlorite, vermiculite, illite, kaolinite, volcanic glass, and apatite. Sedimentary soil mineralogy and mineral abundance were based on soil mineral data from the late Eocene Flournoy formation (Anderson et al. 2002), and from several nearby NCSS-SCD soils developed on similar formations. Sedimentary site mineralogy consisted of albite, biotite, muscovite, vermiculite, kaolinite, apatite, hornblende, and anorthite. In the Oregon Coast Range, mean soil residence times vary between ~7 and 240 ka (Sweeney et al. 2012). Additionally weathering profiles in the Oregon Coast Range average 7 m depth (±3 m s.d.) (Hynicka et al. 2016). These conditions support the use of static mineralogy and mineral surface area input parameters in our ~500 year model simulations. Additional model inputs are described in Supplementary Tables S1 through S4, and a compilation of observed values in the Oregon Coast Range is provided in Table S5.

Calibration

Four specific sites were used for model calibration: a low N sedimentary site (LNS), a low N basaltic site (LNB), a high N sedimentary site (HNS) and a high N basaltic site (HNB) (Tables 1 and 2). NutsFor calibration was carried out by fitting simulated soil solution concentrations of dissolved species to those observed in lysimeter-based datasets. We adjusted soil pore water fluxes during calibration with the ratio of the actual rainfall at each study site relative to the standardized modeled amount of 2500 mm. Calibration occurred over a two-year timeframe of tree growth and differed for basaltic vs. sedimentary sites due to the availability of data. Sedimentary site soil solution concentrations were measured monthly in 2005 and 2006 using lysimeters at 20 and 100 cm depths at LNS and HNS sites (sites 7 and 39, respectively, in Perakis et al. 2013), but similar data do not exist for basalt sites. Conversely, mineral weathering rates at basalt sites were determined using Sr isotopes (Hynicka et al. 2016), but heterogeneity in Sr-isotope end-members at sedimentary sites prevented such calculations for the sedimentary sites. Sedimentary site mineral weathering was instead calibrated such that Ca leaching fluxes and concentrations matched those observed after an initial calibration of soil solution acid-neutralizing capacity.

Process-model calibration follows a hierarchical structure where subsystems with the highest degree of model influence are calibrated first, and the dependent subsystems are calibrated afterward (Munson et al. 1992). The order of subsystem calibration was as follows: hydrology (water yield, evaporation), throughfall and deposition (throughfall concentrations), soil organic matter dynamics (C decomposition, DOC fluxes), N-cycle dynamics (N release), anion chemistry (adsorption, concentrations, and fluxes) and finally cation chemistry (CEC, concentrations, fluxes, and mineral weathering). Once a subsystem is calibrated, model parameters are "locked-in," and the succeeding subsystem is calibrated. A selection of only a few parameters was chosen to calibrate each subsystem to avoid the potential to generate model errors or endless recursive calibration (Sverdrup 1996). The logic behind this calibration process has been described thoroughly in the NuCM and NutsFor user manuals (Munson et al. 1992; Kvindesland 1997; Siah 2022).

Sedimentary calibration

Sedimentary sites were calibrated using soil solution concentrations of major nutrient cations and anions and exchangeable soil chemistry for all cations and Bray-P extractable phosphate (Perakis et al. 2006, 2013). Sedimentary mineral weathering fluxes were calibrated by changing the weatherable mineral surface area parameter until either (a) monthly soil solution cation concentrations (and by association leaching fluxes) matched those observed, or (b) annual nutrient fluxes were within 15% of those observed. Calibration was accepted for this second criteria if the average simulated soil solution concentrations of dissolved species were sufficiently close to the average observed soil solution concentrations at each site, as determined by calibration statistics. The normalized average error (NAE) and normalized mean absolute error (NMAE) statistics were calculated for soil solution concentrations of each species for the 20 and 100 cm lysimeters measured, a NME of less than or equal to ±0.15 or an NMAE of below 0.6 was considered sufficient to end calibration.

Basalt calibration

We used known mineral weathering fluxes of Ca to calibrate our basaltic sites (Hynicka et al. 2016). Fluxes were determined via isotope and element ratio end-member mixing calculations, based on well-constrained atmospheric deposition chemistry and fluxes, as well as foliar chemistry and rock chemistry for the LNB and HNB sites (Table 1, and Hynicka et al. 2016, also see Perakis and Pett-Ridge 2019). The weatherable mineral area parameter was calibrated from initial parameterization until simulated weathering fluxes matched calculated fluxes (2.87 kg Ca ha^{-1} $year^{-1}$ low N basalt (site 19) and 1.05 kg Ca $ha^{-1}yr^{-1}$ high N site (site RR1)).

Analysis of model outputs

Per-rotation biomass yields were tracked over time. The per-rotation yield was compared to the "expected" yield determined via a separate set of auxiliary simulations. In these auxiliary simulations, sites were enriched with base cations, S, and P, and allowed to grow with N limitation as the only constraint on tree growth. The maximum per-rotation biomass achieved for low N and high N sites was then extracted from these auxiliary simulation data and added as a point of reference in the per-rotation biomass plots. Maximum potential yield was based on CIPSANON reference growth rates of a stand with Bruce' Site Index of 80 (Joo et al. 2020). Fertilizer additions were modeled in a separate set of simulations, testing whether the addition of primary limiting nutrients would elicit growth responses in simulated stands. Tracking rotation yields allows for the approximate time period and degree of nutrient limitation to be identified. It also allows for comparisons between simulated yield and expected yields.

Nutrient limitation was represented through calculation of potential uptake (PU) and actual uptake (AU) quantities of nutrients, with declines in AU (relative to PU) diagnosing both the limiting nutrient and the degree to which it is limiting. Potential uptake for each nutrient is defined as the biomass increment multiplied by the tissue's stoichiometry, minus translocation and foliar leaching. Actual uptake for each nutrient is what the stand can extract from soil given model calculated soil parameters, minus the simulated translocation and foliar leaching. The difference between PU and AU ("uptake deficit'', in kg ha^{-1} yr^{-1}) serves as a metric of nutrient limitation (Eq. 1). In general, the higher the uptake deficit is, the greater the degree of nutrient limitation. To facilitate comparison across nutrients, each of which has unique flux requirements for tree growth, a "relative uptake deficit" was quantified as the ratio of the uptake deficit to PU (Eq. 2).

$$\text{Uptake deficit} = PU - AU \tag{1}$$

$$\text{Relative uptake deficit (\%)} = \frac{100 * (PU - AU)}{PU} \tag{1}$$

The relative uptake deficit thus reflects the proportion of N, Ca, Mg, K, S, and P that modeled stands needed for "optimal" growth but could not obtain. The primary limiting nutrient is identified as the nutrient that is most limiting to tree growth at a specific point in time, as defined by the magnitude of the relative uptake deficit.

We quantified the cumulative change in soil nutrient pools by calculating total nutrient loss over 525 years of simulated time. Nutrient losses occur due to leaching and biomass removal in harvest. Leaching losses were further subdivided into "background leaching" and "harvest-stimulated leaching" quantities, to separate excess leaching caused by forest harvest from continuous background leaching. Thus, "harvest-stimulated leaching" indicates only the excess loss that occurs above background levels during forest recovery in the 10 years immediately after logging, which is based on regional field data (Devine et al. 2012). We did not consider effects of potential post-harvest changes in microclimate, which are inconsistent across our study region (Gallo 2017, Littke et al. 2020a). Background leaching was calculated as the average leaching rate after 10 years, which was then applied across all years, to provide a baseline for calculating excess harvest-stimulated leaching (Eq. 3).

$$\text{Harvest-stimulated leaching} = \left(Post_{R_1} - \frac{10 * Back_{R_1}}{21yr}\right) + \Sigma_{i=2}^{n=11}\left(Post_{R_i} - \frac{10 * Back_{R_i}}{32yr}\right) \tag{1}$$

In the calculation, R_i is the rotation "i", "Post" is the 10-year post-harvest total leaching for each rotation, and "Back" is the cumulative background leaching for the rotation. The first half of Eq. 3 only applies to the first rotation R_1, because R_1 is computationally shorter than subsequent rotations, because the model is initialized at age 19 and grows for 21 years before harvest. Thus, the 21 year denominator of R_1 generates a 10-year leaching rate for the first harvest (a rotation that starts at stand age 19, thus 21 years of simulated growth). The 32 year denominator for all other rotations indicates the 32-year time frame considered the background leaching period, as the first 8 years of each rotation are added to the 2-year post-harvest 'gap' period to get the 10 year post-harvest interval. Overall, Eq. 3 estimates the cumulative amount of "harvest-stimulated leaching" that occurs in excess of "background leaching" after correcting for stand age in rotation 1, and for all subsequent rotations out to 525 years.

Sensitivity analyses

Sensitivity analyses were conducted to determine how varying six key model input and parameter values influenced five different model outputs. The inputs and parameters that we varied in this sensitivity analysis included the atmospheric deposition rate, exchangeable pool size, potential tree growth rate, primary mineral surface area (which affects total weathering), percent nitrification, and soil organic matter P access (Table S6). The six inputs and parameters were tested individually following a simple one-at-a-time sensitivity approach (Hamby 1994; Saraiva et al. 2017). Values were varied +/− 50% of base case values, with the exception of potential tree growth which was varied +/− 10% of the base case value (see Appendix for justification). We evaluated their impact on five model outputs including cumulative biomass yield, Ca and K weathering, and Ca and K leaching. The focus on biomass yield examines nutrient limitation, whereas the focus on Ca and K was motivated by our findings that these two nutrients were limiting to tree growth in high N sites. Overall, the goal of this analysis was not to precisely quantify the most controlling input or parameter over the whole model. Instead, the purpose was to qualitatively observe how reasonable variation in key model inputs and parameters might affect changes in model outputs that are important to nutrient limitation and depletion.

Results

Calibration results

Most of the simulated annual nutrient fluxes were adequately (within 15% of observed) matched to that of the observational data from the field sites for the ~2-year timeframe represented (Table 3). Calculated NAE and NMAE values were of varying adequacy (Table S7). In some cases, Na^+, Cl^-, Al, and low concentrations of inorganic N species were difficult to calibrate effectively due to underlying limitations in the model or calibration datasets. Due to reliably dry

Table 3 Model fit of annual leaching (kg ha^{-1} year^{-1})

Site	Leaching	Depth	Ca	Mg	K	Na	NO$_3$	NH$_4$	DON	TP	DOC	SO$_4$	Cl	Al
LNS	Simulated	20	12.6	9.2	5.4	36.8*	0.068	0.328	1.411	0.043	32.5	3.4	83.8	0.0102*
		100	7.0	6.7	2.6	31.1	0.015*	0.237	0.621	0.021	9.4	5.3	46.5	0.0052*
	Observed	20	12.2	8.9	5.6	43.6	0.074	0.307	1.472	0.042	29.1	3.7	82.0	0.5047
		100	7.0	6.4	2.3	29.0	0.110	0.228	0.691	0.019	9.0	5.3	44.1	0.1842
HNS	Simulated	20	17.0	20.1	1.1	34.5*	11.729	2.996*	1.086	0.023	20.8	8.6	82.0*	0.0689*
		100	10.5	12.6	1.1	44.8*	6.927	1.552*	0.081*	0.032	12.6	7.8	50.0*	0.0159*
	Observed	20	17.2	19.4	1.2	101.2	12.296	0.316	1.088	0.020	20.2	8.6	172.8	1.0999
		100	10.2	12.1	1.1	74.5	6.526	0.228	0.736	0.032	11.7	7.5	112.8	0.2273

This table compares simulated and observed soil leaching fluxes of major nutrients, at the 20 and 100 cm depths for the low N sedimentary (LNS) and high N sedimentary (HNS) sites. Observational data was not available for basalt sites

*Indicates that fluxes for a particular species and depth could not be simulated adequately summer conditions causing a lack of lysimeter porewater chemistry data (Perakis et al. 2013), calibrations of porewater chemistry were limited for summer months, but this did not affect total fluxes on annual and greater timescales. Some very low concentration species such as Al were not calibrated well, with the poorer fit likely due to difficulty in accurate measurement, or the limitation that NutsFor does not contain organic-Al chemical speciation. The calibration of Na^+ and Cl^- was less successful at the high N site, likely because the high N field sites tend to be closer to the coast where marine aerosol inputs are higher. Even though low rates of N leaching were difficult to simulate with high accuracy, the model did capture large differences in NO_3^- observed between low N vs. high N sites (Table 3). High N sites showed higher NO_3^- mobility, but lower NH_4^+ and DON mobility, whereas low N sites showed higher NH_4^+ and DON mobility, but lower NO_3^- mobility.

Biomass

In model simulations, low N sites were initially able to reach their theoretical maximum biomass growth rate (i.e., without nutrient limitation), whereas high N sites were consistently beneath the maximum potential biomass (Fig. 2). High N sites displayed a sharp decline in biomass yield after the first rotation on both types of bedrock. Succeeding rotations never reached first rotation yields (Fig. 2, panels B and D).

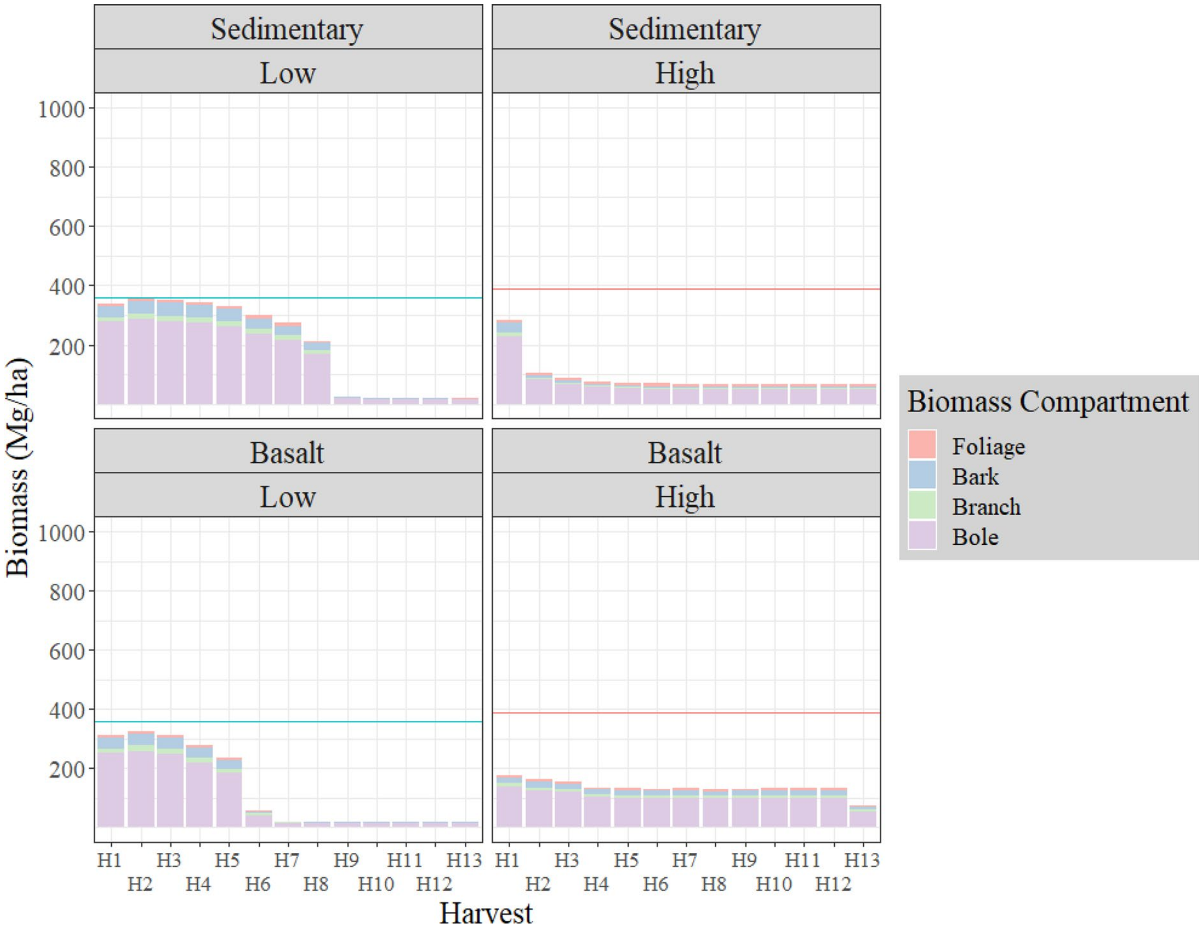

Fig. 2 A site comparison of Douglas-fir total-stand biomass for every harvest event H1-H13, over 525 years. Biomass is separated into Foliage, Bark, Branch, and Bole pools. The red line shows the maximum potential biomass of high N sites, and the blue line the maximum potential biomass of the low N sites. See Methods for more information about the site index. H1 refers to the first harvest cycle, which starts mid-cycle (year 19–40), H2 refers to the second harvest cycle (year 40–80), etc.

In contrast, low N sites maintained more consistent growth over time (Fig. 2A, C). While low N sites generally showed a more gradual biomass decline than high N sites, low N sites also displayed a severe drop in tree growth after five to eight rotations (~ 180 to 300 years), stabilizing to low values < 50 Mg·ha^{-1} biomass accrued per rotation.

Nutrient dynamics

The identity of limiting nutrients varied in our simulations depending on initial soil N content, bedrock type, and time (i.e., successive harvest cycles). We therefore focus on these limiting nutrients: N, Ca, K, and P. Two other macronutrients, Mg and S, did not emerge as limiting in any of our analyses. In all scenarios, cumulative inputs of Mg and S from atmospheric deposition and mineral

Table 4 Cumulative soil nutrient dynamics over 525 years (kg·ha^{-1})

Site	Nutrient	Inputs		Internal Cycling					
		Atmospheric Deposition	Weathering	Total Uptake	Total Litterfall	Total Mineralized	Foliar Leaching	Δ Soil Pool	Inputs/Uptake
LNS									
	Ca	775	645	5198	2371	3742	300	− 1977	0.3
	Mg	1193	503	1285	764	953	144	− 901	1.3
	K	473	280	6140	3091	3843	1369	− 571	0.1
	N	2165	n.a	10,107	6282	9034	0	− 1676	0.2
	P	50	217	1216	841	1570	0	78	0.2
	S	4991	n.a	1375	1057	1430	0	263	3.6
LNB									
	Ca	775	1986	4051	2199	3182	209	− 1117	0.7
	Mg	1193	1157	1050	709	843	100	− 936	2.2
	K	473	286	4788	2824	3316	930	− 327	0.2
	N	2165	n.a	8094	5800	7654	0	− 1203	0.3
	P	50	278	1056	800	1385	0	200	0.3
	S	4991	n.a	999	964	1292	0	2151	5.0
HNS									
	Ca	775	124	2686	1407	2053	285	− 232	0.3
	Mg	1193	127	960	557	719	168	− 174	1.4
	K	473	188	4932	2251	2934	1597	− 220	0.1
	N	2165	n.a	8895	5954	9463	0	− 2543	0.2
	P	50	53	1015	699	1476	0	18	0.1
	S	4991	n.a	785	864	1015	0	279	6.4
HNB									
	Ca	775	825	3937	1739	2841	342	− 57	0.4
	Mg	1193	467	1109	617	806	181	− 58	1.5
	K	473	87	5021	2251	2906	1557	− 25	0.1
	N	2165	n.a	10,139	6609	10,201	0	− 3584	0.2
	P	50	99	1136	772	1639	0	8	0.1
	S	4991	n.a	1001	1027	1062	0	748	5.0

N and S have no values for weathering input because no S– or N-bearing minerals were included in the minerals list

Δ Soil Pool is the sum of Inputs minus the sum of outputs, representing the change in total soil nutrients over the entire simulated period

Table 5 Cumulative nutrient losses and adsorption over 525 years (kg·ha^{-1})

Site	Nutrient	Nutrient Losses				
		Harvested	Leaching	Harvest-Stimulated Leaching	Total	Δ Adsorbed pool
LNS						
	Ca	1301	2161	– 65	3396	n.a.
	Mg	213	2450	– 67	2596	n.a.
	K	972	368	– 16	1324	n.a.
	N	2253	1021	566	3841	n.a.
	P	182	1	7	189	664
	S	798	4019	– 90	4728	1178
LNB						
	Ca	811	3029	39	3878	n.a.
	Mg	133	3142	11	3286	n.a.
	K	592	498	-5	1086	n.a.
	N	1301	1350	716	3368	n.a.
	P	122	1	4	127	687
	S	500	2413	– 73	2840	2977
HNS						
	Ca	399	147	586	1131	n.a.
	Mg	79	1249	165	1493	n.a.
	K	362	519	0	882	n.a.
	N	874	2330	1504	4708	n.a.
	P	73	6	– 2	76	647
	S	321	4460	– 68	4712	900
HNB						
	Ca	733	185	740	1657	n.a.
	Mg	133	1403	182	1718	n.a.
	K	553	25	8	586	n.a.
	N	1431	2088	2230	5749	n.a.
	P	124	6	– 4	127	1094
	S	494	3842	– 92	4243	1396

Harvest-stimulated leaching is the total amount of leached nutrient in excess of the leaching calculated during non-harvest years. Ca, Mg, K, and N were not subject to adsorption in the model

weathering exceeded net plant uptake (Table 4). Biomass removal and leaching did cause net loss of Mg from the soil exchangeable pool (Table 4), and appreciable soil S sorption also occurred (Table 5). However, sustained inputs of Mg and S were sufficiently large that neither element emerged as limiting to tree growth, as indicated by consistently low values of relative uptake deficit (Fig. 3).

Nitrogen

Soil N status determined the occurrence of N limitation as inferred from relative uptake deficits. Low N sites on both basaltic and sedimentary bedrock were primarily N-limited in the first rotation and several succeeding rotations, as indicated by a higher relative uptake deficit for N than for other nutrients (Fig. 3A, C). In contrast, high N sites never experienced primary N limitation. The magnitude of N release from organic matter decomposition differed substantially in low N vs. high N simulations, but there were similar patterns of plant N uptake and N leaching. At low N sites, N mineralization (from litter, SOM, and microbial pools) and atmospheric N deposition closely matched that of gross N uptake by trees throughout simulated time (Table 4), leading to low N leaching loss (Table 3). Over 525 years, low N sites lost 1676 kg N ha^{-1} from the soil at the sedimentary site,

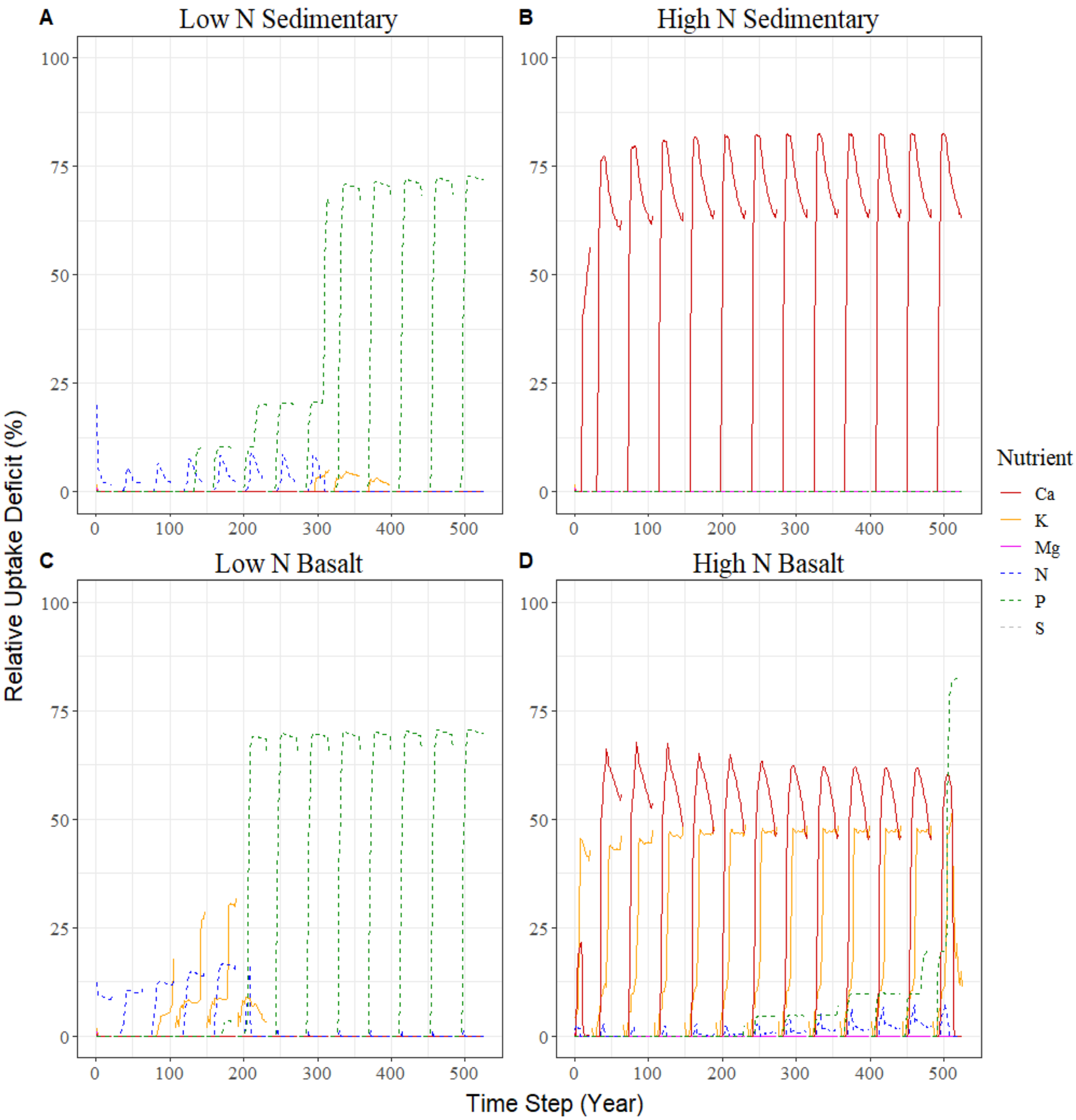

Fig. 3 Relative nutrient uptake deficit, defined as the difference between potential nutrient uptake and actual nutrient uptake, divided by the potential uptake, in percent units. Base cation nutrients are represented with a solid line, and non-base cations with a dashed line. Oscillations reflect harvest events

and 1203 kg N ha^{-1} from the soil at the basalt site (Table 4). This contrasts with the high N sites, where decreases in the soil N pool were larger, with a reduction of 2543 kg N ha^{-1} from the soil at the sedimentary site, and 3584 kg N ha^{-1} from the soil at the basalt site (Table 4).

Harvest generally stimulated additional N leaching, with the magnitude varying by soil N content and bedrock type (Table 5). Most N loss from the low N sedimentary site occurred via biomass removal, whereas the low N basalt site lost a comparable fraction of N to both biomass removal and leaching. In contrast, high N sites lost most N to leaching (81% and 75% of total N loss, for high N sedimentary and basalt, respectively) (Table 5). Although background leaching accounted for most N loss at high N sites, harvest stimulated 19–25% of the total N loss via leaching (high N sedimentary and basalt, respectively).

Calcium

In high N sites, relative uptake deficits of nutrients indicated that the sedimentary site was primarily Ca limited whereas the basalt site was Ca and K limited (Fig. 3B and D). The HNS site maintained consistent Ca limitation both within and across rotations for the full 525-year simulation (Fig. 3B). In contrast, the HNB site generally displayed modest K limitation early in rotations, switching to Ca limitation later in rotations, with larger overall uptake deficits for Ca than for K throughout the 525-year simulations (Fig. 3D).

Calcium losses to leaching were greatly accelerated by harvest at high N sites, but not at the low N sites. High N sites lost most of their Ca during post-harvest periods, whereas low N sites had consistent Ca leaching throughout simulated time (Fig. 3; Table 5). Unlike N, Ca leaching did not always increase post-harvest at low N sites.

Calcium weathering inputs were higher in basalt sites than in sedimentary sites, at both low and high N. Calcium leaching losses were also higher in basalt sites than in sedimentary sites, regardless of soil N contrasts. Compared by soil N status, basalt sites leached 1.3 times (High N sites) and 1.4 times (low N sites) more Ca than sedimentary sites (Table 5). Basalt sites showed higher gross Ca losses (Table 5), but also exhibited smaller reductions in the size of the soil Ca pool (Table 4).

Potassium

While low N sites were primarily N-limited, the low N basalt site shifted to K limitation after ~100 years (Fig. 3C). The high N basalt site was K limited at the onset of simulation, but in subsequent years shifted between K and Ca limitation within harvest cycles (Fig. 3D).

Biomass removal was the largest pathways of K loss for all but the high N sedimentary site (Table 5). Background leaching was also significant for K loss at the low N sites, and for the high N sedimentary site. Harvest-stimulated leaching, in contrast, was not significant for K loss at any site. Overall, cumulative losses of K were greater at sedimentary sites than at basalt sites, leading to larger reductions in soil K pools in sedimentary than basalt sites over the 525-year timeframe (Tables 4 and 5).

Phosphorus

Low N sites on both bedrock types were initially N limited, and shifted over time to P limitation, overshadowing both N and K limitation after ~200 years at the low N basalt site and after ~300 years at the low N sedimentary site (Fig. 3, panels A and C). The high N basalt site experienced minor P limitation after ~250 years, with P becoming limiting only in the final rotation (Fig. 3D). In contrast to base cations and N, the total soil P reservoir increased across all sites over the 525 simulated years (Table 4). Phosphorus limitation was not driven by harvest as with other nutrients, but was associated with a loss of soil organic P and transfer to sorbed P over time (Table 5). Sulfur also accumulated in the soil reservoir over time in model simulations, but no S limitation was evident.

Sensitivity analysis

Biomass yield in high N sites was very sensitive (−27 to 49%) to ±50% changes in atmospheric deposition and moderately sensitive (−25 to 9%) to ±50% changes in soil exchangeable base cation concentrations. In contrast, biomass yield in low N sites was relatively insensitive (<15% change) to all input and parameter variations (Table S8 and Appendix). Weathering release of K at all sites was highly insensitive (<5% change) to all input and parameter variations. Weathering of Ca was sensitive only to primary mineral surface area, responding approximately ±40% to ±50% changes in primary mineral surface area. Cumulative leaching of Ca was most sensitive to changes in atmospheric deposition at high N sites and to changes in primary mineral surface area and the size of the exchangeable pool in basaltic sites. Leaching of K exhibited the greatest sensitivity in basaltic sites and was influenced most by changes in atmospheric deposition and the exchangeable pool size. Neither cumulative biomass growth, Ca or K weathering, nor Ca or K leaching were consistently sensitive to changes in changes in tree growth, percent nitrification and SOM-P access.

Discussion

Model evaluation

We used the process-oriented model NutsFor to estimate potential changes in forest growth and nutrient cycling over multiple harvest cycles. While it is not possible to specifically validate NutsFor performance in response to harvest, because the calibration data did not span entire harvest cycles, we can look at prior model performance, pre-harvest calibration, sensitivity analyses, and comparisons of the model output to empirical studies in the same region as a means of evaluation. NutsFor was built from a combination of existing models: the NuCM and ForSAFE models that simulate pools and fluxes of chemical species in forests, the WATfor water balance model, and the PROFILE model of mineral weathering. Each of the component models have a history of successful validation in other forest ecosystem studies (e.g. Jönssen et al., 1995; Johnson et al. 1995; Fenn et al. 1996; Legout et al. 2016). In addition, a previous application of the combined NutsFor model successfully reproduced major element behavior in a nutrient-poor forest site in the Morvan Mountains in France (van der Heijden et al. 2017a, b).

Model calibrations were based on comparisons against soil porewater chemistry and flux data for the two sedimentary sites (Perakis et al. 2013) and against weathering rates calculated from isotopic mass balance for the two basaltic sites (Hynicka et al. 2016, (*and see methods in* Perakis and Pett-Ridge 2019)). As two different approaches were used for determining weathering fluxes, depending on bedrock type, the interpretation of model results based on varying N status within a bedrock type may be more robust than the comparisons between bedrock types. We note, however, that both approaches are similar in that they are reliant on measurements reflecting mobile base cations (rather than changes in soil phases), and both approaches are similar in that they determine weathering fluxes on a ~ 1–3 year timescale. These four sites are well-representative of forests of the Oregon Coast Range (Perakis et al. 2006; Hynicka et al. 2016), though lower N sites occur in other areas of the Pacific Northwest (Littke et al. 2016). The model calibration was successful in reproducing porewater chemistry and fluxes for key nutrient species including Ca, Mg, and K. It also successfully reproduced the large NO_3^- flux at the high N field site, where substantial NO_3- leaching occurs, as well as the small NO_3^- leaching flux at 20 cm depth at the low N field site (Table 3). The weathering flux calibration at the basaltic sites was also successful. The sensitivity analysis results indicate that simulations of biomass yield, base cation leaching and weathering were not particularly sensitive to model parameterizations of tree growth, nor to the internal dynamics of N and P cycling in the model. This suggests that the newly added parameter of direct tree N and P uptake from soil organic matter did not have a strong influence on the model outputs. Instead, model outputs were most sensitive to base cation nutrient availability via atmospheric deposition, available mineral surface area (which affects weathering rate), and the initial reservoir of soil exchangeable cations. The relative insensitivity of the model to K weathering, despite the emergence of K limitation on basalt sites, is reasonable given the low abundance of K-bearing minerals in Oregon Coast Range soils, as well as the low mass fraction of K within those minerals (Tables S1 through S4).

The NutsFor model simulations indicate that forest nutrient dynamics depend on all three factors that we investigated: site N status, bedrock type, and harvest. We also observed interactive effects among these factors, particularly at high N sites with simulated forest harvest. Our application of NutsFor to the Oregon Coast Range extends application of the model to high N sites and to explicit examination of forest harvest effects on long-term nutrient dynamics. Model limitations, such as biogeochemical processes absent from the model and uncertainties for some input variables, are discussed in later sections. We also note that our simulations focused on nutrient cycling and limitation, and do not address the full suite of non-nutrient stressors that can influence forest growth. For example, high N forests of the Coast Range support higher loads of the native fungal pathogen *Nothophaeocryptopus gaeumannii*, which can reduce tree growth

(Waring et al. 2000). Likewise, the model does not evaluate potential site differences in summer drought that could arise if soil N and Ca fertility affect plant water use and soil water depletion (Cornejo-Oviedo et al. 2017; Lanning et al. 2019). Such multi-factor interactions highlight how the preferential accumulation of one nutrient (in this case, high N from legacies of biological N fixation) could lead to nutrient imbalances that lower forest productivity and promote eventual ecosystem retrogression (Peltzer et al. 2010).

Longer-term modeling exercises have inherent uncertainty, but our overall finding that high N sites can display severe base cation deficiency is consistent with predictions from current observational and experimental data in the region (Perakis et al. 2006; Hynicka et al. 2016; Mainwaring et al. 2014). Uncertainties in model structure and parametrization will reduce the accuracy of soil fertility predictions over time, but given the strongly contrasting sites considered in our simulations, the model remains a valuable tool to assess likely trends and understand drivers of soil fertility change. The overall concordance of model behaviors with field and experimental data suggests that our simulation results provide reasonable indications of both the identity of nutrient limitation and relative nutrient dynamics as a function of N status, bedrock type, and forest harvest over time.

Nutrient limitation and nutrient budgets over time

Comparing rates of nutrient input to plant uptake can identify which nutrient(s) are likely present in excess in the system versus nutrients that have potential to limit plant growth. In the Oregon Coast Range, four key nutrients –N, P, Ca, and K– have lower inputs from deposition and weathering compared to plant uptake (Table 4), suggesting high reliance on internal recycling. Generally speaking, forest ecosystem modeling studies have shown that low ratios of inputs relative to internal cycling can lead to synchronization and co-limitation by multiple elements (e.g. Rastetter et al. 2013). Model simulations of relative nutrient uptake deficit (i.e., the ratio of plant demands to internal and external supply) confirmed these four elements as candidate limiting nutrients (Fig. 3). In contrast, inputs of Mg and S from atmospheric deposition and mineral weathering consistently exceeded plant uptake (Table 4), and neither Mg nor S displayed signs of uptake deficits at any time in any simulations (Fig. 3). Of the four limiting nutrients, the particular identity of the nutrient(s) that limited growth in the model varied with N status, bedrock type, and time elapsed (i.e., number of forest harvest cycles experienced). Multiple nutrient limitation also occurred in some cases, including both N and P, both N and K, and both Ca and K. This finding is broadly consistent with fertilization studies that identify either multiple nutrient limitation and/or within region heterogeneity in nutrient limitation in forest ecosystems (Vadeboncoeur 2010; Wurzburger and Wright 2015; Goswami et al. 2018).

Nitrogen is a critical nutrient that regulates the cycling of other essential elements. However, due to complexity in N cycling, simulation models often struggle to reproduce the observed behavior of various N species (Aber et al. 1997; van der Heijden et al. 2011). Our NutsFor model simulations were effective at capturing N cycling processes that are characteristic of ecosystem N scarcity or abundance. In simulations of contrasting low versus high N sites, the model showed good agreement between simulated and observed nitrate leaching fluxes. In the first century of simulations, low N sites displayed N-limited plant growth and low nitrate leaching, whereas high N sites displayed high nitrate loss (Fig. 3; Table 5) and non-N nutrient limitation (Fig. 3). These findings are consistent with detailed field studies of low versus high N forests in the Oregon Coast Range (Perakis and Sinkhorn 2011; Mainwaring et al. 2014) and more broadly across the Pacific Northwest (Peterson and Hazard 1990; Slesak et al. 2009; Littke et al. 2014) and worldwide (Niu et al. 2016). We note, however, that the low N sites we simulated for the Oregon Coast Range are fairly N-rich and productive, and that even more intense N limitation can occur elsewhere in the Pacific Northwest (Peterson and Hazard 1990; Littke et al. 2016).

High N sites displayed a relatively strong degree of nutrient limitation in NutsFor that was attributable to insufficient base cation availability, primarily of Ca on both types of bedrock, and secondarily of K in basalt sites (Fig. 3 and S3). This simulated Ca limitation at high N sites is supported by field fertilization experiments using Ca-only additions (as $CaCl_2$) at multiple sites across our study area (Mainwaring et al. 2014). While Ca limitation is generally not as common as N or P limitation, it nevertheless occurs in many regions worldwide, especially on highly weathered soils or in areas with histories of acid pollutant deposition (Federer et al. 1989; Mann et al. 1988; Huggett et al. 2007; Likens et al. 1998; Nykvist 2000; Bullen and Bailey 2005; Vadeboncoeur 2010; Bigelow and Canham 2007; Bauters et al. 2022; Vanguelova et al. 2022; Oursin et al. 2023). Our modeled sites differ notably from these by having only very low atmospheric N deposition and moderately weathered soils (Hynicka et al. 2016). Instead, our high N sites display Ca depletion and limitation due to long-term legacies of prior N accumulation from symbiotic N-fixing red alder (Perakis et al. 2011), which accelerates nitrification, soil acidification, mineral weathering, and coupled Ca and nitrate leaching (Homann et al. 1992; Perakis et al. 2013; Perakis and Pett-Ridge 2019). Indeed, Ca leaching at high N sites can be so intense that it exhausts weatherable Ca from soils, with tau calculations that show up to 96% depletion of Ca relative to the total Ca content of fresh bedrock (Hynicka et al. 2016).

Additional factors besides the low initial pool of exchangeable Ca likely contributed to Ca limitation at high N sites. The model was initialized with a 20-year old forest, with potential for rapid biomass growth and associated Ca uptake. Estimated rates of external Ca input from deposition and weathering are insufficient for annual plant Ca uptake, placing particular importance on exchangeable pools as a source of Ca (Table 4). The model also does not account for less-recognized sources of cations in soil besides the typically extracted exchangeable pool, including Ca in Ca-oxalate (Dauer and Perakis 2013; Oursin et al. 2023), rock fragments (Hynicka et al. 2016), sorbed to soil organic matter or non-crystalline secondary minerals (van der Heijden et al. 2017a; van der Heijden et al. 2017b; Bel et al. 2020) or unmeasured forms of atmospheric deposition (Bockheim and Langley-Turnbaugh 1997; Pett-Ridge et al. 2009). However, none of these possible Ca sources alone would likely provide Ca sufficiency. Indeed, our sensitivity analyses found that increasing Ca availability within reasonable bounds for the three main Ca sources individually (atmospheric deposition, mineral weathering, and the soil exchange reservoir) led to only small growth responses and did not alleviate Ca limitation in high N sites (Table S8).

Douglas-fir physiological demands for Ca are typically met through root uptake in the transpiration stream, because resorption of Ca from senescing tissues is widely considered negligible in conifers (McLaughlin and Wimmer 1999; Vergutz et al. 2012). While excess Ca uptake can be sequestered as calcium-oxalate and recycled via litterfall (Borer et al. 2004; Dauer and Perakis 2014), low Ca presents problems for cell integrity, lignin formation, disease resistance, and other functions (McLaughlin and Wimmer 1999). If NutsFor simulations show more sensitivity to low Ca than field-growth trees, it is possible that field trees are adjusting tissue Ca uptake below deficiency levels identified in the literature for Douglas-fir (Walker and Gessel 1991). Across our study area, sites with low soil exchangeable Ca show asymptotic declines in foliar Ca to slightly below deficiency levels (Perakis et al. 2006). Wood is also a significant Ca sink in growing trees, but data on how wood Ca varies with soil Ca are lacking for our region, and no clear pattern existed in the regional Douglas-fir data used to parameterize NutsFor (Binkley et al. 1992; Schowalter and Morrell 2002; Perakis et al. 2013). If trees can form woody tissue with less Ca than assumed in our model (7.5 μmol g^{-1} bole, 63.6 μmol g^{-1} branches), then tree growth could persist at low soil Ca for longer than simulated, though an eventual emergence of Ca limitation remains very likely (Mainwaring et al. 2014).

Bedrock mineralogy was important in structuring base cation limitation in our simulations, leading to Ca limitation on sedimentary bedrock and Ca and K co-limitation on basaltic bedrock. Weathering on basaltic sites supplied more Ca and less K than on sedimentary sites, and provided especially low K relative to tree demands, which intensified K limitation over time especially on high N basaltic soils (Fig. 3). Sedimentary sites, in contrast, had an abundance of K-bearing minerals and higher initial soil K contents (Table 2, S1–S4) that prevented K limitation. In support of these findings, leaching experiments with nitric acid have shown that sedimentary bedrock in the Oregon Coast Range releases more K than basaltic bedrock (Hynicka et al. 2016). Despite this, our simulations of Ca fertilization on high N sedimentary sites drove an immediate shift to K limitation, suggesting important roles for both Ca and K on both bedrock types (Fig. S3). Overall, we conclude that mineral weathering does not keep pace with Ca and K loss in these managed forests, similar to estimates for other temperate forests (Vadeboncoeur et al. 2014). Further, for high N sites, bedrock type exerts a strong influence on whether K versus Ca emerge as single or co-limiting nutrients over the course of multiple forest harvest rotations.

Factors besides mineral weathering could also influence the emergence of K limitation in forests, with biological cycling of K being of particular importance (Tripler et al. 2006). Notably, foliar leaching is higher for K than Ca, and we simulated that leaching ranges from 19 to 32% of tree K uptake versus only 5 to 11% of tree Ca uptake (Table 4). We also observed very different couplings between K and N dynamics in the model than was observed for Ca and N. During post-harvest periods, high N sites showed high Ca leaching, and overall the cumulative harvest-stimulated leaching of Ca exceeding background Ca leaching (Table 5). This reflects known geochemical couplings of N and Ca via acid-base mechanisms, which are stronger than biotic Ca retention in our system (Perakis et al. 2013). In contrast, N and K couplings in our high N simulations appeared to be dominated by biotic processes, as in many forests worldwide (Tripler et al. 2006), with larger fractional K losses occurring via biomass removal than via harvest-stimulated leaching (Table 5).

Our finding that K may be a limiting nutrient in these forests has not been emphasized in prior work; to our knowledge no previous fertilizer trials have shown K limitation in Pacific Northwest forests. However, there is extensive evidence of the occurrence of K limitation in other tropical, temperate, and boreal forests (Stevens et al. 1995; Tripler et al. 2006; Wright et al. 2011; Ouimet and Moore 2015; Sardans and Peñuelas 2015; Schlesinger 2021; Stone and Kszystyniak 1977). Organic matter removal during harvesting in the Pacific Northwest can lower soil exchangeable K, but it has been unclear whether K is depleted enough to be limiting (Littke et al. 2020a). Efficient recycling of K between plants and soils (Vitousek and Sanford 1986) and relatively high K supply from atmospheric deposition can often alleviate K limitation (Vitousek 1984; Chadwick et al. 1999). In our model simulations, sensitivity analyses using + 50% increase in base cation supply from atmospheric deposition, mineral weathering, or mineral abundance showed a wide range of tree growth responses, from a mere + 1% increase (mineral abundance) to + 35% increase (atmospheric deposition) on the high N basalt site (Table S8). This suggests that unmeasured inputs of K in atmospheric deposition (e.g., via fog or dust) could be a potentially significant source of K in these systems. We suggest that K limitation merits keen attention as a concern especially in high N basalt sites. Additional model simulations for a fertilization scenario showed that increases in site K (and Ca) supply within likely model uncertainly are sufficient to at least partially alleviate nutrient limitation (Fig. S3).

The occurrence of P limitation in model simulations at low N sites, but not at high N sites, contrasts with P limitation theory derived from tropical soils (Chadwick et al. 1999; Vitousek et al. 2010), as well as experimental fertilization that shows slight P limitation at some high N sites in the Oregon Coast Range (Mainwaring et al. 2014). As soils age and accumulate N over millennia, the pool of weatherable P is increasingly cycled, occluded, and lost, eventually causing a transition from N to P limitation (Vitousek et al. 2010; Du et al. 2020). However, in the Oregon Coast Range, soils with the most N also contain the most organic P, which could buffer against P limitation in high N sites (Hynicka et al. 2016; Perakis et al. 2017). Consistent with this idea, our simulated low N sites were more prone to P limitation than high N sites (Fig. 3). Phosphorus limitation developed over time in our simulations of low N sites because processes of organic P mineralization, plant P uptake and recycling caused some annual P cycling as phosphate, which was susceptible to adsorption in mineral soil. Roughly 4–8 fold more P was transferred to adsorption on soil minerals than was lost to harvest and leaching in our simulations, in contrast to large off-site losses for N and base cations (Table 5). While all simulated soils tended to gain P due to low leaching losses, most of this P was unavailable due to phosphate adsorption, leading to a gradual depletion of soil organic P and the emergence of P limitation in low N sites (Fig. 3). This finding highlights major knowledge gaps in P nutrition of both accurately defining the plant-available P pool in soil and of understanding whether long-term biological P cycling accelerates the transfer of organic forms of P to sorbed inorganic P in soil. Overall, while N limitation in the model was controlled by variation in soil N accumulation, the model instead shows that P dynamics were controlled by interactions between initial P status, tree uptake, recycling, and adsorption. Improved model representation of mechanisms of biotic access to soil organic P (Zhang et al. 2014; Meeds et al. 2021) is needed to better represent P cycling in NutsFor and in biogeochemical models in general.

Forest management impacts on nutrient sustainability

Our 525-year simulations exceed most planning horizons for forest management, yet they are brief compared to long-term processes of nutrient input and loss that shape landscape-scale heterogeneity in soil biogeochemistry. Soils of the Oregon Coast Range display substantial biogeochemical heterogeneity compared to many other temperate regions, in particular ranging from naturally N-limited to N-saturated due symbiotic N fixation legacies spanning thousands of years (Perakis et al. 2011). Such high N inputs are unlikely to continue in most managed forests of the region, however, as the economics usually favor conifer production and the elimination of competing N-fixing red alder. Consequently, contemporary soil heterogeneity across the landscape represents a range of "starting conditions" for ongoing forest management. However, this underlying variability is rarely captured in coarse-grained analyses of nutrient depletion (de Oliveira Garcia et al. 2018), nor has been used to inform soil nutrition management besides routine N fertilization (Peterson and Hazard 1990; Littke et al. 2014).

We observed a wide range of nutrient depletion in our simulations, sometimes severe, with large declines for Ca, K and N, and declines in potentially available (i.e., non-adsorbed) forms of P. It is noteworthy that our estimated rates of Ca input from atmospheric deposition and mineral weathering could sustain growth and biomass removals for only 1–2 rotations at high N sites, especially given that background variability in soil N enrichment and base cation depletion occurred over millennia of soil development. Atmospheric nutrient deposition has also been declining in many regions (Lajtha and Jones 2013) and future changes in mineral weathering may vary in complex ways due to interactions with elevated CO_2, climate and ecosystem biology (Taylor et al. 2012). At present, it seems unlikely that future nutrient supplies will sustain long-term tree requirements in managed forests of our study area without direct fertilization or changes in forest management. While remedial fertilization is feasible on many sites, using other forms of forest management (rotation lengths, target species) to alleviate nutrient depletion may be difficult in high N sites where soil base cations are already at critical levels (Hynicka et al. 2016) and where high nitrate leaching is likely to persist for centuries (Perakis and Sinkhorn 2011). Our simulations suggest which nutrient(s) require the most monitoring and attention for sustainability in the near term, to detect and minimize potential future nutrient deficiencies to forest growth across this biogeochemically heterogeneous landscape.

The degree to which different nutrients declined over the course of our 525-year simulations varied interactively with soil N status and bedrock type. For N, *absolute* declines in the total soil reservoir were greatest on high N sites due to sustained high nitrate leaching, whereas *relative* declines in soil N were greater on low N sites due to harvest effects on lower starting N pools. For P, both absolute and relative declines in potentially available (i.e., non-adsorbed) soil pools were equal or greater on low N sites, due to higher sustained tree growth and subsequent P removal to harvest as well as adsorption. For base cations, the *absolute* decline in the size of the soil reservoir was greater for low N sites, though this primarily reflected their larger starting pool compared to high N sites (Table 4). The *relative* decline in the soil base cation reservoir was greater in the high N sites, indicating their greater sensitivity to loss. These losses mirrored the emergence of severe and persistent Ca limitation in sedimentary sites and a shift from Ca to both Ca and K limitation in basaltic sites with harvests over time. Thus, while natural processes of long-term N enrichment have improved short-term tree growth in some cases (Gessel et al. 1973, Stegemoeller and Chappell 1989, Littke et al. 2014), our simulations suggest that at least some of these initially productive high N forests are also poised to severe depletion of Ca and/or K within decades of continued intensive forest management. We expect these risks are most acute in forests where long-term soil N enrichment has led to the exhaustion of weatherable rock nutrients, and has caused forests to rely on dilute nutrient inputs from atmospheric deposition (Hynicka et al. 2016).

The pathway of nutrient loss (i.e., background leaching, biomass removal, or harvest-induced leaching) can influence whether changes in forest management promote nutrient sustainability. In field studies, harvest-induced losses of N, Ca, and K occur both via the removal of nutrient-containing biomass

(Duchesne and Houle 2008) and by accelerated leaching after logging (Brown et al. 1973; Mann et al. 1988; Likens et al. 1994; Devine et al. 2012), whereas losses are much less in the absence of disturbance (Vitousek and Reiners 1975). In our simulations, harvest-related loss pathways make up a large fraction of the total losses for N, Ca, and K when compared to background leaching. Generally, the sum of biomass harvest and harvest-stimulated leaching removed a greater amount of N and K than did the background leaching, and the same was also true for Ca at high N sites (Table 5). This raises the possibility that less frequent logging could be effective in conserving these nutrients (Siah *in prep*). At a finer grain, the proportion of nutrients lost to biomass removal is much higher for K than Ca, which suggests that leaving nutrient-rich bark, branches, and foliage onsite following logging may forestall K limitation more than Ca limitation (Littke et al. 2020 b, Siah et al., *in prep*). Potential Ca limitation is therefore likely to be a more persistent problem, requiring novel fertilization, less frequent harvest, or selection of tree species with low Ca demands to maintain productivity. Where management can sustain and even increase soil exchangeable Ca to where it no longer severely limits growth, then tree biological control of coupled Ca–N cycling may also reduce excess N leaching (Groffman and Fisk 2011; Perakis et al. 2013), at least between large leaching pulses that occur when logging high N sites (Brown et al. 1973).

Conclusion

In this study, the Nutrient Cycling in Forest Ecosystems Model (NutsFor) was used to evaluate how site differences in soil N enrichment and bedrock type affect long-term nutrient supply in Pacific Northwest Douglas-fir forests of the Oregon Coast Range under a common 40-year bole-only harvest regime. The model simulations indicate that low N sites display N-limited forest growth and low nitrate leaching, whereas high N sites display other non-N nutrient limitations on forest growth and nitrate loss. At high N sites, model simulations with sedimentary bedrock revealed a rapid onset of Ca limitation of forest growth, while model simulations with basaltic bedrock found both Ca and K limitation. Both biomass removal and harvest-stimulated leaching were major nutrient loss pathways for N, Ca, and K in simulations. Specifically, the proportion of nutrients lost to biomass removal was higher for K than Ca, while the proportion lost to harvest-stimulated leaching was higher for Ca than for K.

Our simulations are the first to use a process-based biogeochemical model to evaluate multi-nutrient interactions and limitation in intensively managed forests of the Pacific Northwest. The NutsFor model was modified for this study to include disturbance-namely forest harvest rotations. The ability of the model to simulate nutrient responses over multiple harvest rotation cycles suggests that the model could also be utilized to investigate other types of forest disturbance in future studies elsewhere. We show that, within just one or two 40-year rotations, high N sites underlain by basalt bedrock can become severely Ca and K limited, while sedimentary sites become Ca limited. Low N sites show expected initial N limitation, with emergence of K limitation after ~ 100 years on basalt, and P limitation after ~ 200 to 300 years on both rock types. While the model was parameterized using data from Oregon Coast Range forests, many of the underlying behaviors emerge from general biogeochemical relationships of N with bedrock chemistry. Consequently, the findings of this work may be conceptually and qualitatively useful in other forests that display N saturation and base cation depletion, such as forests polluted by atmospheric N deposition (Peterjohn et al. 1996d) rich tropical forests growing on moderately weathered soils (Lu et al. 2018). The wide range of limiting nutrients that we simulated across a relatively small geographic area also illustrate the importance of capturing local heterogeneity in soil conditions, as the most sensitive sites of greatest concern for sustainability can elude more coarse-grained spatial analyses (de Oliveira Garcia et al. 2018).

The simulations shown here illustrate the key role that bedrock type (and associated mineral abundances) can play in shaping nutrient limitation at high N sites. For instance, high N sedimentary sites had less severe K limitation than basalt sites, while the reverse was true for Ca. Nevertheless, variation in mineral weathering was less important than atmospheric deposition in shaping long-term base cation supply at high N sites. Overall the model generally represented base cation cycling well, following heuristic principles of internal nutrient redistribution as sites underwent base cation depletion. The high likelihood of simulated base cation limitation differs from conventional theories that emphasize a long-term shift from N to P limitation under high N conditions (Chadwick et al. 1999; Vitousek et al. 2010; Du et al. 2020) and is more akin to effects of acidic deposition that preferentially deplete soil base cations, especially Ca (Niu et al. 2016). The findings show that harvest is the primary driver of soil nutrient depletion on short (multi-decadal) time scales, driving forests towards base cation limitation within 1 to 2 harvest cycles on high N sites.

Acknowledgements We thank Doug Maguire, Kim Littke and anonymous reviewers for suggestions that improved the manuscript.

Funding The research was supported by NSF award EAR – 2045135 awarded to J.C. Pett-Ridge and S.S. Perakis.

Data Availability The datasets generated during and/or analyzed during the current study are available in the GitHub repository, https://github.com/Coffee-Powered-Scientist/NutsFor_OR2.

Declarations

Author Contributions All authors contributed to the study conception and design. Modeling, data collection and analysis were performed by Kaveh Siah, with input from Julie Pett-Ridge, Steven Perakis, and Gregory van der Heijden. The first draft of the manuscript was written by Kaveh Siah and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest The authors have no 10.1007/s10533-023-01039-6 relevant financial or non-financial interests to disclose. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Code Availability The code written to generate figures and analyze data is located in the GitHub repository, https://github.com/Coffee-Powered-Scientist/NutsFor_OR2.

References

Aber JD, Ollinger SV, Driscoll CT (1997) Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. Ecol Model 101:61–78. https://doi.org/10.1016/S0304-3800(97)01953-4

Anderson SP, Dietrich WE, Brimhall GH Jr (2002) Weathering profiles, mass-balance analysis, and rates of solute loss: linkages between weathering and erosion in a small, steep catchment. Geol Soc Am Bull 114(9):1143–1158. https://doi.org/10.1130/0016-7606(2002)114%3C1143:WPMBAA%3E2.0.CO;2

Bauters M, Janssens IA, Wasner D et al (2022) Increasing calcium scarcity along afrotropical forest succession. Nat Ecol Evol 6(8):1122–1131. https://doi.org/10.1038/s41559-022-01810-2

Bel J, Legout A, Saint-André L, Hall SJ, Löfgren S, Laclau JP, van der Heijden G (2020) Conventional analysis methods underestimate the plant-available pools of calcium, magnesium and potassium in forest soils. Sci Rep 10(1):1–13. https://doi.org/10.1038/s41598-020-72741-w

Berendse F, Aerts R, Bobbink R (1993) Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In: Vos CC, Opdam P (eds) Landscape ecology of a stressed environment. Springer, Dordrecht, pp 104–121. https://doi.org/10.1007/978-94-011-2318-1_5

Bigelow SW, Canham CD (2007) Nutrient limitation of juvenile trees in a northern hardwood forest: calcium and nitrate are preeminent. For Ecol Manage 243(2–3):310–319. https://doi.org/10.1016/j.foreco.2007.03.027

Binkley D, Sollins P, Bell R et al (1992) Biogeochemistry of adjacent Conifer and Alder-Conifer stands. Ecology 73(6):2022–2033. https://doi.org/10.2307/1941452

Binkley D, Cromack K, Baker DD (1994) Nitrogen fixation by red alder: biology, rates, and controls. In: Hibbs DE, DeBell DS, Tarrant RF (eds) The biology and management of red alder. Oregon State University Press, Oregon, pp 57–72

Bockheim JG, Langley-Turnbaugh S (1997) Biogeochemical cycling in coniferous ecosystems on different aged marine terraces in coastal Oregon. J Environ Qual 26:292–301. https://doi.org/10.2134/jeq1997.00472425002600010041x

Borer CH, Schaberg PG, DeHayes DH, Hawley GJ (2004) Accretion, partitioning and sequestration of calcium and aluminum in red spruce foliage: implications for tree health. Tree Physiol 24:929–939. https://doi.org/10.1093/treephys/24.9.929

Brown GW, Gahler AR, Marston RB (1973) Nutrient losses after clear-cut logging and slash burning in the Oregon Coast Range. Water Resour Res 9:1450–1453. https://doi.org/10.1029/WR009i005p01450

Bullen TD, Bailey SW (2005) Identifying calcium sources at an acid deposition-impacted spruce forest: a strontium isotope, alkaline earth element multi-tracer approach. Biogeochemistry 74:63–99. https://doi.org/10.1007/s10533-004-2619-z

Chadwick OA, Derry LA, Vitousek PM et al (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397:491–497. https://doi.org/10.1038/17276

Cornejo-Oviedo EH, Voelker SL, Mainwaring DB, Maguire DA, Meinzer FC, Brooks JR (2017) Basal area growth, carbon isotope discrimination, and intrinsic water use efficiency after fertilization of Douglas-fir in the Oregon Coast Range. For Ecol Manag 389:285–295. https://doi.org/10.1016/j.foreco.2017.01.005

Dauer JM, Perakis SS (2013) Contribution of calcium oxalate to soil-exchangeable calcium. Soil Sci 178(12):671–678. https://doi.org/10.1097/SS.0000000000000029

Dauer JM, Perakis SS (2014) Calcium oxalate contribution to calcium cycling in forests of contrasting nutrient status. For Ecol Manag 334:64–73. https://doi.org/10.1016/j.foreco.2014.08.029

de Oliveira Garcia W, Amann T, Hartmann J (2018) Increasing biomass demand enlarges negative forest nutrient budget areas in wood export regions. Sci Rep 8:1–7. https://doi.org/10.1038/s41598-018-22728-5

Devine WD, Footen PW, Strahm BD et al (2012) Nitrogen leaching following whole-tree and bole-only harvests on two contrasting Pacific Northwest sites. For Ecol Manag 267:7–17. https://doi.org/10.1016/j.foreco.2011.11.043

Du E, Terrer C, Pellegrini AFA et al (2020) Global patterns of terrestrial nitrogen and phosphorus limitation. Nat Geosci 13:221–226. https://doi.org/10.1038/s41561-019-0530-4

Duchesne L, Houle D (2008) Impact of nutrient removal through harvesting on the sustainability of the boreal forest. Ecol Appl 18:1642–1651. https://doi.org/10.1890/07-1035.1

Erickson HE, Perakis SS (2014) Soil fluxes of methane, nitrous oxide, and nitric oxide from aggrading forests in coastal Oregon. Soil Biol Biochem 76:268–277. https://doi.org/10.1016/j.soilbio.2014.05.024

Federer CA, Hornbeck JW, Tritton LM et al (1989) Long-term depletion of calcium and other nutrients in eastern US forests. Environ Manage 13:593–601. https://doi.org/10.1007/BF01874965

Fenn ME, Poth MA, Johnson DW (1996) Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. For Ecol Manag 82:211–230. https://doi.org/10.1016/0378-1127(95)03668-7

Franklin WT (1971) Mineralogical and chemical characteristics of western Oregon Andic Soils, Dissertation edn. Oregon State University

Gallo AC (2016) Response of soil temperature, moisture, and respiration two years following intensive organic matter and compaction manipulations in Oregon Cascade forests. MS Thesis, Oregon State University

Gessel SP, Cole DW, Steinbrenner EC (1973) Nitrogen balances in forest ecosystems of the Pacific Northwest. Soil Biol Biochem 5:19–34. https://doi.org/10.1016/0038-0717(73)90090-4

Goswami S, Fisk MC, Vadeboncoeur MA et al (2018) Phosphorus limitation of aboveground production in northern hardwood forests. Ecology 99:438–449. https://doi.org/10.1002/ecy.2100

Groffman PM, Fisk MC (2011) Calcium constrains plant control over forest ecosystem nitrogen cycling. Ecology 92:2035–2042. https://doi.org/10.1890/11-0461.1

Hamby DM (1994) A review of techniques for parameter sensitivity analysis of environmental models. Environ Monit Assess 32(2):135–154. https://doi.org/10.1007/BF00547132

Homann PS, van Miegroet H, Cole DW, Wolfe GV (1992) Cation distribution, cycling, and removal from mineral soil in Douglas-fir and red alder forests. Biogeochemistry 16:121–150. https://doi.org/10.1007/bf00002828

Homann PS, McKane RB, Sollins P (2000) Belowground processes in forest-ecosystem biogeochemical simulation models. For Ecol Manag 138:3–18. https://doi.org/10.1016/S0378-1127(00)00408-4

Huggett BA, Schaberg PG, Hawley GJ, Eager C (2007) Long-term calcium addition increases growth release, wound closure, and health of sugar maple (*Acer saccharum*) trees at the Hubbard brook experimental forest. Can J For Res 37:1692–1700. https://doi.org/10.1139/x07-042

Hume AM, Chen HYH, Taylor AR (2018) Intensive forest harvesting increases susceptibility of northern forest soils to carbon, nitrogen and phosphorus loss. J Appl Ecol 55:246–255. https://doi.org/10.1111/1365-2664.12942

Hynicka JD, Pett-Ridge JC, Perakis SS (2016) Nitrogen enrichment regulates calcium sources in forests. Glob Change Biol 22:4067–4079. https://doi.org/10.1111/gcb.13335

Johnson DW, Lindberg SE (1992) Processing of acidic deposition. In: Johnson DW, Lindberg SE (eds) Atmospheric deposition and forest nutrient cycling: a synthesis of the integrated forest study. Springer, New York, pp 426–466. https://doi.org/10.1007/978-1-4612-2806-6_11

Johnson DW, Binkley D, Conklin P (1995) Simulated effects of atmospheric deposition, harvesting, and species change on nutrient cycling in a loblolly pine forest. For Ecol Manag 76:29–45. https://doi.org/10.1016/0378-1127(95)03565-R

Jönsson C, Warfvinge P, Sverdrup H (1995) Uncertainty in predicting weathering rate and environmental stress factors with the PROFILE model. Water Air Soil Pollut 81(1):1–23. https://doi.org/10.1007/BF00477253

Joo S, Mainwaring DB, Hann DW, Osborne NL, Maguire DA (2020) User's Manual for CIPSR Version 4.0. 0. Center for Intensive Planted-forest Silviculture (CIPS), College of Forestry, Oregon State University. http://cips.forestry.oregonstate.edu/cipsanon. Accessed 20 February, 2020

Kranabetter JM, McLauchlan KK, Enders SK et al (2016) A framework to assess biogeochemical response to ecosystem disturbance using nutrient partitioning ratios. Ecosystems 19:387–395. https://doi.org/10.1007/s10021-015-9934-1

Kvindesland SHSB (1997) The nutrient cycling model (NuCM) user manual. Agricultural University of Norway Department of Soil and Water Sciences. http://hdl.handle.net/11250/2502953 Accessed 20 February, 2020

Lajtha K, Jones J (2013) Trends in cation, nitrogen, sulfate and hydrogen ion concentrations in precipitation in the United States and Europe from 1978 to 2010: a new look at an old problem. Biogeochemistry 116:303–334. https://doi.org/10.1007/s10533-013-9860-2

Lanning M, Wang L, Scanlon TM, Vadeboncoeur MA et al (2019) Intensified vegetation water use under acid deposition. Sci Adv 5(7):5168. https://doi.org/10.1126/sciadv.aav5168

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379. https://doi.org/10.1890/06-2057.1

Legout A, van der Heijden G, Jaffrain J et al (2016) Tree species effects on solution chemistry and major element fluxes: a case study in the Morvan (Breuil, France). For Ecol Manag 378:244–258. https://doi.org/10.1016/j.foreco.2016.07.003

Leys BA, Likens GE, Johnson CE et al (2016) Natural and anthropogenic drivers of calcium depletion in a northern forest during the last millennium. PNAS 113:6934–6938. https://doi.org/10.1073/pnas.1604909113

Likens GE, Bormann FH, Johnson NM et al (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecol Monogr 40:23–47. https://doi.org/10.2307/1942440

Likens GE, Driscoll CT, Buso DC et al (1994) The biogeochemistry of potassium at Hubbard Brook. Biogeochemistry 25:61–125. https://doi.org/10.1007/BF00000881

Likens GE, Driscoll CT, Buso DC et al (1998) The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry 41:89–173. https://doi.org/10.1023/A:1005984620681

Littke KM, Harrison RB, Zabowski D et al (2014) Prediction of Douglas-fir fertilizer response using biogeoclimatic properties in the coastal Pacific Northwest. Can J For Res 44:1253–1264. https://doi.org/10.1139/cjfr-2014-0190

Littke KM, Harrison RB, Zabowski D (2016) Determining the effects of biogeoclimatic properties on different site index systems of Douglas-fir in the coastal Pacific Northwest. For Sci 62:503–512. https://doi.org/10.5849/forsci.15-191

Littke KM, Harrington TB, Slesak RA et al (2020a) Impacts of organic matter removal and vegetation control on nutrition and growth of Douglas-fir at three Pacific Northwestern Long-Term Soil Productivity sites. For Ecol Manag 468:118176. https://doi.org/10.1016/j.foreco.2020.118176

Littke KM, Harrington TB, Holub SM et al (2020b) Douglas-fir biomass allocation and net nutrient pools 15–20 years after organic matter removal and vegetation control. Forests 11:1022. https://doi.org/10.3390/f11091022

Lu X, Vitousek PM, Mao Q et al (2018) Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. PNAS 115:5187–5192. https://doi.org/10.1073/pnas.1720777115

Mainwaring DB, Maguire DA, Perakis SS (2014) Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington. For Ecol Manag 327:178–188. https://doi.org/10.1016/j.foreco.2014.05.005

Mann LK, Johnson DW, West DC et al (1988) Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital, and regrowth. For Sci 34:412–428

McLaughlin SB, Wimmer R (1999) Tansley Review No. 104 calcium physiology and terrestrial ecosystem processes. New Phytol 142(3):373–417. https://doi.org/10.1046/j.1469-8137.1999.00420.x

Meeds JA, Kranabetter MJ, Zigg I et al (2021) Phosphorus deficiencies invoke optimal allocation of exoenzymes by ectomycorrhizas. ISME 15:1478–1489. https://doi.org/10.1038/s41396-020-00864-z

Menge DNL, Wolf AA, Funk JL, Perakis SS, Akana PR, Arkebauer R, Bytnerowicz TA, Carrera Pereira KA, Huddell AM, Kou-Giesbrecht S, Ortiz SK (2023) Tree symbioses sustain nitrogen fixation despite excess nitrogen supply. Ecol Monogr. https://doi.org/10.1002/ecm.1562

Mika PG, Moore JA (1990) Foliar Potassium Status Explains Douglas Fir Response to Nitrogen Fertilization in the Inland Northwest, USA. In: Zöttl HW, Hüttl RF (eds) Management of Nutrition in Forests under Stress: Proceedings of the International Symposium, Springer Netherlands, Dordrecht, pp 477–491. https://doi.org/10.1007/BF02385240

Munson RK, Liu S, Gherini SA et al (1992) NuCM Code Version 2.0: an IBM PC Code for simulating Nutrient Cycling in Forest Ecosystems. Tetra-Tech, Hadley, Massachusetts

National Atmospheric Deposition Program (NRSP-3) (2022) NADP Program Office, Wisconsin State Laboratory of Hygiene, 465 Henry Mall, Madison, WI 53706

Niu S, Classen AT, Dukes JS, Kardol P et al (2016) Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. Ecol Lett 19:697–709. https://doi.org/10.1111/ele.12591

Nykvist N (2000) Tropical forests can suffer from a serious deficiency of calcium after logging. Ambio 29:310–313. https://doi.org/10.1579/0044-7447-29.6.310

Ouimet R, Moore JD (2015) Effects of fertilization and liming on tree growth, vitality and nutrient status in boreal balsam fir stands. For Ecol Manag 345:39–49. https://doi.org/10.1016/j.foreco.2015.02.032

Oursin M, Pierret MC, Beaulieu É, Daval D, Legout A (2023) Is there still something to eat for trees in the soils of the Strengbach catchment? For Ecol Manag 537:120583. https://doi.org/10.1016/j.foreco.2022.120583

Peltzer DA, Wardle DA, Allison VJ, Baisden WT et al (2010) Understanding ecosystem retrogression. Ecol Monogr 80(4):509–529. https://doi.org/10.1890/09-1552.1

Perakis SS, Maguire DA, Bullen TD et al (2006) Coupled nitrogen and calcium cycles in forests of the Oregon Coast Range. Ecosystems 9:63–74. https://doi.org/10.1007/s10021-004-0039-5

Perakis SS, Sinkhorn ER (2011) Biogeochemistry of a temperate forest nitrogen gradient. Ecology 92:1481–1491. https://doi.org/10.1890/10-1642.1

Perakis SS, Sinkhorn ER, Compton JE (2011) δ^{15}N constraints on long-term nitrogen balances in temperate forests. Oecologia 167:793–807. https://doi.org/10.1007/s00442-011-2016-y

Perakis SS, Sinkhorn ER, Catricala CE et al (2013) Forest calcium depletion and biotic retention along a soil nitrogen gradient. Ecol Appl 23:1947–1961. https://doi.org/10.1890/12-2204.1

Perakis SS, Tepley AJ, Compton JE (2015) Disturbance and topography shape Nitrogen availability and δ15N over long-term forest succession. Ecosystems 18:573–588. https://doi.org/10.1007/s10021-015-9847-z

Perakis SS, Pett-Ridge JC, Catricala CE (2017) Nutrient feedbacks to soil heterotrophic nitrogen fixation in forests. Biogeochemistry 134:41–55. https://doi.org/10.1007/s10533-017-0341-x

Perakis SS, Pett-Ridge JC (2019) Nitrogen-fixing red alder trees tap rock-derived nutrients. PNAS 116:5009. https://doi.org/10.1073/pnas.1814782116

Peterjohn WT, Adams MB, Gilliam FS (1996) Symptoms of nitrogen saturation in two central Appalachian hardwood forest ecosystems. Biogeochemistry 35:507–522. https://doi.org/10.1007/BF02183038

Peterson CE, Hazard JW (1990) Regional variation in growth response of Coastal Douglas-fir to nitrogen fertilizer in the Pacific Northwest. For Sci 36(3):625–640. https://doi.org/10.1093/forestscience/36.3.625

Pett-Ridge JC, Derry LA, Barrows JK (2009) Ca/Sr and 87Sr/86Sr ratios as tracers of ca and sr cycling in the Rio Icacos watershed, Luquillo Mountains, Puerto Rico. Chem Geol 267:32–45. https://doi.org/10.1016/j.chemgeo.2008.11.022

PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, Accessed 7 Mar 2020

Ranger J, Turpault MP (1999) Input–output nutrient budgets as a diagnostic tool for sustainable forest management. For Ecol Manag 122:139–154. https://doi.org/10.1016/S0378-1127(99)00038-9

Rastetter EB, Yanai RD, Thomas RQ, Vadeboncoeur MA, Fahey TJ, Fisk MC, Kwiatkowski BL, Hamburg SP (2013) Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecol Appl 23(3):621–642. https://doi.org/10.1890/12-0751.1

Sachs D, Sollins P (1986) Potential effects of management practices on nitrogen nutrition and long-term productivity of western hemlock stands. For Ecol Manag 17:25–36. https://doi.org/10.1016/0378-1127(86)90073-3

Saraiva JP, Lima BS, Gomes VM et al (2017) Calculation of sensitivity index using one-at-a-time measures based on graphical analysis. In: 2017 18th International Scientific Conference on Electric Power Engineering (EPE). pp 1–6. https://doi.org/10.1109/EPE.2017.7967329

Sardans J, Peñuelas J (2015) Potassium: a neglected nutrient in global change. Glob Ecol Biogeogr 24(3):261–275. https://doi.org/10.1111/geb.12259

Schlesinger WH (2021) Some thoughts on the biogeochemical cycling of potassium in terrestrial ecosystems. Biogeochemistry 154(2):427–432. https://doi.org/10.1007/s10533-020-00704-4

Schowalter T, Morrell J (2002) Nutritional quality of Douglas-fir wood: effect of vertical and horizontal position on nutrient levels. Wood Fiber Sci 34:158–164

Siah K (2022) The NutsFor user Manual. Github. https://github.com/Coffee-Powered-Scientist/NutsFor_OR2/blob/master/Manual/The%20NutsFor%20User%20Manual.pdf Accessed Mar 22 2022

Slesak RA, Schoenholtz SH, Harrington TB, Strahm BD (2009) Dissolved carbon and nitrogen leaching following variable logging-debris retention and competing-vegetation control in Douglas-fir plantations of western Oregon and Washington. Can J For Res 39:1484–1497. https://doi.org/10.1139/X09-067

Sposito G (1977) The Gapon and the Vanselow selectivity coefficients. Soil Sci Soc Am J 41:1205–1206. https://doi.org/10.2136/sssaj1977.03615995004100060040x

St. Clair SB, Sharpe WE, Lynch JP (2008) Key interactions between nutrient limitation and climatic factors in temperate forests: a synthesis of the sugar maple literature. Can J For Res 38:401–414. https://doi.org/10.1139/X07-161

Stegemoeller KA, Chappell HN (1990) Growth response of unthinned and thinned Douglas-fir stands to single and multiple applications of nitrogen. Can J For Res 20:343–349. https://doi.org/10.1139/x90-050

Stevens PA, Norris DA, Williams TG et al (1995) Nutrient losses after clearfelling in Beddgelert Forest: a comparison of the effects of conventional and whole-tree harvest on soil water chemistry. Forestry: Int J For Res 68:115–131. https://doi.org/10.1093/forestry/68.2.115

Stokely TD, Verschuyl J, Hagar JC, Betts MG (2018) Herbicides and herbivory interact to drive plant community and crop-tree establishment. Ecol Appl 28:2011–2023. https://doi.org/10.1002/eap.1777

Stone EL, Kszystyniak R (1977) Conservation of potassium in the Pinus resinosa ecosystem. Science 198(4313):192–194. https://doi.org/10.1126/science.198.4313.192

Sullivan BW, Alvarez-Clare S, Castle SC et al (2014) Assessing nutrient limitation in complex forested ecosystems: alternatives to large-scale fertilization experiments. Ecology 95:668–681. https://doi.org/10.1890/13-0825.1

Sverdrup H (1996) Geochemistry, the key to understanding environmental chemistry. Sci Total Environ 183:67–87. https://doi.org/10.1016/0048-9697(95)04978-9

Sverdrup H, Warfvinge P (1988) Weathering of primary silicate minerals in the natural soil environment in relation to a chemical weathering model. Water Air Soil Pollut 38:387–408. https://doi.org/10.1007/BF00280768

Sverdrup H, Warfvinge P (1993) Calculating field weathering rates using a mechanistic geochemical model PROFILE. Appl Geochem 8:273–283. https://doi.org/10.1016/0883-2927(93)90042-F

Sweeney KE, Roering JJ, Almond P, Reckling T (2012) How steady are steady-state landscapes? Using visible–near-infrared soil spectroscopy to quantify erosional variability. Geology 40(9):807–810. https://doi.org/10.1130/G33167.1

Taylor LL, Banwart SA, Valdes PJ, Leake JR, Beerling DJ (2012) Evaluating the effects of terrestrial ecosystems, climate and carbon dioxide on weathering over geological time: a global-scale process-based approach. Philos Trans R Soc Lond B Biol Sci 367:565–582. https://doi.org/10.1098/rstb.2011.0251

Terrer C, Jackson RB, Prentice IC et al (2019) Nitrogen and phosphorus constrain the CO2 fertilization of global plant biomass. Nat Clim Change 9:684–689. https://doi.org/10.1038/s41558-019-0545-2

Thiffault E, Hannam KD, Paré D et al (2011) Effects of forest biomass harvesting on soil productivity in boreal and temperate forests — a review. Environ Rev 19:278–309. https://doi.org/10.1139/A11-009

Tripler CE, Kaushal SS, Likens GE, Walter MT (2006) Patterns in potassium dynamics in forest ecosystems. Ecol Lett 9:451–466. https://doi.org/10.1111/j.1461-0248.2006.00891.x

Vadeboncoeur MA (2010) Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Candian J For Res 40:1766–1780. https://doi.org/10.1139/X10-127

Vadeboncoeur MA, Hamburg SP, Yanai RD, Blum JD (2014) Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. For Ecol Manag 318:194–205. https://doi.org/10.1016/j.foreco.2014.01.012

Valipour M, Driscoll CT, Johnson CE, Battles JJ, Campbell JL, Fahey TJ (2018) The application of an integrated biogeochemical model to simulate dynamics of vegetation, hydrology and nutrients in soil and streamwater following a whole-tree harvest of a northern hardwood forest. Sci Total Environ 645:244–256. https://doi.org/10.1016/j.scitotenv.2018.07.066

van der Heijden G, Legout A, Nicolas M et al (2011) Long-term sustainability of forest ecosystems on sandstone in the Vosges Mountains (France) facing atmospheric deposition and silvicultural change. For Ecol Manag 261:730–740. https://doi.org/10.1016/j.foreco.2010.12.003

van der Heijden G, Belyazid S, Dambrine E et al (2017a) NutsFor a process-oriented model to simulate nutrient and isotope tracer cycling in forest ecosystems. Environ Model Softw 95:365–380. https://doi.org/10.1016/j.envsoft.2017.06.003

van der Heijden G, Legout A, Mareschal L et al (2017b) Filling the gap in ca input-output budgets in base-poor forest ecosystems: the contribution of non-crystalline phases evidenced by stable isotopic dilution. Geochim et Cosmochimia Acta 209:135–148. https://doi.org/10.1016/j.gca.2017.04.018

van der Heijden G, Hinz A, Didier S et al (2019) Quantifying the uncertainty in modeled water drainage and nutrient leaching fluxes in forest ecosystems. Ecosystems 22:677–698. https://doi.org/10.1007/s10021-018-0295-4

Vanguelova E, Benham S, Nisbet T (2022) Long term trends of base cation budgets of forests in the UK to inform sustainable harvesting practices. Appl Sci 12:2411. https://doi.org/10.3390/app12052411

Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol Monogr 82:205–220. https://doi.org/10.1890/11-0416.1

Vicca S, Luyssaert S, Peñuelas J et al (2012) Fertile forests produce biomass more efficiently. Ecol Lett 15:520–526. https://doi.org/10.1111/j.1461-0248.2012.01775.x

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298. https://doi.org/10.2307/1939481

Vitousek PM, Reiners WA (1975) Ecosystem Succession and Nutrient Retention: a hypothesis. Bioscience 25:376–381. https://doi.org/10.1890/0012-9623-95.3.234

Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forest. Ann Rev Ecol Syst 17:137–167. https://doi.org/10.1146/annurev.es.17.110186.001033

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl 20:5–15. https://doi.org/10.1890/08-0127.1

Walker RB, Gessel SP (1991) Mineral Deficiencies of Coastal Northwest Conifers. Institute of Forest Resources Contribution No. 70, College of Forest Resources. University of Washington, Seattle

Wallman P, Svensson MGE, Sverdrup H, Belyazid S (2005) ForSAFE—an integrated process-oriented forest model for long-term sustainability assessments. For Ecol Manag 207:19–36. https://doi.org/10.1016/j.foreco.2004.10.016

Waring RH, Boyle J, Cromack K Jr, Maguire D, Kanaskie A (2000) Researchers offer new insights into swiss needle cast. Western Forester 45:10–11

Wright SJ, Yavitt JB, Wurzburger N et al (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625. https://doi.org/10.1890/10-1558.1

Wurzburger N, Wright SJ (2015) Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. Ecology 96:2137–2146. https://doi.org/10.1890/14-1362.1

Zhang L, Wang MX, Li H et al (2014) Mobilization of inorganic phosphorus from soils by ectomycorrhizal fungi. Pedosphere 24:683–689. https://doi.org/10.1016/S1002-0160(14)60054-0