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Long-term nutrient cycling patterns in Douglas-fir and red alder stands: a simulation study

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Abstract

Long-term patterns in nutrient cycling in regrowing Douglas-fir (*Pseudosuga menziesii* Mirb. Franco) and red alder (*Alnus rubra* Bong.) on native soils plus soils previously occupied by other species were simulated using the nutrient cycling model. Simulations of regrowing stands were also compared with observations of nutrient cycling in mature Douglas-fir and red alder. We hypothesized that (1) prolonged presence of red alder will cause a depletion in soil base cations due to increased nitrification and NO_3^- leaching; (2) lower base cation availability under red alder will ultimately cause biomass production to decline; (3) high N availability in red alder soils will favor regrowth of Douglas-fir; (4) higher base cation and P status of the Douglas-fir soils will favor growth of red alder both in the short- and long-term, since N is not limiting to red alder; and (5) in regrowing red alder, NO_3^- leaching will increase with time as a result of increased N fixation. All hypotheses were confirmed, but the effect of soil type on biomass production was minimal both for red alder and Douglas-fir. The higher soil organic matter content in the mature red alder stand most likely reflected previous occupation by old-growth Douglas-fir and also a large litter input from the understory vegetation. In general, the nutrient cycling model simulated differences in nutrient cycling patterns at least qualitatively between Douglas-fir and red alder and was helpful in identifying potential gaps in the understanding of biogeochemical cycling as well as uncertainties in the data. The nutrient cycling model did not fully elucidate differences in P cycling between Douglas-fir and red alder and overestimated weathering rates under Douglas-fir. Uncertainties in the data included: (1) temporal patterns in N fixation in the regrowing stands; (2) understory litterfall; and (3) site history and, consequently, presence of pre-existing differences in site conditions.

Keywords: Nutrient cycling; Douglas-fir; Red alder; Nitrogen fixation

1. Introduction

In large areas of the Pacific Northwest, red alder (*Alnus rubra* Bong.) is a prominent species, especially in areas that have been recently disturbed. Red alder is able to symbiotically fix atmospheric N_2 with reported N fixation rates ranging from 50 to 200 kg N ha^{-1} per year (Cole et al., 1978; DeBell and Radwan, 1979; Binkley, 1981). Several studies have shown that continued presence of red alder increases total and available N in the soil (Cole et al., 1978; Bormann and DeBell, 1981). Mixing red alder with non-N-fixing species such as Douglas-fir (*Pseudotsuga menziesii*

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(Mirbel.)) provides an important management option in addition to direct fertilization to increase biomass production (Miller and Murray, 1978).

In addition to providing N inputs from N fixation, the presence of red alder causes increases in N mineralization, nitrification, and nitrate leaching. This can, in turn, cause acidification of soils, and soil and surface waters (Van Miegroet and Cole, 1984, 1985; Binkley and Sollins, 1990; Van Miegroet et al., 1992). Removal of mature red alder and replanting with either Douglas-fir or red alder saplings, however, caused nitrate concentrations in soil solution to decrease to trace levels within four years (Van Miegroet et al., 1992; Homann et al., 1994). It is very likely, however, that under regrowing red alder, nitrate concentrations will increase again as N fixation increases. Because the presence of red alder can cause depletion of exchangeable base cations and increases in soil acidity, continued rotations of red alder might result in deficiencies in nutrients other than N (see, e.g. Binkley, 1992). Still, Homann et al. (1992) observed that weathering rates under red alder were high enough to supply the exchangeable pools with Ca, Mg and K. Brozek (1990) noted that foliar P levels were lower in Douglas-fir planted on red alder soils than when planted on Douglas-fir soils. Compton and Cole (1998) found soil available P levels were 11 times higher under mature Douglas-fir than under red alder soils, indicating that the latter species may deplete available P pools (Binkley, 1992). The amount of P present in the red alder forest floor, however, was three times higher under red alder than under Douglas-fir. Binkley (1992) suggested that the differences in extractable P between tree species reflect differences in soil conditions prior to planting. Giardina et al. (1995) observed that P availability for Douglas-fir was higher when mixed with red alder.

As most of the reported experiments represent a limited time series (typically <10 years), the long-term effects of tree species on soil conditions and vice versa are unclear. For instance, Van Miegroet et al. (1990) observed that red alder produces more biomass on soils previously occupied by Douglas-fir during the first three years of regrowth, perhaps due to the larger amount of base cations or extractable P present in the soil. Initially, however, Douglas-fir produced equal amounts of biomass on soils previously occupied by Douglas-fir and red alder. By contrast, Brozek (1990) found higher biomass in a Douglas-fir stand after 6 years of growth on red alder soils than after a similar growth period on Douglas-fir soil. Still, no long-term data are present to assess whether these short-term trends will be sustained.

In this paper, we present a modeling approach to assess the potential long-term effects of red alder and Douglas-fir vegetation on biomass production, soil nutrient status and water quality. We simulated both red alder and Douglas-fir regrowing on their native soils as well as on soils previously occupied by other species, similar to the experiment described in Van Miegroet et al. (1992). These simulations were compared with simulations of mature red alder and Douglas-fir. For this assessment, we used the nutrient cycling model (NuCM; Liu et al., 1991). This model has been previously used to study effects of acid deposition, harvesting and liming on nutrient cycling in forest ecosystems (Johnson et al., 1993, 1995a, b) covering a wide range of geographical and, thus, climatic conditions.

We hypothesized that:

1. prolonged presence of red alder will cause a depletion in soil base cations due to increased nitrification and NO_3^- leaching;
2. lower base cation availability under red alder will ultimately cause biomass production to decline;
3. high N availability in red alder soils will favor regrowth of Douglas-fir (although a lower availability of base cations may lower growth rates on the long term);
4. higher base cation and P status of the Douglas-fir soils will favor growth of red alder both on the short and long term since N is not limiting to red alder; and
5. in regrowing red alder, NO_3^- leaching will increase with time as a result of increased N fixation.

Finally, we wanted to assess whether NuCM reflects our current understanding of biogeochemical cycling in forested ecosystems.

2. Nutrient cycling model (NuCM)

The NuCM model was developed to explore potential effects of atmospheric deposition, fertilization and harvesting in forest ecosystems. As a stand-level model, NuCM incorporates all major nutrient cycling processes (uptake, translocation, leaching, weathering, organic matter decay and accumulation). Vegetation is divided into leaf, bole and root compartments for under- and overstory vegetation. NuCM simulates the cycling of N, P, K, Ca, Mg, Na and S based on expected optimal growth rates (input by the user and reduced in the event of nutrient limitation), user-defined litterfall, weathering, N and S mineralization rates, soil minerals composition, initial litter, soil organic matter pools and C/N ratios. The soil can be divided into as many as 10 different layers each having its own physical and chemical characteristics. Movement of water is simulated using the continuity equation, Darcy's equation for permeable media flow and Manning's equation for free surface flow (Munson et al., 1992). Percolation between the different layers occurs as a function of permeability and gradients in moisture content. The model treats decomposition as a three-stage process (litter moves into fine litter and two soil organic fractions) during which nutrients are released from litter at rates depending on litterfall inputs and C/N ratios of litter and microbes. The model simulates non-competitive adsorption of sulfate, phosphate and organic acids. Sulfate adsorption is described by a Langmuir adsorption isotherm. Phosphate adsorption is represented by a linear isotherm. Cation exchange is described by the Gapon equation. Mineral weathering rates depend on the mass of the mineral present and the dissolved proton concentration raised to a fractional power. The model has previously been calibrated for different vegetation types, including a loblolly pine (*Pinus taeda* L.) stand at Duke University (Johnson et al., 1995a), a mixed deciduous stand at Walker Branch (Johnson et al., 1993) and a red spruce (*Picea rubens* Sarg.) stand in the Great Smoky Mountains (Johnson et al., 1996).

3. Model calibration

The Thompson research site used to calibrate NuCM for this study is located in the Cedar River watershed. The site is in the foothills of the Cascade Range, 56 miles southeast of Seattle, Washington. The site climate is maritime with cool dry summers and wet moderate winters. Mean annual temperature is 9.8°C; and mean annual precipitation is $\approx$1300 mm, most of which falls as rain between October and March. The site is representative of large parts of the Cascade Range in Oregon and Washington. In the fall of 1984, all overstory vegetation was removed from a 1.0-ha area in adjacent Douglas-fir and red alder sites (Van Miegroet et al., 1992). In February 1985, one-half of each clear-cut area was replanted with red alder and one-half with Douglas-fir seedlings, yielding four 0.5 ha conversion units: alder-to-alder (RA–RA), alder-to-Douglas-fir (RA–DF), Douglas-fir-to-alder (DF–RA) and Douglas-fir to Douglas-fir (DF–DF). Plots in undisturbed 60-year-old red alder (RA) and Douglas-fir (DF) stands were used as controls. Meteorological data were taken from a local weather station at the Thompson research site. Soil and vegetation data for the reference stands were taken from Johnson and Lindberg (1992). Since we wanted to investigate vegetation growth response to different soil conditions, we used a nominal high value for tree growth rates so actual growth rates would reflect any nutrient or water limitations. An important unknown in the simulations (and measurements), in general, is the weathering rate of primary minerals. The observed high base cation leaching in the mature red alder stand suggests that weathering rates were high enough to compensate for any base cation leaching due to nitrate production. We did not, however, have any data on time course of exchangeable cations. Weathering rates were, therefore, set to maintain sufficient leaching of base cations. Dependence of weathering rates on proton concentration and total mineral mass were set the same for both red alder and Douglas-fir soils.

Note that N fixation is currently not simulated explicitly in NuCM. In our study, we therefore increased NH_4^+ in wet deposition to account for extra N inputs through N fixation. In the mature stands, total N fixation equaled 100 kg N ha^{-1} per year. In the regrowing alder stands, we gradually increased NH_4^+ in deposition from 0 at Year 1 to 100 kg N ha^{-1} per year in Year 40.

4. Results and discussion

4.1. Comparison of field and model results for mature red alder and Douglas-fir stands

In Table 1, we summarize the comparison between simulations and field data for the mature red alder and

Table 1
Comparison of field measurements and model simulations of nutrient pools (kmol ha^{-1}) and fluxes (kmol ha^{-1} per year) in mature Douglas-fir and red alder stands

	N		P		Ca		Mg		K	
	Field	Model	Field	Model	Field	Model	Field	Model	Field	Model
Douglas-fir										
Ecosystem pools										
vegetation	27.29	25.91	1.65	1.51	7.91	7.78	1.60	1.02	4.09	3.16
soil, exchange	0.00	0.02	2.32	2.31	27.25	27.25	4.12	3.89	6.73	7.35
soil, total	390	327	119	73	1157	1158	1185	1189	609	595
Ecosystem fluxes										
deposition	0.35	0.41	0.00	0.00	0.09	0.09	0.04	0.03	0.06	0.07
throughfall	0.09	0.38	0.00	0.00	0.24	0.19	0.05	0.09	0.20	1.29
litterfall	0.56	1.36	0.10	0.14	0.27	0.28	0.04	0.05	0.07	0.23
leaching	0.00	0.06	0.00	0.00	0.26	0.18	0.06	0.10	0.03	0.04
Red alder										
Ecosystem pools										
vegetation	77.43	68.49	1.84	1.47	17.00	16.55	3.29	2.73	12.94	10.00
soil, exchange	0.00	0.11	0.13	0.12	22.54	28.03	3.05	3.72	3.71	3.38
soil, total	620	371	60	58	733	750	835	826	394	413
Ecosystem fluxes										
deposition	0.34	7.53[a]	0.00	0.00	0.09	0.09	0.03	0.03	0.06	0.07
throughfall	0.10	7.56[a]	0.00	0.00	0.14	0.09	0.07	0.04	0.32	0.07
litterfall	4.20	2.55	0.07	0.10	0.85	0.34	0.19	0.14	0.34	0.44
leaching	2.98	2.35	0.00	0.00	0.94	0.87	0.30	0.27	0.20	0.27

[a] Includes N input through N fixation.

Douglas-fir stands. For Douglas-fir, both throughfall and litterfall were higher in the simulations than measured in the field. Changing the wet and dry deposition trapping efficiency of the canopy affected throughfall values, but the effects were different for the various nutrients. Although translocation of N and K was set at 40%, N in litterfall was more than two times and K more than three times higher in the simulations than the measured amounts. Johnson et al. (1996) also observed that NuCM overestimated litterfall N and K fluxes when simulating a red spruce stand in the Great Smoky Mountains. The simulated amount of nutrients in red alder biomass was generally lower than the measured amount, suggesting that the total amount of nutrients in foliage was underestimated. This may also explain the relatively low simulated litterfall N and P fluxes. Increasing the amount of foliage, however, caused the model to crash suggesting that nutrient requirements and supply were not in balance. This may have been due to inconsistent data or errors in the model definitions. Johnson et al. (1996) noted disparities between simulations and measurements caused by the model structure, the way that data were measured or a combination of these factors. For example, NuCM does not include a branch pool, but somehow these nutrients must be included. In this study, we included these nutrients in the bole pool.

The simulated total amount of soil N was 16% lower than the measured amount for Douglas-fir and as much as 40% lower for red alder (Table 1). In NuCM, the forest floor and soil organic matter are combined and attributed to organic matter in the mineral soil. Because total organic matter mass is expressed as a percentage of soil mass in the topsoil, there is an upper limit to how much organic matter can be assigned to the topsoil. Simulated deposition and throughfall fluxes for red alder are difficult to compare with measured data since we included extra N to account for N fixation. In the case of red alder, nutrient leaching is an important efflux from the ecosystem. Simulated leaching matched the observations very

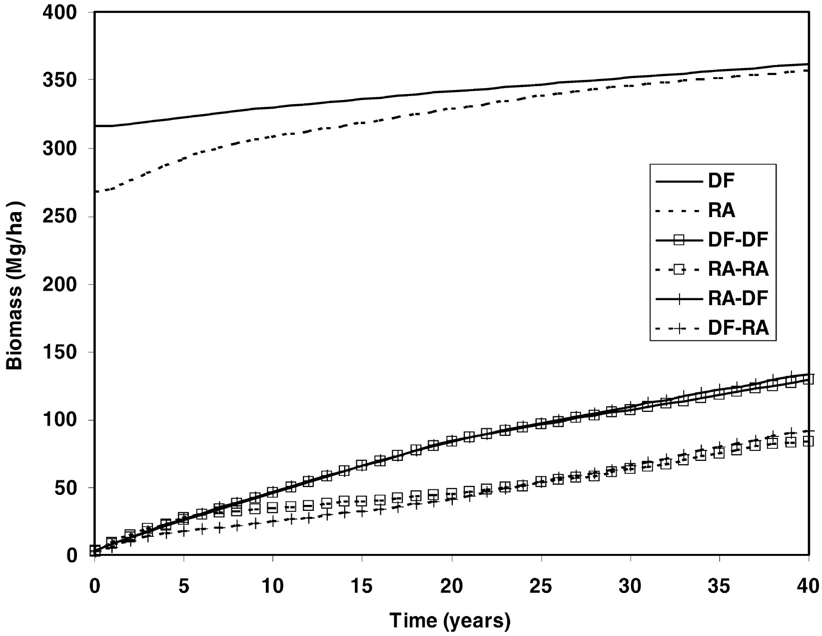

Fig. 1. Simulated biomass for: (1) mature Douglas-fir (DF); (2) red alder (RA); (3) regrowing Douglas-fir on Douglas-fir soil (DF–DF); (4) regrowing Douglas-fir on red alder soil (RA–DF); (5) regrowing red alder on red alder soil (RA–RA); and (6) regrowing red alder on Douglas-fir soil (DR–RA).

well for Douglas-fir. For red alder, simulated N leaching was 21% lower than observed.

Although measured parameters and simulations did not always agree, the main differences in patterns in nutrient pools and fluxes in red alder and Douglas-fir stands were mimicked by the simulations. Therefore, we feel confident that the model is suitable for at least qualitatively describing nutrient cycling in red alder and Douglas-fir.

4.2. Biomass

Total biomass in the uncut reference stand for Douglas-fir was initially 42 Mg ha^{-1} higher than for red alder, but the difference decreased through time as the simulations progressed (Fig. 1). During the first six years, growth rates for the regrowing stands were equal, except for DF–RA which had a lower initial growth rate. After 40 years, total biomass of Douglas-fir was 50% or 43 Mg ha^{-1} higher than that of red alder. For red alder, after 40 years, biomass was 10% higher when trees were planted on soils previously occupied by Douglas-fir. Douglas-fir biomass was only 3% higher on soils previously occupied by red alder. Brozek (1990) observed that Douglas-fir seedlings had higher biomass after growing for four years on red alder soils than after growing for the same period of time on Douglas-fir soils. Cole et al. (1995) observed that biomass was only slightly higher in the RA–DF than in the DF–DF plots after seven years of growth. Our simulations do not show clear differences in growth between DF–DF and RA–DF in the early growth years.

In general, the simulated growth rates of the regrowing stands appeared to be too low. Biomass of the mature forest at 60 years was ≈320 Mg ha^{-1} for the Douglas-fir and 270 Mg ha^{-1} for red alder (Johnson and Lindberg, 1992). After 40 years, simulated biomass of the regrowing stands was below 133 Mg ha^{-1}. A potential explanation is that estimates for litterfall rates for the regrowing stands were too high. NuCM calculates nutrient uptake based on demand for tree growth and litterfall. High litterfall rates will increase uptake demand so nutrient deficiencies and, consequently, lower growth rates are likely to occur much earlier than when all nutrients can be used for tree growth. For the regrowth simulations, litterfall rates were assumed to equal litterfall in the mature stand after canopy closure which was set at 10 years after planting. When the model was run with litterfall rates set at zero, the biomass of regrowing stands was even higher than of the mature stands after 40 years of simulation (data not shown).

Accumulation of N, P, Ca, Mg and K in the Douglas-fir biomass was generally higher for the regrowing than for the mature stands (Table 2). In contrast, for most nutrients accumulation in mature red alder was higher than in the regrowing stands reflecting the lower biomass of the regrowing red alder. Total accumulation of nutrients was higher in red alder than in Douglas-fir. The bole of red alder, which accounts for 72% of the total biomass in the mature stand (Johnson and Lindberg, 1992), has a higher nutrient content than the bole of Douglas-fir.

Total litterfall N, Mg and K fluxes were higher for red alder than for Douglas-fir irrespective of soil type (Table 2). Litterfall P was higher for Douglas-fir. Litterfall Ca was higher for red alder in the mature stand, but lower in the regrowing stands. The patterns in litterfall between regrowing and mature stands

Table 2
Simulated cumulative ecosystem fluxes and changes in ecosystem pools (Δ) during a 40-year simulation (kmol ha^{-1}) in mature Douglas-fir (DF), red alder (RA), regrowing Douglas-fir on Douglas-fir soil (DF–DF), regrowing red alder on red alder soil (RA–RA), regrowing red alder on Douglas-fir soil (DR–RA), and regrowing Douglas-fir on red alder soil (RA–DF)

		Deposition	Vegetation increment	Litterfall	Δ Exchang.	Weathering	Leaching	Δ Organic matter
N	DF	16.81	3.53	56.24	0.00	0.00	3.12	4.39
	RA	272.47[a]	28.53	114.78	0.05	0.00	228.86	−12.80
	DF–DF	15.30	9.10	69.49	−0.01	0.00	8.06	10.97
	RA–RA	169.67[a]	24.64	101.91	0.02	0.00	137.02	−17.10
	DF–RA	169.67[a]	26.29	108.66	0.08	0.00	88.03	34.85
	RA–DF	15.35	9.74	50.46	−0.02	0.00	26.98	−29.18
P	DF	0.06	0.25	6.38	−1.85	0.00	0.05	1.60
	RA	0.06	0.46	4.16	−0.34	0.00	0.00	−0.72
	DF–DF	0.06	0.56	5.59	−1.50	0.00	0.05	1.16
	RA–RA	0.06	0.44	3.64	−0.43	0.00	0.00	−0.93
	DF–RA	0.06	0.52	4.22	−2.78	0.00	0.01	1.30
	RA–DF	0.06	0.57	5.10	0.63	0.00	0.06	−1.16
Ca	DF	3.94	0.54	12.15	25.82	27.68	4.54	0.19
	RA	3.70	4.08	16.13	−18.67	29.85	44.97	3.17
	DF–DF	3.72	2.20	13.45	26.04	30.67	4.60	0.49
	RA–RA	3.53	2.56	10.49	−5.34	25.03	31.19	0.32
	DF–RA	3.53	3.17	12.99	7.77	31.92	18.25	5.33
	RA–DF	3.72	2.85	14.76	16.74	19.06	8.97	−5.77
Mg	DF	1.54	0.04	3.17	4.26	7.73	5.06	−0.24
	RA	1.44	0.66	7.06	−2.51	9.40	11.59	1.06
	DF–DF	1.45	0.28	3.97	4.34	8.63	5.13	0.06
	RA–RA	1.37	0.37	4.59	−1.32	7.89	10.34	−0.21
	DF–RA	1.37	0.52	5.71	−0.06	8.98	7.46	2.21
	RA–DF	1.45	0.59	3.85	3.89	5.94	5.08	−2.21
K	DF	2.96	0.31	12.15	8.48	3.87	1.10	−0.69
	RA	2.70	2.38	24.26	−2.30	4.70	5.18	−0.56
	DF–DF	2.72	0.99	14.91	5.46	4.32	1.10	0.30
	RA–RA	2.51	2.00	17.57	−1.95	3.95	7.02	−3.96
	DF–RA	2.51	2.30	20.67	−6.31	4.49	1.08	6.55
	RA–DF	2.72	1.21	14.35	8.96	2.97	4.42	−8.28

[a] Includes N input through N fixation.

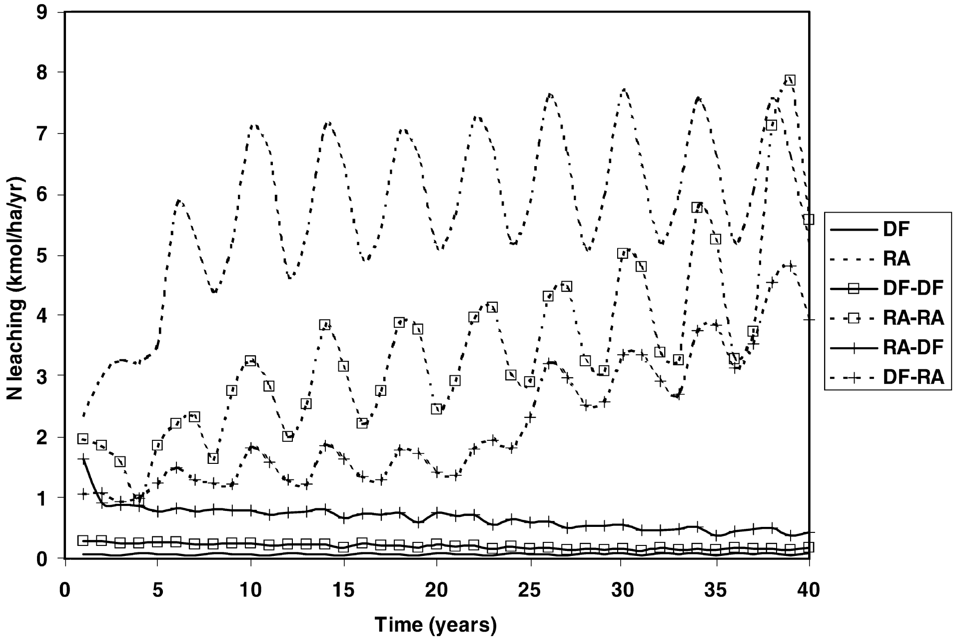

Fig. 2. Simulated N leaching for mature and regrowing Douglas-fir and red alder stands.

varied by nutrient and stand; but, in general, cumulative litterfall was higher for the regrowing than for the mature stands of Douglas-fir. The opposite was true of red alder.

4.3. Leaching

NuCM simulated higher N leaching for the red alder than for the Douglas-fir sites for all soil types. Nitrogen leaching was lowest in the mature Douglas-fir and highest under the mature red alder (Table 2; Fig. 2). For RA–DF and DF–DF, simulated N leaching decreased with time but remained higher than that for the mature Douglas-fir (DF). For both regrowing red alder stands, N leaching increased with time to reach levels comparable to the reference plots. Van Miegroet et al. (1992) observed that nitrate leaching from the A horizon decreases after harvesting red alder and replanting with either red alder or Douglas-fir (presumably leaching from the soil profile decreases as well). In the same plots, Homann et al. (1994) observed a strong decrease in soil solution nitrate concentrations in the O, A and B horizons. Simulated N leaching in the red alder soils after removal of the vegetation decreased for the first few years. Still, levels stayed higher than observed by Van Miegroet et al. (1992).

In the first 15 years, Ca^{2+} was the main cation accompanying N leaching under red alder (Fig. 3); but, after 25 years, H^+ leaching accounted for almost 50% of the cation leaching, suggesting thereby that the weathering rates were too low to sustain Ca^{2+} leaching. The efflux of Mg^{2+} and Ca^{2+} through leaching exceeded deposition, most likely due to the high nitrate leaching and associated production of H^+ from nitrification (Table 2). Leaching of K^+ exceeded deposition inputs only in the red alder soils. Simulated P leaching was close to zero in all cases. Measured P leaching from the mature Douglas-fir and red alder stands was negligible (Johnson and Lindberg, 1992; Compton and Cole, 1998).

4.4. Soil nutrients

Most of the soil N is contained in organic matter. The initial amount of litter N in the mature stands was higher in red alder than in Douglas-fir soils (Table 2). In the mature Douglas-fir stand, simulated litter N increased by 10%, whereas it decreased by 9% in the red alder stand. Litter N increased by 25% in the

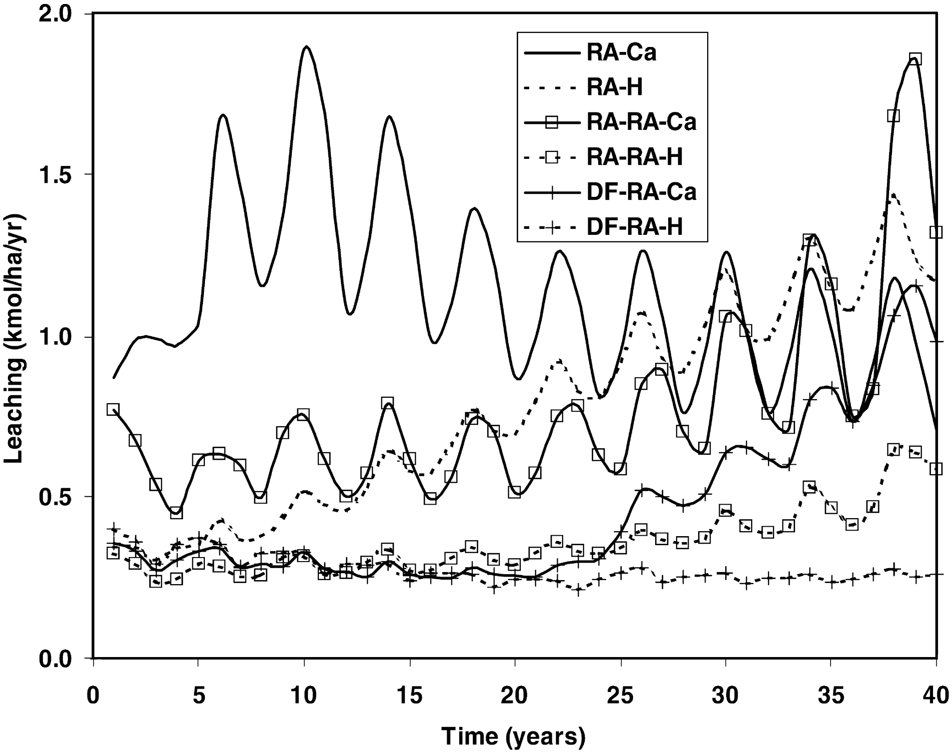

Fig. 3. Simulated Ca and H leaching for mature and regrowing red alder stands.

DF–DF stand and by almost 65% in the DF–RA stand (Fig. 4). In the RA–RA stand, however, litter N decreased by 12% and in the RA–DF stand by 25%. None of the regrowing stands reached a steady state even after 40 years of simulation. The data showed that the amount of organic matter in the forest floor was almost three times higher under mature red alder than under mature Douglas-fir. In the RA and RA–RA stands, however, litter N, P and K decreased. Assuming that there were no major changes in the litter/nutrient ratios, presumably the total litter pool decreased. The mature red alder stand developed on soils formerly occupied by old-growth Douglas-fir/western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) (Turner et al., 1976; Compton and Cole, 1998) and followed the DF–RA path so the higher organic matter content may reflect a previous occupation by Douglas-fir.

The simulations suggested an increase in litter N in the DF and DF–DF stands. Turner (1975) observed that under Douglas-fir, litter N continues to accumulate until the stand reaches an age of ≈70 years. Cole et al. (1995) studied C accumulation in the organic O horizon in the same plots and observed that C accumulated in the DF–RA and DF–DF plots, but decreased in the RA–DF and RA–RA plots after 7 years of harvest. Our simulations are consistent with these observations, but in the simulations the patterns are spread out over a longer time period. Especially under red alder, the understory vegetation, most notably swordfern, may significantly contribute to the litter production. Exact numbers are very sparse, however, and litterfall patterns may change with time due to changes in competition between under- and overstory vegetation (Cole et al., 1995). Although we included understory litterfall, the simulated amounts were relatively constant with time.

In the RA and RA–RA stands, the amount of exchangeable Ca^{2+} (Table 2; Fig. 5) and Mg^{2+} (Table 2) decreased with time. In the other stands, exchangeable Ca^{2+} increased with time. Exchangeable K increased under Douglas-fir, but decreased

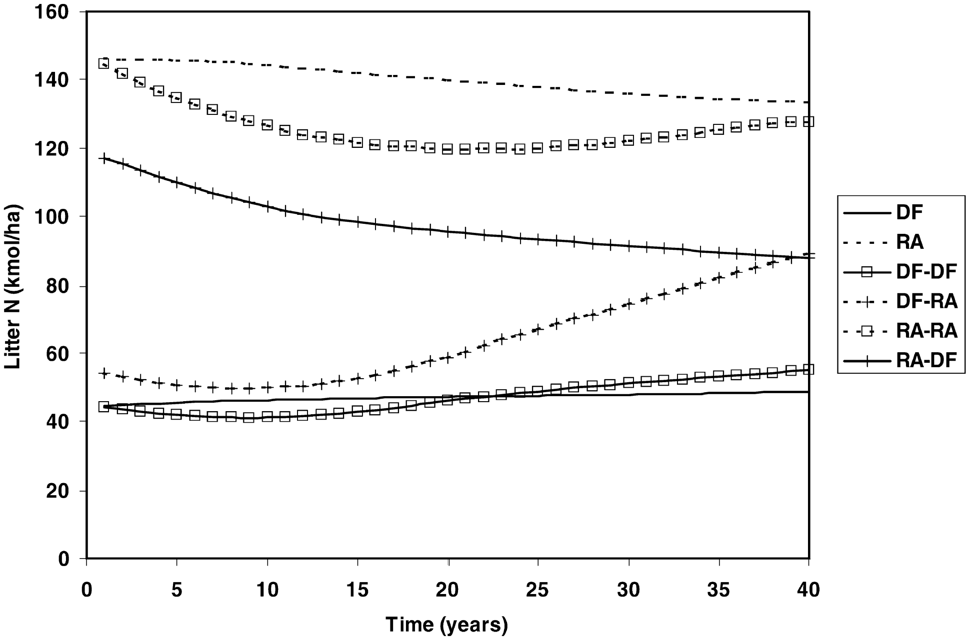

Fig. 4. Simulated litter N pool.

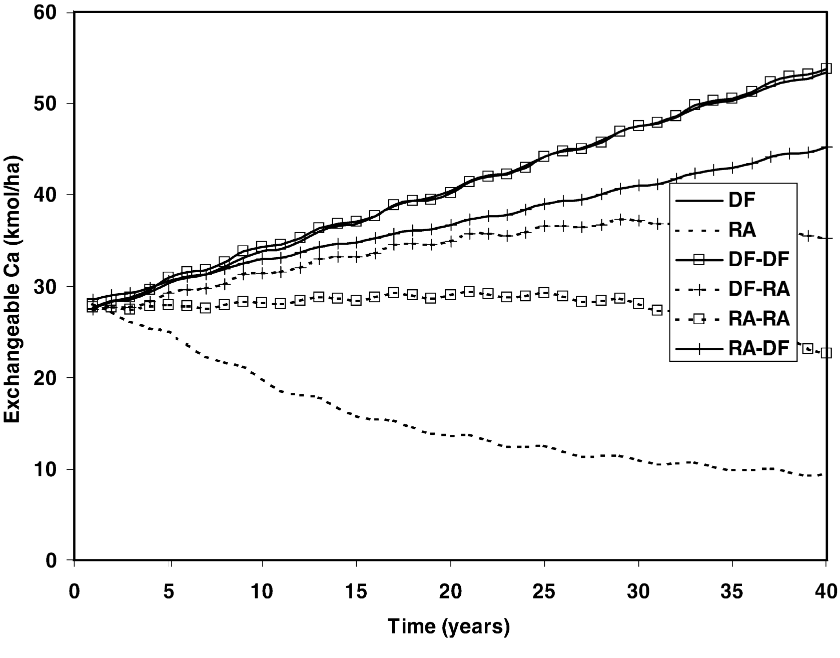

Fig. 5. Simulated total exchangeable Ca in mature and regrowing Douglas-fir and red alder stands.

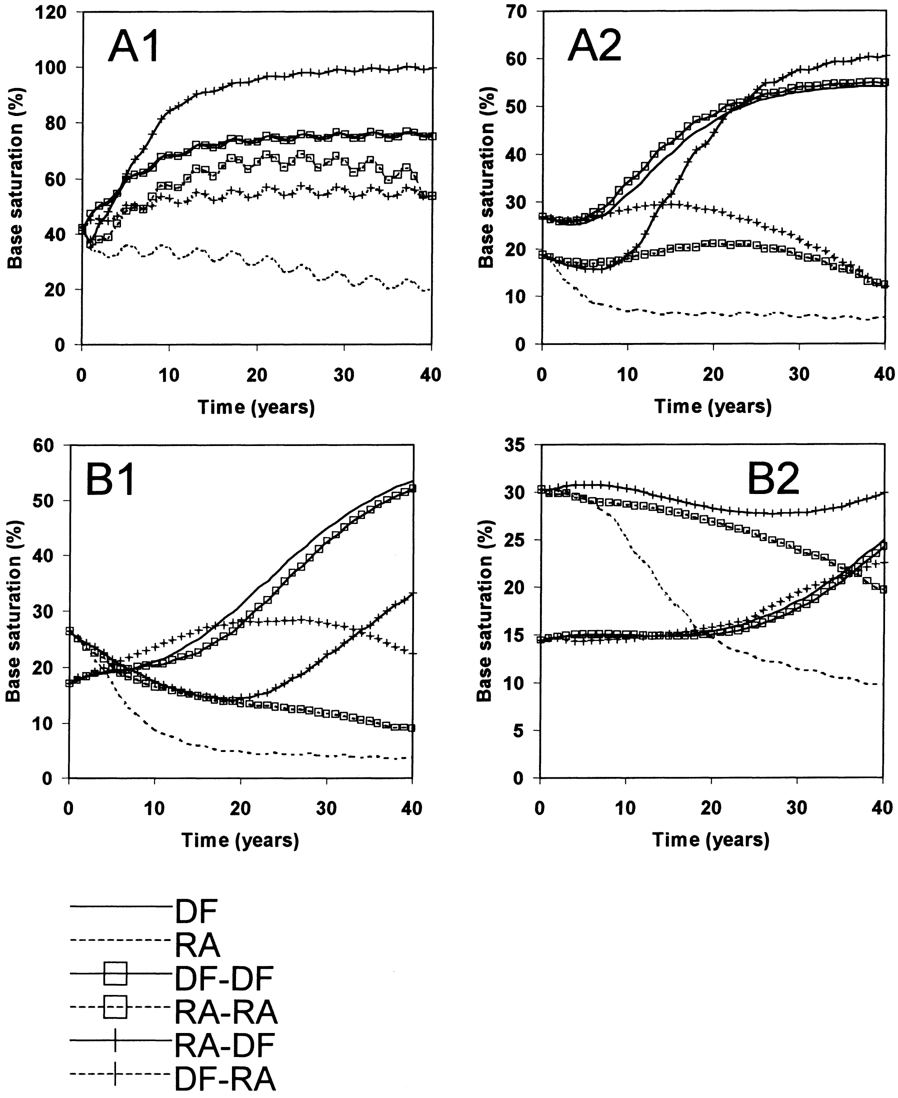

Fig. 6. Base saturation in mature and regrowing Douglas-fir and red alder stands in the A1, A2, B1 and B2 horizon.

under red alder (Table 2). In the A1 horizon, base saturation decreased in the RA stand (Fig. 6), but increased in all other stands. In the A2, B1 and B2 horizons, base saturation increased under Douglas-fir and decreased under red alder. The patterns in exchangeable cations and base saturation are highly dependent on weathering rates. Since weathering rates in NuCM are dependent on proton concentration, we expected weathering rates to be much higher under red alder due to proton production associated with nitrification. Surprisingly, weathering fluxes were comparable for both vegetation types (Table 2). This may be caused by the lower total amount of minerals under red alder. Homann et al. (1992) calculated that net cation removal from the soil must have been almost an order of magnitude higher under red alder than under Douglas-fir to explain changes in nutrient accumulation in vegetation and the O horizon. In NuCM, the dependence of weathering rates on proton concentration appears to be too low to cause differences in weathering fluxes between red alder and Douglas-fir. In the case of Douglas-fir, most of the weathered cations were transferred to the exchange complex (Table 2). Consequently, if weathering rates are lower under Douglas-fir, our simulations overestimated the increase in base cations.

The patterns in extractable P seemed to reflect soil type more than vegetation; extractable P decreased more rapidly in Douglas-fir soils than in red alder soils irrespective of vegetation growing on these soils (Table 2). Extractable P even increased for Douglas-fir regrowing on red alder soils. Lower extractable P values under red alder have been ascribed to adsorption and precipitation of P with Al and Fe due to a lowering of the pH (Bohn et al., 1985) and microbial immobilization (Wood et al., 1984) or increased phosphatase activity (Binkley, 1992). For the mature stands, however, total extractable P losses were higher under Douglas-fir. In the mature red alder stand, the amount of P present in the litter pool decreased slightly. In the mature Douglas-fir stand, a reallocation of P from the exchange complex through the vegetation into the litter pool seemed to take place resulting in an increase in the litter P pool. This appears to contradict the data from Johnson and Lindberg (1992) and Compton and Cole (1998), showing that much more P is present in the organic surface horizons under red alder than under Douglas-fir. It may also be that the mature red alder stands reflects the DF–RA path where depletion of the exchange complex is largest and P accumulates in the litter layer. Still, there were discrepancies between the simulations and field observations in terms of internal P cycling. The simulated litterfall P flux for the mature stand was higher for Douglas-fir than for red alder even though several studies show the opposite (Fig. 7; e.g. Turner et al., 1976; Johnson and Lindberg, 1992; Compton and Cole, 1998). Uptake was twice as high for the red alder; but for both Douglas-fir and red alder, simulated uptake flux was much higher than measured. Especially under red alder, this will cause a rapid depletion of the extractable P pool without the litter pool being replenished. The only way to increase the litterfall would be to decrease P resorption from foliage. Compton and Cole (1998) observed, however, that in fact P resorption was much higher for red alder (61%) than for Douglas-fir (38%). In addition, decreasing resorption would most likely decrease total biomass due to the higher nutrient requirement as a result of increased litterfall.

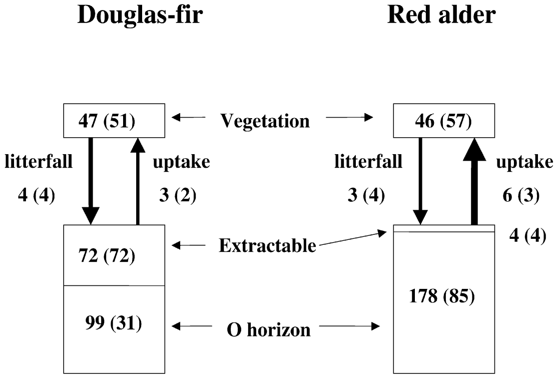

Fig. 7. P fluxes (kg ha^{-1} per year) and pools (kg ha^{-1}) in Douglas-fir and mature red alder stands. Numbers in brackets represent measured pools and fluxes reported in Johnson and Lindberg (1992). Sizes of boxes and arrows correspond to their magnitude.

An idea of the effects of vegetation alone on soil properties can be gained by comparing the DF–DF and DF–RA simulations, because both started with the same soil properties. Fig. 8 shows the nutrient pools at the end of the 40-year simulations. The red alder stand contained much more N in vegetation and forest floor pools, as expected. Red alder also caused reduced extractable P and exchangeable Ca^{2+}, K^{+} and Mg^{2+}, as has been observed in the field (Brozek, 1990). In each case, these reductions in soil pools were greater than could be explained by accumulations in either vegetation or forest floor pools.

4.5. Long-term effects on nutrient cycling

We hypothesized that Douglas-fir trees will produce more biomass when grown on red alder and vice versa. The simulations supported this hypothesis for both Douglas-fir and red alder, but the total biomass increases were relatively small (<10%). In the case of RA–DF, we hypothesized that high N availability may lead to higher biomass production even though base status of the soil is lower. Indeed, the lower base status did not appear to be limiting biomass production, since none of the base cations were fully depleted. The lower soil horizons were almost fully depleted of NH_4^+; but in the upper horizons, NH_4^+ was not limiting.

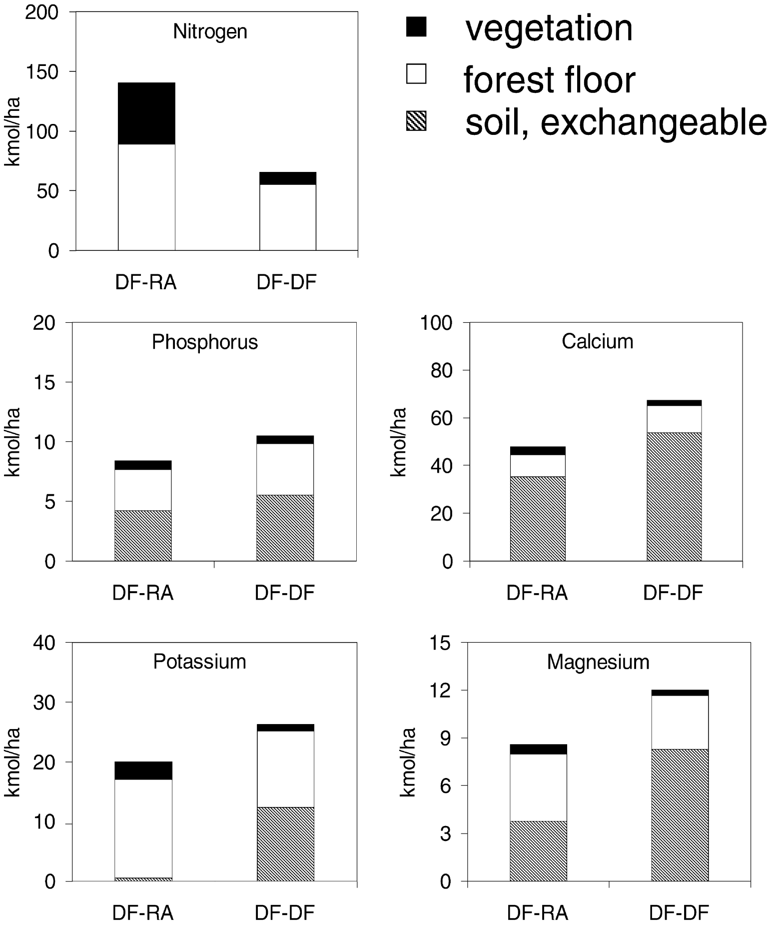

Fig. 8. Final N, P, K, Ca and Mg contents of vegetation, forest floor and soil exchangeable pools in Douglas-fir soils planted with red alder (DF–RA) and Douglas-fir (DF–DF).

In the RA and RA–RA stands, litter N decreased, whereas in the DF–RA stand it strongly increased. This suggests that the high organic matter content in the mature red alder stand in the field reflects other factors such as the presence of large amounts of sword fern in the understory or previous occupation by old-growth Douglas-fir. In the DF and DF–DF stands, litter N increased, which agrees with observed patterns (e.g. Turner, 1975). Extractable P seemed to decrease most rapidly in Douglas-fir soils regardless of vegetation type. Still, the red alder soil contained the lowest amount of extractable P which may reflect the DF–RA path or differences in soil conditions prior to planting, as suggested by Binkley (1992). In terms of internal P cycling, NuCM was not able to fully reproduce measured patterns. NuCM suggested a slower internal recycling of P for red alder than for Douglas-fir where most experimental studies indicate the opposite. Mature red alder appeared to deplete the soils for base cations during the 40-year simulation mostly due to leaching. Weathering rates were high enough to at least partly supply the exchange complex. Douglas-fir tended to increase exchangeable base cations in the soil, but this may have been due to an overestimation of weathering rates under Douglas-fir. It appears that dependence of weathering rates on pH was too low compared to the dependence on total amount of minerals. Regrowing Douglas-fir on red alder soils may be favorable for biomass production, and our simulations suggest that Douglas-fir may help to resupply the exchange complex with base cations. Potentially, continued growth of red alder may deplete the exchange complex in the long term which no doubt will affect forest productivity. An adverse side effect of high nitrification is the potential acidification and eutrophication of leaching water. This leaching water may ultimately end up in downstream surface waters which could affect aquatic life (Wright and Schindler, 1995).

As large quantities of nutrients are stored in the organic surface horizons, the removal of litter after clearcutting may rapidly decrease the amount of available nutrients. Decomposition of old litter may provide the exchange complex with nutrients even though, at least initially, litterfall from the regrowing vegetation is low. For the simulation, this poses a potential problem in selecting parameters describing the decomposition processes. Where trees are grown on soils that previously supported other species, a mixture of litter types will be present. Initially, decomposition parameters reflect the previous vegetation, whereas the influence of new litter will increase with time. Edmonds (1980) and Cole et al. (1995) observed that during the first 2-to-3 years, red alder litter decomposes faster than Douglas-fir litter. After this period, however, Douglas-fir litter appears to decompose faster; mass loss of red alder litter after a 6-year incubation was $\approx$70% vs. 75% for Douglas-fir litter (Cole et al., 1995). We used the same decomposition rate constant for red alder and Douglas-fir which appeared to be a good compromise between the different short-term and long-term patterns.

The aim of the simulations was to explore potential effects of species change and forest regrowth on nutrient cycling. Although there were some clear trends for soil nutrients and leaching, several uncertainties remain. We had very little, if any, data on the rate of N fixation in the regrowing red alder stands, for instance. If N fixation exceeds uptake by the vegetation (which, at least, is the case for mature red alder), subsequent nitrification and nitrate leaching will cause base cations to be depleted. In the simulations of the regrowing stands, N fixation also exceeded N demand by the vegetation as evidenced by the high leaching rates. We simulated N fixation by increasing NH_4^+ deposition. Although this may have affected canopy exchange processes, it should not have affected ecosystem nutrient budgets. Nitrification may have been overestimated, however. In our simulations, N enters the system directly as inorganic N, whereas with N fixation atmospheric N is converted to organic N. Subsequently, the organic N is converted to NH_4^+ and released through mineralization.

Another important unknown is the extent to which nutrients are translocated before leaf senescence. This process is hardly ever measured, but Johnson (1999) showed that translocation may have a significant impact on, for instance, N cycling. We included nutrient translocation both for the red alder and Douglas-fir after modifying the model to allow for nutrient translocation in coniferous species which was not included in earlier versions of the model (Kvindesland, 1997). The time series of the data available for calibrating the reference sites was also limited; only two full years of measurements were present to calculate ecosystem nutrient budgets. Consequently, data on different processes may not have been internally consistent, since ecosystem processes may contain a carryover from previous years. In addition, little of the site history is known; and the time series given in the data, such as exchangeable cations in the soil, provided just a snapshot of the development of the stand. Given these uncertainties, the simulations showed potential long-term trends in the biogeochemistry of red alder and Douglas-fir ecosystems.

5. Conclusions

The findings described above confirmed our original five hypotheses:

1. Prolonged presence of red alder caused a depletion in soil base cations due to increased nitrification and NO_3^- leaching. Weathering rates appeared to be high enough, however, to at least partly supply the exchange complex with cations.
2. Lower base cation availability under red alder (RA–RA) ultimately caused biomass production to decline compared to the DF–RA scenario. The difference in total biomass was small, however.
3. High N availability in red alder soils favored regrowth of Douglas-fir. Again, the difference was small.
4. Higher base cation and P status of the Douglas-fir soils favored the growth of red alder both in the short- and long-term, since N was not limiting.

5. N leaching in the regrowing red alder stands increased with time as N fixation increased.

The purpose of these simulations was not to verify the NuCM model, since verification would imply that the model represents the absolute truth (Oreskes et al., 1994). At best, we could show that the model "does not contain known or detectable flaws and is internally consistent" (Oreskes et al., 1994). Our purpose was to examine whether our current understanding of biogeochemical processes can be summarized in a model like NuCM. Overall, the NuCM model was able to simulate the main features of each of the different stands; but some processes were not simulated accurately (e.g. mineral weathering and N fixation). We conclude that the NuCM model was helpful in assessing potential gaps in data as well as aspects of nutrient cycling that require more research.

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