



On the modeling paradigm of plant root nutrient acquisition

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Abstract Plant root nutrient acquisition, and to a lesser extent foliar nutrient uptake, maintain plant metabolism and strongly regulate terrestrial biogeochemistry and carbon-climate feedbacks. However, terrestrial biogeochemical models differ in their representations of plant root nutrient acquisition, leading to significantly different, and uncertain, carbon cycle and future climate projections. Here we first review biogeochemical principles and observations relevant to three essential plant root nutrient acquisition mechanisms: activity of nutrient acquiring proteins, maintenance of nutrient stoichiometry, and energy expenditure for these processes. We next examine how these mechanisms are considered in three existing modeling paradigms, and conclude by recommending the capacity-based approach, the need for observations, and necessary modeling developments of plant root nutrient acquisition to improve carbon-climate feedback projections.

Keywords Plant root nutrient acquisition · Nutrient limitation · Biogeochemistry-climate feedback · Plant-microbial competition · Nutrient stoichiometry · Terrestrial biogeochemical modeling

Introduction

Since plants often live in environments with a limited supply of macronutrients (i.e., nitrogen and phosphorus), they must actively acquire these nutrients to fulfill their metabolic needs, such as surviving environmental stress, increasing biomass, and producing offspring (e.g., Cronan 2018). Plants procure these nutrients primarily by roots, through complex interactions and competition with soil microbes, other plants, and abiotic processes. A smaller proportion of these nutrients are obtained via foliar nutrient uptake (Fernandez and Brown 2013; Lambers et al. 2009; Sparks 2009; Wittwer and Teubner 1959). In order to predict how plants and therefore terrestrial ecosystems interact with the changing environment, modelers have developed and implemented various plant root nutrient acquisition paradigms in terrestrial biogeochemical models (Achat et al. 2016). Nonetheless, despite decades of research, there has been no consensus on which paradigm to use in terrestrial biogeochemical models (Wang et al. 2010; Yang et al. 2014; Zhu et al. 2017), resulting in large uncertainty, and degrading the fidelity of biogeochemistry-climate feedback projections (e.g., Fleischer et al. 2019).

We identified three paradigms (or approaches) that have been used to conceptualize and simplify the very complex process interactions affecting plant root nutrient acquisition: (1) the relative demand approach (Goll et al. 2012; Hidy et al. 2016; Wang et al. 2010; Yang et al. 2014); (2) the capacity-based approach (Medvigy et al. 2019; Tang and Riley 2013; Yu et al. 2020; Zhu et al. 2016), and (3) the much less used thermodynamic

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flow-force approach (Le Deunff et al. 2019; Thellier et al. 2009). The relative demand approach assumes that, in acquiring a given nutrient, the capabilities of all competitors are instantaneously proportional to their respective nutrient demands, which for plants are driven by their attempt to maintain stoichiometric balance under nutrient dilution caused by CO₂ assimilation.

In the capacity-based approach, plants spend metabolic energy or take advantage of the chemical potential gradient of nutrient molecules inside and outside root (or mycorrhizal) surfaces to acquire nutrients via special nutrient acquiring proteins (pumps, transporters, and channels; Taiz and Zeiger 2006). In this approach, microbes and abiotic competitors, such as mineral surfaces, are analogously characterized with acquisition capabilities (i.e., how effective and how fast nutrients can be acquired).

In the thermodynamic flow-force approach (derived from non-equilibrium thermodynamics; Thellier 1971), plant root nutrient acquisition also follows the chemical potential gradient of nutrient molecules inside and outside the roots (or mycorrhizae) with associated conductance parameters determined by environmental conditions and plant traits.

Among these three approaches, an important distinction is that for both the capacity-based approach and the thermodynamic flow-force approach, plant root nutrient acquisition is tied to root activity, and can occur in the absence of photosynthesis. In contrast, the relative demand approach is implemented without explicitly considering root activity. Recently, Riley et al. (2018) implemented both the relative demand approach and the capacity-based approach in the terrestrial biogeochemical module of the Energy Exascale Earth System Model (E3SM), and found that these two approaches resulted in large differences in predicted global N₂O emission warming potential (2.4 Pg CO₂ yr⁻¹) and nitrogen leaching (96% difference), highlighting the need to develop an accurate and mechanistically realistic plant root nutrient acquisition paradigm to improve modeling of biogeochemistry-climate feedbacks.

In this opinion piece, we review the soil and plant biogeochemistry and competition processes affecting plant root nutrient acquisition, synthesize existing observations, examine how related mechanisms are resolved in the three modeling approaches, and conclude by discussing the need for observations and how terrestrial biogeochemical models can update their paradigms to better represent the relevant mechanisms. Although

our review of biological mechanisms below is succinct, we believe it is sufficient to recommend a paradigm of plant root nutrient acquisition amenable to terrestrial biogeochemical models. For discussions of detailed molecular-level biological mechanisms, including plant shoot-root development, molecular sensing of nutrient molecules, and plant-mycorrhizal interactions, we refer readers to other excellent reviews (e.g., Gent and Forde 2017; Lambers et al. 2009; Oldroyd and Leyser 2020).

Biogeochemical processes controlling plant root nutrient acquisition

Plant root nutrient acquisition occurs in soil through competition with microbes and abiotic competitors (Fig. 1), all of which are modulated by transport (e.g., diffusion, dispersion and advection; Tinker and Nye 2000). In this review we do not discuss how plants spend energy on growing roots or mycorrhizae, but note that these processes are also critical for modeling plant root nutrient acquisition, and are often (implicitly) considered in models as part of the plant allometric relationships for carbon and nutrients (e.g., Zhu et al. 2019). Mechanistically, both plant and microbial nutrient acquisition involve three broad and closely coupled classes of biogeochemical processes: (NA1) activity of nutrient acquiring proteins, (NA2) maintenance of nutrient stoichiometry, and (NA3) energy expenditures for these processes. These three processes are asynchronous in plants (as we explain in more detail below) because of their size and the time taken to transport carbon and nutrients from one plant organ to another (e.g., Taiz and Zeiger 2006). In contrast, by being much smaller, microbes have shorter time lags between expressing a nutrient acquiring protein and securing nutrient molecules with that protein (Madigan et al. 2009), justifying the synchrony assumption often made in models like *ecosys* (Grant 2013) which uses a 60 minute time step or the global-scale models like ELM (Zhu et al. 2019) and CLM (Lawrence et al. 2019) which use a 30 minute time step. However, for some fungi having effective hyphae lengths comparable to those of plant roots, asynchrony may become important (e.g., Watanabe 2002). Moreover, when nutrients are abundant, microbes produce storage materials, which may be used to fuel survival under prolonged starvation (Ji et al. 2015).

The first class of nutrient acquisition processes, NA1, can be divided into three components: (NA1a) use of

different nutrient acquiring proteins for different nutrient molecules, (NA1b) environmental modulation of the activity of these proteins, and (NA1c) trade-offs among these protein activities. An example of NA1a is that plants can take up and assimilate different nitrogen forms (e.g., ammonium, nitrite, nitrate, urea, amino acids), often with preference (e.g., Masclaux-Daubresse et al. 2010; Miller and Cramer 2004). Consequently, the nitrogen forms plants and microbes acquire depend strongly on the soil physical and biogeochemical conditions that determine the bioavailability of related molecules or ions (i.e., NA1b). In low pH and anaerobic natural soils, ammonium produced from organic matter decomposition is the primary nitrogen form. Under aerobic or high pH conditions, rapid nitrification can make nitrate the primary inorganic nitrogen form (Miller and Cramer 2004). In cold environments, such as tundra and boreal forests where organic matter mineralization is so slow that inorganic nitrogen forms become limiting, amino acids may serve as an important form for plant root nutrient acquisition (Nasholm et al. 2009). In agricultural ecosystems, besides ammonium and nitrate, urea from fertilizers may become an important nitrogen source, although it may be hydrolyzed into ammonium before it is assimilated for biomass (e.g., Pinton et al. 2016; Witte 2011).

Similar to diauxic microbial growth on different carbon substrates (i.e., because of NA1b) (Erickson et al. 2017; la Cecilia et al. 2019), plants respond to different soil nitrogen forms by regulating the expression of corresponding nutrient acquiring proteins to enhance or repress the uptake of one nitrogen form over another (NA1c; Miller and Cramer 2004). For instance, nitrate is often found to suppress ammonium uptake, even though using ammonium for biomass synthesis costs plants less energy (Lee and Drew 1989). In crop plants, simultaneous application of urea and nitrate is found in the short term to lower nutrient acquiring protein expression for both nitrogen forms compared to when they are applied alone (Zanin et al. 2015). However, in the long term, crop plants grow better and increase their nitrogen use efficiency when both nitrate and urea are applied (Pinton et al. 2016). Besides diauxic growth on different nutrients, trade-offs among different nutrient acquiring proteins may also arise from the competition of metabolic energy required for plant root nutrient acquisition (i.e., NA3), such that more uptake of one form often lowers the uptake of others. Additionally, because the oxidation

of organic carbon produces metabolic energy, this energy trade-off also explains why assimilating organic nitrogen may increase overall nitrogen use efficiency (Franklin et al. 2017).

Energy required for plant root nutrient acquisition is provided by ATP (or proton motive force) harvested from root respiration using either photosynthates or carbon from the acquired organic nutrient (Franklin et al. 2017; Masclaux-Daubresse et al. 2010). For intracellular processes, nitrogen is primarily used to construct proteins and nucleotides (and some forms may be used as signal molecules, e.g., nitrate and nitrite (Maathuis 2009)), and the energy cost for assimilating each nitrogen form may be approximately ranked by their reduction status with respect to the nitrogen valence in the amino group. However, with the extra energy incurred to handle indirect biochemical feedbacks, such as maintaining cellular pH homeostasis accompanying ammonium or nitrate assimilation or energy produced from oxidizing the extra carbon associated with the organic nitrogen (Feng et al. 2020), the actual energy cost (and therefore efficiency) for nitrogen assimilation may differ from this ranking in a given environment (Franklin et al. 2017; Raven and Smith 1976).

Unlike microbes that can directly assimilate phosphorus from dissolved small organic molecules (van Veen et al. 1987), plants primarily take up inorganic soil phosphorus (i.e., dissolved and dissociated forms of H_3PO_4 , aka Pi; but see Mckercher and Tollefson (1978) for exceptions), which is provided either by external sources or organic matter mineralization. Therefore, plant phosphorus acquisition is limited by factors regulating soluble Pi availability, such as phosphatase activity, sorptive interactions with abiotic mineral soil surfaces, pH, etc. (Schachtman et al. 1998). Indeed, the soluble Pi form is a strong function of pH (with $\text{pK} = 2.1$ for H_3PO_4 , and 7.2 for H_2PO_4^- , respectively). Consequently, for a typical soil pH of 6.0, H_2PO_4^- dominates, followed by H_3PO_4 and HPO_4^{2-} . Corresponding to this ranking of Pi availability, most studies observe that plants primarily take up H_2PO_4^- (e.g., Furihata et al. 1992). Similar to nitrogen, plant root phosphorus uptake is also regulated by the coupling between three processes (Fig. 1) as a function of substrate bioavailability in different soil conditions (Bucher et al. 2001; Smith 2002).

explaining why girdling may slow plant root nutrient acquisition (Jordan et al. 1998).

Plants move mobile nutrients like nitrate, amino acids, and Pi taken up by roots through xylem to leaves for assimilation (NA2; e.g., Tegeer and Masclaux-Daubresse 2018). Organic nutrients may move with carbon through the phloem, but generally at a lower speed than in xylem (Jensen et al. 2016). Overall, since phloem and xylem flows are on the order of 10^{-3} m s^{-1} or less, plant root nutrient acquisition and photosynthesis are probably asynchronous even in the short term (days). Consequently, processes that adjust nutrient stoichiometry (NA2) are not as closely coupled to the other two plant root nutrient acquisition processes as in microbes for typical numerical time steps used by terrestrial biogeochemical models. The usually large distance between carbon source and use also explains why plants with foliar nutrient uptake may possess an advantage for canopy development, a phenomenon that has significant ramifications for cropping and certain natural ecosystems, but is missing in most models we are aware of (Al Harbi et al. 2013; Kannan and Charnel 1986; Sparks 2009).

From the processes reviewed above, we thus infer that the overall plant nutrient stoichiometry emerges dynamically from the elemental composition of different cells in the various organs (Taiz and Zeiger 2006). Indeed, plant stoichiometry is often measured at the level of organs (Kattge et al. 2011), such as leaves, stems, roots, etc. In contrast, many terrestrial biogeochemical models assume that each plant organ has fixed nutrient stoichiometry, and plants maintain the overall nutrient balance (i.e., NA2) through energy-dependent translocation of internal nutrients and assimilation from external sources (e.g., Wang et al. 2010; Yang et al. 2014). However, because of the coupling among the three classes of processes, at the cellular-level, plant nutrient stoichiometry should vary in ways similar to that of single-cell microbes. Microbes modify their internal nutrient concentrations and macromolecular compositions to adapt their growth rates to changes in environmental conditions (Garcia et al. 2016; Madigan et al. 2009), while for newly formed cells in a plant organ the environmental conditions are established mostly by existing neighbor cells. Even when cells built from new photosynthates can maintain nutrient stoichiometry using nutrients translocated from their neighbors, because nutrient translocation takes time, and such time is longer for plants of greater sizes, the nutrient

stoichiometry of a plant organ and consequently the whole plant will fluctuate in response to fluctuating environmental conditions (Jing et al. 2017; Taiz and Zeiger 2006). In summary, plant and soil biogeochemistry together make plant nutrient uptake and nutrient use for forming new biomass intrinsically asynchronous.

Observations revealing photosynthesis-independent plant root nutrient acquisition

A major inference we derive from the biogeochemical processes reviewed above is that photosynthesis and root nutrient uptake in plants are intrinsically asynchronous. We next corroborate this assertion with observations of diurnal and seasonal plant root nutrient acquisition dynamics.

We identified 14 experiments (Table S1) that measured the diurnal cycle of plant root nutrient acquisition in crops. For example, Pan et al. (1987) studied nitrate, potassium, and phosphate uptake by seedlings of five corn genotypes, and Okuyama et al. (2015) observed nitrogen and potassium absorption by cucumber, komatsuna, tomato, and water spinach. Most experiments, except Okuyama et al. (2015), collected measurements using artificial light conditions and nutrient solutions without soil, and we found no measurements of diurnal plant root acquisition of phosphate in soil. For natural ecosystems, we only found one observational study (Schimel et al. 1989) that measured nighttime and daytime cumulative ammonium and nitrate uptake by plants and microbes in a grassland ecosystem.

For the diurnal cycle reported in Okuyama et al. (2015; Fig. 2a), cucumber nitrate uptake showed two peaks, one in the light and one in the dark. Others observed similar patterns using artificial light sources (e.g., Pan et al. 1987). Albornoz and Lieth (2015), who switched plants between constant light and dark conditions in their experiments, observed more than three diurnal peaks for almost all nutrients studied. Although it is hard to extrapolate these patterns observed in greenhouses to field conditions, these many studies we identified showed that 30 ~ 60% of plant root nutrient acquisition occurred during the night; that is, none of these observations showed that plant root nutrient acquisition is synchronous with photosynthesis (Table S1). These crop-based studies also observed significant nighttime plant root nutrient efflux, a process that likely occurs

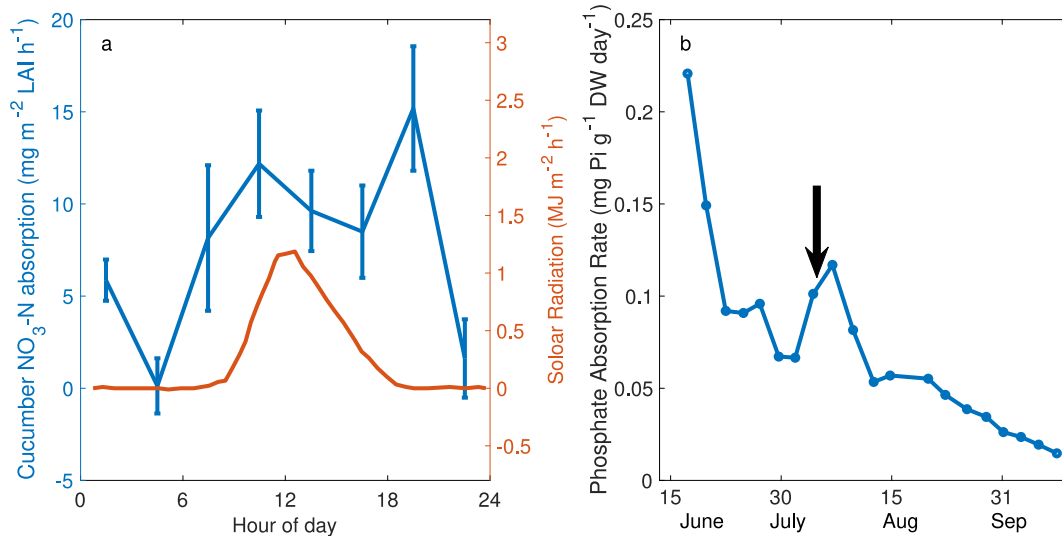


Fig. 2 **a** Observed diurnal pattern of cucumber nitrate uptake (with standard deviation) showing high uptake during the dark (Okuyama et al. 2015. LAI means leaf area index ($\text{m}^2 \text{m}^{-2}$). **b** Observed seasonal pattern of tundra graminoid (Dupontia

phosphate uptake showing that about half of the seasonal uptake occurred after plants started translocating nutrients to roots for winter storage (indicated by the thick black arrow; Chapin and Bloom 1976). DW means dry weight

less frequently in nutrient-limited natural ecosystems. Nonetheless, in fertilization experiments, which often apply nutrients to levels much higher than natural inputs (e.g., Bouskill et al. 2014), or in agroecosystems where fertilizer is generally applied more than needed (Good and Beatty 2011), efflux could be significant. However, nutrient efflux is rarely considered in current terrestrial biogeochemical models. *Ecosys* is the only model we identified which explicitly prognoses this process, and showed that efflux may be important for accurately representing plant-microbial interactions (Grant 2013).

Many observations have quantified plant root nutrient acquisition dynamics during the non-growing season or leafless period (Table S2). One study suggested that in graminoid tundra ecosystems nearly half of the phosphate was taken up after plant shoots had begun senescence and translocating nutrients to roots for storage during winter Chapin and Bloom 1976; Chapin et al. 1975; Fig. 2b). In another study of a subarctic heath system, Larsen et al. (2012) used an ¹⁵N-labeled glycine tracer and detected that graminoids, evergreen dwarf shrubs, and mosses were able to take up nitrogen during late winter and early spring, although with different temporal patterns. Nishitani et al. (2013) observed that a juvenile winter-green perennial herb actively took up nitrogen during its leafless period. Together, these observations confirm that plant root

nutrient acquisition and photosynthesis can occur independently and that, like microbes (e.g., Ji et al. 2015), plants maintain flexible nutrient stoichiometry.

Updating the paradigm of plant root nutrient acquisition for terrestrial biogeochemical models

Above we showed that both biogeochemical principles and observations suggest that plant root nutrient acquisition involves multiple kinetically-interacting nutrient forms, and is at most loosely coupled with instantaneous photosynthesis (i.e., plants maintain variable nutrient stoichiometry at the diurnal time scale). In particular, plants are able to take up nutrients in the absence of active photosynthesis. Therefore, the time lag between a plant signaling nutrient demand and taking up the nutrient by nutrient acquiring proteins is probably much greater than the numerical time step of most terrestrial biogeochemical models. We next examine how the relevant biogeochemical processes and in particular the asynchrony between photosynthesis and plant root nutrient uptake have been represented in the three modeling paradigms surveyed in this review.

The commonly applied relative demand approach assumes that plants maintain fixed nutrient stoichiometry in different organs during growth (thereby a synchronicity between plant root nutrient acquisition and

photosynthesis) so that, for each numerical time step, a nutrient demand is computed based on a stoichiometric ratio with respect to new photosynthates (as net primary productivity) that cannot be balanced from nutrient translocation. Since the relative demand approach represents microbial nutrient demand analogously, it effectively assumes that microbes and plants are kinetically equivalent with respect to nutrient acquisition (i.e., no consideration of the kinetic difference in various nutrient acquiring proteins of plants and microbes). This approach would therefore not be able to resolve the observed diauxic growth of plants and microbes on various nutrients (e.g., Madigan et al. 2009; Taiz and Zeiger 2006). Rather, the relative demand approach either has to treat different nutrient forms as equally assimilable or force plants and microbes to take the nutrients with a presumed order (e.g., first ammonia, then nitrate, etc.). All these assumptions are inconsistent with the biogeochemical processes and observations reviewed above. Consequently, the traditional relative demand approach may at most be a good approximation at large time scales (e.g., monthly or seasonally), even though such a potential has not been demonstrated with observations. Therefore, considering that current terrestrial biogeochemical models often operate with 30 to 60-minute time steps, the existing relative demand approach is neither appropriate to represent the flexible nutrient stoichiometry of both plants and microbes, nor capable of resolving their diauxic growth on different nutrients.

The thermodynamic flux-force approach is first-principle based and was derived based on non-equilibrium thermodynamics (Thellier 1971). It has been proposed to explain the “dual mechanisms” of ionic nutrient uptake by higher plants, i.e., experimentalists often found that there are both high and lower affinity nutrient acquiring proteins when Michaelis-Menten kinetics is used to fit observed nutrient uptake dynamics (Thellier et al. 2009). However, the thermodynamic flux-force approach relies on empirical regressions to account for the variability of its conductance parameters and it has yet to be applied in terrestrial biogeochemical models with coupled biogeochemical processes (Le Deunff et al. 2019). Therefore, it remains unclear how the thermodynamic flux-force approach can be applied consistently to resolve plant-microbe competition, although its similarity with the linlog kinetics (which has been used to model *E. coli*'s central metabolism; Tusek and Kurtanjek 2010) suggests that

such applications may be feasible. Nonetheless, the thermodynamic flux-force approach may have difficulty in resolving the diauxic growth on multiple substitutable nutrients (associated with NA1 and NA3; Fig. 1), even though it has the potential to resolve the asynchrony between photosynthesis and plant root nutrient uptake.

Unlike the relative demand approach and the thermodynamic flux-force approach, the capacity-based approach explicitly considers the three classes of processes affecting plant root nutrient acquisition (Fig. 1), and therefore allows for observed asynchrony between plant root nutrient acquisition and photosynthesis. In the capacity-based approach, nutrient uptake is decoupled from photosynthesis, and thus this approach is intrinsically compatible with the observation that plants are flexible in their organ and overall elemental stoichiometry (Mariotte et al. 2017). This flexibility allows the modeled plant to naturally include dynamic shoot-root nutrient and carbon exchanges and more advanced model representation of nutrient translocation (Grant 1998), thereby making the modeled system more realistically resilient to perturbations (Zaehle et al. 2014). Further, the capacity-based approach enables explicit incorporation of kinetic traits (e.g., affinity parameters and maximum uptake rates for substrates of nutrient acquiring proteins as have been used in the Michaelis-Menten kinetics) for both plants and microbes, providing a more direct link to biology. This approach thus extends the classic Nye-Tinker-Barber model that uses a single Michaelis-Menten kinetics to model nutrient uptake (Barber 1995; Roose et al. 2001; Tinker and Nye 2000), at the risk of including more model parameters (Zhu et al. 2017). However, the risk of including more model parameters can be alleviated by using improved mathematical formulations, e.g., the Equilibrium Chemistry Approximation (ECA) theory that is first-principle based and was derived from the law of mass action. ECA is an extension of the classic Michaelis-Menten kinetics for a network of many substrates and many consumers (Tang and Riley 2013, 2017), and enables a mechanistically tighter coupling between plants, microbes (including mycorrhizae), and soil abiotic factors (including diffusive nutrient transport; e.g., Tang and Riley 2019a, b). With the tighter coupling provided by ECA, the computed nutrient fluxes are less sensitive to individual model parameters than when the Michaelis-Menten kinetics are used (as in the Nye-Tinker-Barber model). The parametric robustness of ECA over the Michaelis-Menten kinetics is discussed in detail in Tang

and Riley (2013, 2017). Moreover, by explicitly considering internal nutrient concentrations, the capacity-based approach is also able to represent nutrient efflux, a feature that cannot be consistently incorporated into the relative demand approach (but can be resolved with the thermodynamic flux-force approach). Lastly, by incorporating the Goldman ionic flux equation (e.g., Bowman and Baglioni 1984), ECA (and therefore the capacity-based approach) will be able to thermodynamically account for the “dual mechanisms” captured by the thermodynamic flux-force approach (Gerson and Poole 1971).

Conclusions

The relative demand, capacity-based approach, and thermodynamic flux-force approaches are three modeling paradigms that have been used to approximate the complex set of plant root nutrient acquisition processes operating in nature. As we describe here, only the capacity-based approach can comprehensively incorporate known soil and plant biogeochemistry and observed shoot-root asynchrony in nutrient uptake and phytomass synthesis, and has been successfully applied in several terrestrial biogeochemical models (Grant 2013; Medvigy et al. 2019; Yu et al. 2020; Zhu et al. 2019).

To further improve the modeling of nutrient regulation of plant and ecosystem biogeochemistry, additional observational and modeling developments are needed. Regarding observations, more measurements are needed of plant root nutrient acquisition, and plant shoot-root nutrient coupling in natural ecosystems for different plant species and ages and covering both diurnal and seasonal dynamics. Existing observations mostly focus on grasses and shrubs, while observations of diurnal and seasonal nutrient acquisition dynamics of trees are rare, and coverage of ecosystems in different geographical regions is sparse. Characterization of nutrient relevant traits (e.g., root nutrient acquiring protein density and capacity) and their trade-offs in more vegetation types and age groups are required to form a better representation of plant root nutrient acquisition. For modeling, new capacity-based algorithms should consider plant root nutrient acquisition regulation by plant stoichiometric plasticity (e.g., Zhu et al. 2019), the close coupling between plant hydraulics and metabolite transport, and foliar nutrient uptake. Finally, more advanced numerical methods that enable close coupling of

different plant-microbial processes should be explored (Tang and Riley 2016). With these developments, we expect that the modeling of nutrient regulation of terrestrial carbon-climate feedbacks can be made more realistic and accurate.

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