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Title
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Abstract

Terrestrial carbon–climate feedbacks depend on two large and opposing fluxes—soil organic matter decomposition and photosynthesis—that are tightly regulated by nutrients[1,2]. Earth system models (ESMs) participating in the Coupled Model Intercomparison Project Phase 5 represented nutrient dynamics poorly[1,3], rendering predictions of twenty-first century carbon–climate feedbacks highly uncertain. Here, we use a new land model to quantify the effects of observed plant nutrient uptake mechanisms missing in most other ESMs. In particular, we estimate the global role of root nutrient competition with microbes and abiotic processes during periods without photosynthesis. Nitrogen and phosphorus uptake during these periods account for 45 and 43%, respectively, of annual uptake, with large latitudinal variation. Globally, night-time nutrient uptake dominates this signal. Simulations show that ignoring this plant uptake, as is done when applying an instantaneous relative demand approach, leads to large positive biases in annual nitrogen leaching (96%) and N_2O emissions (44%). This N_2O emission bias has a GWP equivalent of ~2.4 $PgCO_2\,yr^{-1}$, which is substantial compared to the current terrestrial CO_2 sink. Such large biases will lead to predictions of overly open terrestrial nutrient cycles and lower carbon sequestration capacity. Both factors imply over-prediction of positive terrestrial feedbacks with climate in current ESMs.

Introduction

Earth's greenhouse gases (that is, CO_2, CH_4 and N_2O), and therefore radiative budgets over the twenty-first century, are strongly dependent on how terrestrial ecosystems respond to expected changes in atmospheric CO_2 and other environmental factors[4,5,6]. These terrestrial responses are dependent on plant and microbial interactions that are often nitrogen and/or phosphorus limited[7,8]. In response, Earth system model (ESM) land models have integrated a variety of approaches to couple carbon and nutrient (mostly nitrogen, but some with phosphorus) dynamics, plant–microbial competition for nutrients[9], and nutrient regulation of photosynthesis, carbon allocation, and so on (Supplementary Table 1). Here, we focus on an important aspect of these interactions: nutrient competition and acquisition at the root–soil interface. Our review (below) of empirical studies indicates that plant nutrient uptake is often decoupled from instantaneous photosynthetic nutrient demand, such that a significant fraction of nutrient uptake occurs at night and during the non-growing season. To our knowledge, observational studies have not addressed the role of this decoupling in the context of

ecosystem responses to changing climate and atmospheric CO_2 concentrations. Furthermore, many ESM land models either do not allow for this decoupling or do not resolve diurnal biogeochemical cycles (Supplementary Table 1). The most common modelling approach to resolving the intense nutrient competition between plants and microbes is based on the relative demand concept, which assumes that a competitor's nutrient acquisition can be calculated based on its proportional demand relative to other competitors. In this approach, plant demand is typically related to its instantaneous potential (that is, not nutrient constrained) photosynthesis rate. To our knowledge, only two published ESM land models (the one we apply here (ELMv1-ECA-CNP (Q. Zhu et al., manuscript in preparation); hereafter, ELMv1-ECA) and O-CN[10]) link nutrient uptake to root traits and dynamics that are independent of instantaneous plant demand, thereby allowing for night-time and non-growing season nutrient uptake. The enhanced nutrient uptake associated with these processes would probably reduce simulated leaching and gas losses, thereby creating a more closed nitrogen cycle and benefiting plant growth. In addition, since warming and increased nitrogen and phosphorus availability from enhanced mineralization are expected over the twenty-first century, we hypothesized that representing nutrient acquisition consistently with these observed mechanisms would lead to weaker predicted positive terrestrial feedbacks with the atmosphere and climate.

The observational studies we reviewed indicated that night-time nitrogen uptake occurs widely (Supplementary Table 2); night-time phosphorus uptake is less commonly studied but also observed[11]. For example, more than half of diurnal nitrogen uptake occurred at night in a California annual grassland[12]. Over a 6 d experiment with Italian ryegrass, about as much nitrogen was taken up during the 8 h of darkness as during the 16 h light period[13]. In *Arabidopsis*, the night-time NO_3^- uptake rate was ~50% of the peak daytime value, but the integrated night-time uptake was larger than the integrated daytime uptake[14]. About 40% of daily plant nitrogen uptake occurred during night-time in five different agricultural plants[15]. Across the observational studies we identified, about ~30–60% of diurnal nitrogen uptake occurred at night. Additionally, the observational literature indicates significant non-growing season nutrient uptake, particularly at high latitudes. For example, in a coastal heath system, roots acquired soil nitrogen after canopy senescence, and winter nitrogen uptake was comparable to growing season uptake[16]. In a study of mountain birch in Sweden, winter nitrogen uptake varied between 10 and 29% of annual nitrogen uptake at two sites[17]. Finally, about half of the annual phosphate acquired by tundra graminoids near Barrow, Alaska was acquired after the growing season[18].

Since nutrient limitations are common in terrestrial plants[7,8], night-time plant uptake can reduce these limitations at relatively low cost, because the uptake machinery (that is, root structure and transporters) is already established. The wide range of reported night-time nutrient uptake

proportions has been hypothesized to occur for several reasons. First, night-time root metabolism is expected to differ between plant types and times of year because of differences in photosynthate inputs to roots[12]. Second, variability in plant transport and metabolism during the night may affect nutrient uptake[19]. Third, roots may be more competitive against microbes during the night[12], possibly because of reduced root exudation and resulting energy limitations on decomposing microbes. Autotrophic nitrification, however, would not be hindered by this labile carbon constraint, and because of its higher mobility, the competition for NO_3^- may be even more heavily weighted towards roots than the competition for NH_4^+. For example, NO_3^- and NH_4^+ uptake rates were observed to be 210 and 50% higher, respectively, at night-time than during the day in a California annual grassland[12]. The disconnect between this wide range of observed nutrient uptake dynamics and the inconsistent treatment in current ESM land models motivates our analysis here and the need for relevant observations in more ecosystems, particularly forests.

To extrapolate these observed nutrient uptake patterns globally and estimate their effects on large-scale nutrient cycling, we applied the new land model ELMv1-ECA (Methods). In contrast with demand-based models, ELMv1-ECA explicitly represents plant uptake capacity as a function of root biomass (as a proxy for surface area and transporter enzymes) and substrate affinity. The model represents competitive interactions between root, microbial and abiotic processes using equilibrium chemistry approximation (ECA) kinetics[20], which has been shown to accurately represent observed nutrient uptake patterns in several model–data comparisons[9,21,22]. We note that, although leaching and gaseous nitrogen losses remain uncertain in global models, our recent work has improved these predictions (Q. Zhu et al., manuscript in preparation)[23]. Here, we use ELMv1-ECA to quantify global spatial patterns of photosynthesis-inactive-period root nitrogen and phosphorus uptake, and the implications of ignoring these dynamics. We also make recommendations for measurements, model structures and benchmarking approaches needed in next-generation nutrient-enabled ESM land models.

Although observational constraints are insufficient to test the model's simulated nutrient uptake diurnal cycle in forested systems, analysis of individual grid-cell simulations of agricultural and grassland systems indicate good agreement with available observations. The simulated diurnal cycle, with nitrogen uptake lagging net primary production (NPP) by a few hours over the daytime and then declining slowly during the night (Fig. 1a), is consistent with observed patterns in many of the fine temporal-resolution site observations listed in Supplementary Table 2. In the California annual grassland mentioned above[12], the observed night-time nitrogen uptake was 1.2 ± 0.4 times as large as daytime nitrogen uptake (Fig. 1b), which is comparable to the ELMv1-ECA simulated value (1.1 ± 0.1) for that model grid cell (centred at 49° N and 122° E). We also evaluated the model's ability to

simulate short-term (1–7 d) microbial versus plant nitrogen uptake against a synthesis of 123 observations from 23 sites distributed globally (including 6 woody plant sites; Supplementary Fig. 1). Using ELMv1-ECA estimates from the appropriate grid cell and time, we found good agreement between the modelled (2.7 (1.8, 4.7)) and observed (2.5 (1.0, 7.9)) median (25 and 75% percentile) ratios of short-term microbial to plant nitrogen uptake (Fig. 1c). The much larger observed than simulated range for the uptake ratio probably results from inaccurate model representation of specific site properties and climate forcing[24]. However, the model's relatively accurate simulations of nitrogen uptake patterns give confidence in its underlying mechanistic treatment of these processes.
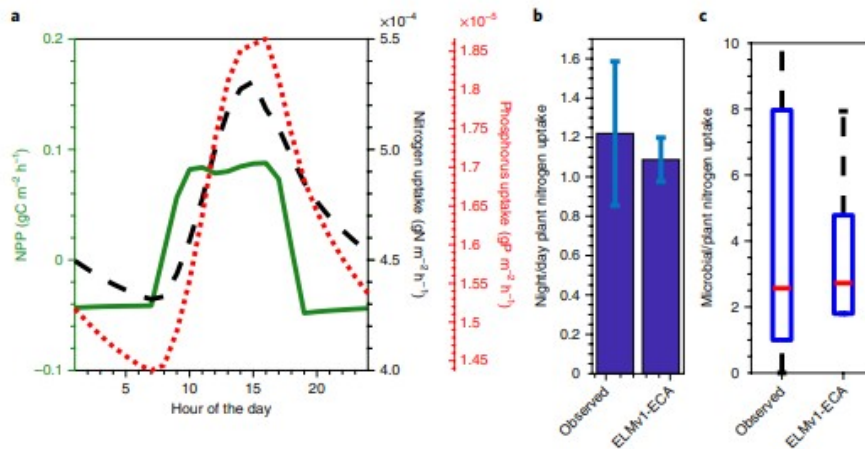
Fig. 1 | ELMv1-ECA accurately represents observed short-term nutrient uptake patterns. a, Simulated diurnal cycles of NPP, nitrogen uptake and phosphorus uptake in October in the northern California grid cell (49°N and 122°E) corresponding to the observations in Schimel et al.[12] (note the different y axis ranges). **b**, Observed and ELMv1-ECA simulated ratios between night-time and daytime nitrogen uptake in the same California grassland as in **a** (bars show means, with error bars representing s.d.). **c**, Observed and ELMv1-ECA simulated ratios of microbial to plant nitrogen uptake synthesized from 123 short-term isotopic tracer studies from 23 sites (the median, 25th and 75th percentiles (box edges), and upper and lower limits (bars) of distribution are shown; Supplementary Table 3).

The baseline ELMv1-ECA simulation indicates that the zonal mean fraction of annual nitrogen and phosphorus uptake that occurred during photosynthesis-inactive periods ranged from ~15% at high latitudes to ~50% in the tropics (Fig. 2a,b,d,e). Globally, NPP-weighted nitrogen and phosphorus uptake in the absence of photosynthesis accounted for ~45 and ~43%, respectively, of the annual uptake. Most of this uptake occurred at night, rather than in the non-growing season (the non-growing season being much more important at high latitudes; compare Fig. 2b with 2c and Fig. 2e with 2f).
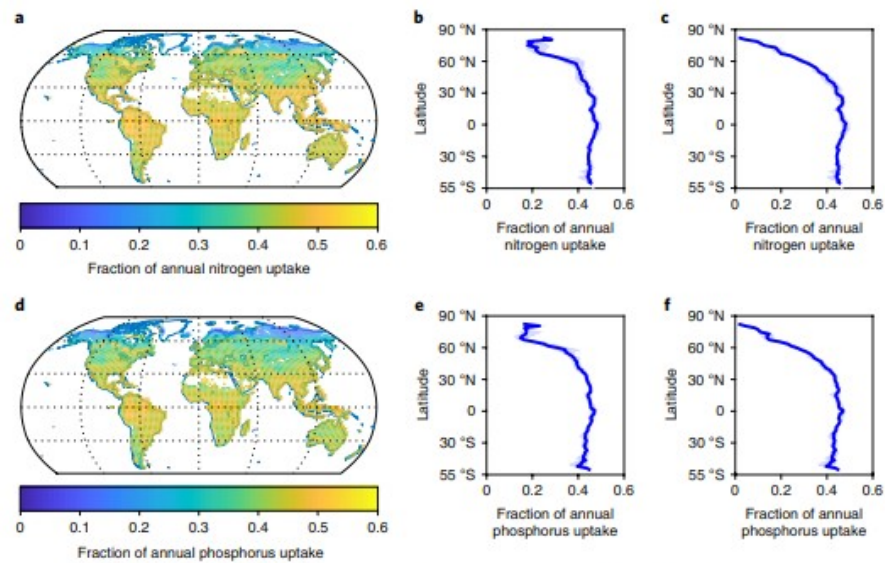
Fig. 2 | Photosynthesis-inactive period nutrient uptake is a large proportion of annual uptake globally. a,b,d,e, ELMv1-ECA simulations of the fraction of annual plant nitrogen (**a** and **b**) and phosphorus (**d** and **e**) uptake during photosynthesis-inactive periods globally (**a** and **d**) and zonally (**b** and **e**). **c,f,** Fraction of plant annual nitrogen (**c**) and phosphorus (**f**) uptake at night during the growing season zonally. The lines in **b, c, e** and **f** represent the median, and the shading the 25th and 75th percentiles.

Land models that apply a relative demand-based nutrient uptake approach, yet predict reasonable spatial patterns of GPP and NPP, may have offset the night-time and non-growing season nutrient uptake by, for example, enhancing daytime uptake or modifying plant stoichiometric constraints. We used ELMv1-ECA to evaluate how ignoring these nutrient uptake processes could affect simulated nitrogen and phosphorus losses and, by extension, carbon dynamics. For example, NO_3^- leaching and N_2O emissions depend nonlinearly on vertically resolved NO_3^- concentrations. NO_3^- concentrations are probably biased low during the day and high during the night if night-time plant and microbe competition for NO_3^- is ignored.

We performed three perturbation model scenarios to investigate the implications of excluding photosynthesis-inactive-period nutrient uptake. Scenario 1 was a ten-year simulation initialized from the baseline simulation in 2001 and excludes photosynthesis-inactive-period nutrient uptake. This perturbation led to small changes compared with the baseline simulation in global GPP and NPP (−3.5 and −2.9%, respectively; Supplementary Fig. 2c,d), and modest reductions in global plant nitrogen and phosphorus uptake (−6.0 and −13%, respectively; Supplementary Fig. 3c,d). However, the effects on annual global nitrogen leaching (16 TgN yr^{-1}; 96%), N_2O emissions (5.7 TgN yr^{-1}; 44%) and phosphorus leaching (1.3 TgP yr^{-1}; 19%) were larger, with the largest changes in tropical and boreal forest regions (Fig. 3). Interannual variability in these effects was small (a global mean interannual coefficient of variation of ~4% for plant nitrogen and phosphorus uptake; Supplementary Fig. 4), indicating robust effect sizes from this perturbation.
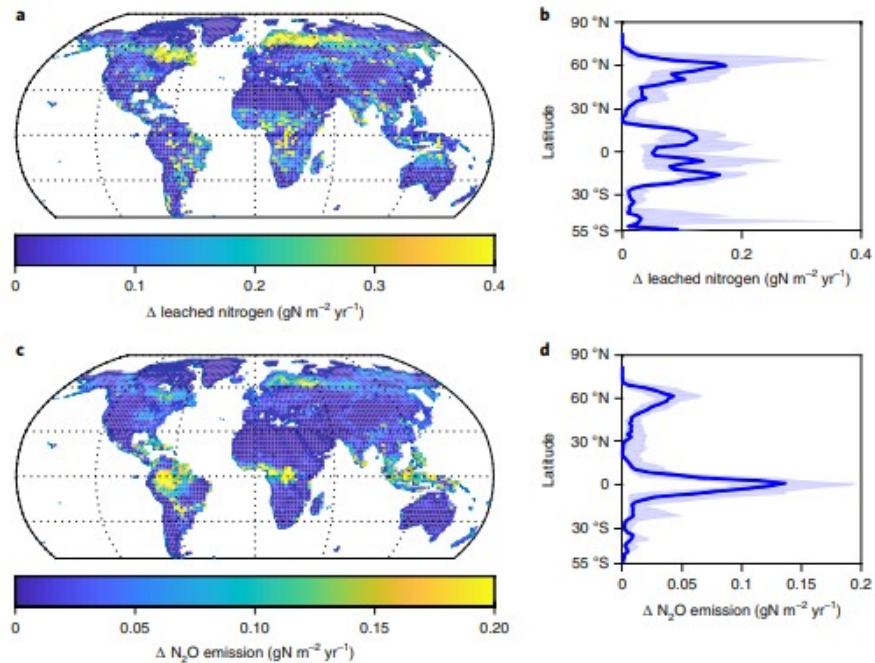
Fig. 3 | Ignoring photosynthesis-inactive-period nitrogen uptake has large effects on nitrogen leaching and gaseous losses. a–d, ELMv1-ECA simulations of the differences (scenario 1 compared with baseline) in nitrogen leaching (**a** and **b**) and N_2O emissions (**c** and **d**) globally (**a** and **c**) and zonally (**b** and **d**), caused by eliminating photosynthesis-inactive period nitrogen and phosphorus uptake. The bias in global N_2O emissions (5.7 TgN yr^{-1}) has an equivalent GWP of ~2.4 Pg CO_2 yr^{-1}. The lines in **b** and **d** represent the median, and the shading the 25th and 75th percentiles.

To further evaluate whether these results were affected by our experimental protocol, we also fully spun up a model version with no photosynthesis-inactive-period nutrient uptake (scenario 2) and compared it with a ten-year simulation (scenario 3) with full nutrient uptake initialized from scenario 2 in 2001. This perturbation again led to large biases in global nitrogen leaching (19 TgN yr^{-1}; 100%) and N_2O emissions (7.2 TgN yr^{-1}; 85%) and comparably low interannual variability. In both comparisons, biases in modelled annual nitrogen leaching, N_2O emissions and phosphorus leaching were not spatially correlated with annual total or night-time precipitation, indicating that biases in these nitrogen and phosphorus loss pathways are not simply related to total precipitation amounts. The scenario 1 bias in global N_2O emissions from the baseline simulation (5.7 TgN yr^{-1}) has an equivalent global warming potential (GWP) of ~2.4 Pg CO_2 yr^{-1} (the GWP of N_2O is 265 times that of CO_2[25]).

Our estimates of night-time and non-growing season nitrogen and phosphorus uptake are consistent with available observational constraints. Furthermore, the relatively large simulated global effects of ignoring these dynamics on nutrient losses indicate that the long-term carbon cycle implications may be large. We found that the relative demand approach that many ESM land models apply to resolve the complex competitive interactions that affect plant and microbial nutrient acquisition ignores important observed processes that in turn affect terrestrial carbon cycle and nitrogen loss predictions. We show here that night-time nitrogen and

phosphorus uptake by plants has a clear spatial pattern, with night-time uptake being relatively more important at lower latitudes. Non-growing season nitrogen and phosphorus uptake have the opposite spatial pattern. Almost half of annual plant nutrient acquisition occurs during photosynthesis-inactive periods. Accounting for these uptake pathways decreases simulated nitrogen leaching and N_2O gaseous losses, resulting in a tighter terrestrial nitrogen cycle and a substantial reduction in potential greenhouse gas forcing associated with N_2O emissions and terrestrial carbon storage. We therefore recommend a several-pronged approach to developing realistic representations of the diurnal and seasonal cycles of plant nutrient uptake: (1) models should not apply the instantaneous relative demand approach to resolve nutrient competition; (2) multiple competitor–multiple nutrient interactions require new model representations, such as the ECA approach; and (3) many more observational constraints of these dynamics, particularly in forests, are required to confirm our model predictions and develop and test model structures to represent these processes.

Methods

ELMv1-ECA description

Our experiments and analyses use the new ELMv1-ECA model (Q. Zhu et al., manuscript in preparation)[26], which recently branched from the Community Earth System Model version 1.0 Community Land Model 4.5 (refs 27,28,29,30,31,32). ELMv1-ECA simulates global terrestrial carbon, nitrogen and phosphorus cycles with representation of below-ground nutrient competition between plants and soil biotic and abiotic competitors using the ECA[20,21,33]. The model uses an explicit trait-based approach to nutrient competitive interactions so that uptake capacities and affinities are dynamically calculated independent of instantaneous photosynthetic demand. A generic dynamic allocation scheme based on water, nitrogen, phosphorus and light availability[34] is used with flexible plant nutrient stoichiometry and constraints on photosynthesis. The model explicitly represents several root traits that are important for nutrient acquisition: (1) root nutrient carrier enzyme kinetics; (2) activation and deactivation of nutrient carrier enzymes controlled by plant nutritional level; (3) direct plant competition with other soil nutrient consumers (for example, microbes); and (4) nutrient carrier enzyme-mediated resource uptake preference (for example, NH_4^+ versus NO_3^-; refs 21,33). The model applies a general allocation framework[34,35] that considers multiple resource availability (that is, nitrogen, phosphorus and water). Finally, carbon:nitrogen:phosphorus stoichiometry is flexible around a baseline value and prognostically determined by leaf level carbon fixation versus root nutrient uptake. The baseline carbon:nitrogen:phosphorus ratios are derived from the TRY database[36] and a recent synthesis of global fine root, sapwood and heartwood carbon:nitrogen:phosphorus, which included more than 6,000 plant species. Root nutrient uptake is regulated so that plant tissue

nutritional levels are maintained within the range of observed natural variability.

We have benchmarked the global model using the International Land Model Benchmarking package[37,38]. Compared with the precursor Community Land Model 4.5, ELMv1-ECA better predicted global-scale gross primary production, ecosystem respiration, leaf area index, vegetation biomass, soil carbon stocks and evapotranspiration (Q. Zhu et al., manuscript in preparation). For the baseline simulations used here, we initialize the model version with a 500-year spin-up simulation[27] followed by a transient simulation from 1850 to 2010 with observed nitrogen and phosphorus deposition[39,40], diagnostic CO_2 concentration[41] and Global Soil Wetness Project Phase 3 climate forcing[42].

We analysed the photosynthesis-inactive-period nutrient dynamics using hourly model predictions for the years 2001–2010. We separated non-growing and growing seasons based on the first and last occurrence when predicted GPP was zero during the year. The calculation was made for each grid cell, which gave a conservative estimate of individual plant functional type (PFT) values, since the grid-cell values consolidated the individual PFT carbon cycle dynamics. Individual PFT photosynthesis-inactive-period uptake proportions are probably larger than calculated for the consolidated grid cell.

To quantify the effects of photosynthesis-inactive-period nitrogen and phosphorus plant uptake on ecosystem nutrient and carbon dynamics, we performed three additional simulations. First, initializing from the baseline simulation in 2001, we disabled root uptake during photosynthesis-inactive periods for 2001–2010 (scenario 1). Second, we performed a new fully spun-up simulation with disabled root uptake during photosynthesis-inactive periods (scenario 2). Finally, we performed a simulation (scenario 3) initialized from scenario 2 in 2001, but enabling root nutrient uptake during photosynthesis-inactive periods. Scenario 2 and 3 simulations allowed us to evaluate whether our predictions of enhanced nitrogen losses are consistent with this different model structure that is conceptually similar to most other ESM-scale land models (that is, with respect to plant nutrient uptake).

We report the proportion of nitrogen and phosphorus plant uptake during photosynthesis-inactive periods as NPP-weighted values by grid cell to highlight the relative importance of this mechanism on the terrestrial carbon cycle (for example, a large ratio in a grid cell with low NPP would not substantially contribute to the global NPP-weighted value).

Data availabilty

The data that support the findings of this study are available from the corresponding author upon request.

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