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The nitrogen gap in soil health concepts and fertility measurements

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A B S T R A C T

Soil nitrogen (N) often limits productivity in agroecosystems, prompting fertilizer applications that increase crop yields but can degrade the environment. Nitrogen's dual role in both productivity and environmental quality should center it in soil health frameworks. We use recent evidence to argue that N availability is an emergent property of the integrated soil biogeochemical system and is strongly influenced by plant traits and their interactions with microbes and minerals. Building upon this, we theorize that the sources of plant and microbial N shift across soil health gradients, from inorganic N dependence in ecologically simple systems with poor soil health to a highly networked supply of organic N in healthy soils; ergo, investments in soil health should increase ecological complexity and the pathways by which plants can access N, leading to more resilient nutrient supplies and yields in a variable climate. However, current N assessment methods derive from a historical emphasis on inorganic N pool sizes and are unable to capture the shifting drivers of N availability across soil health gradients. We highlight the need to better understand the plant-microbial-mineral interactions that regulate bioavailable N as a first step to improving our ability to measure it. We conclude it will be necessary to harness agroecosystem complexity, account for plant and microbial drivers, and carefully integrate external N inputs into soils' internal N network to expand the routes by which N from organic pools can be made bioavailable. By emphasizing N in soil health concepts, we argue that researchers can accelerate advances in N use efficiency and resiliency.

1. Introduction

Nitrogen (N) fertilizer inputs can be necessary to optimize yields but only about 40–45% of applied synthetic N fertilizer is recovered in crops within the year of its application (Gardner and Drinkwater, 2009; Lassaletta et al., 2014; Yan et al., 2020). The excess N causes eutrophication, deleterious health outcomes, and air pollution, and amplifies climate change (Erisman et al., 2013; West et al., 2014). Capable of both dramatically increasing food production and also diminishing environmental quality, N fertilizers are a double-edged sword. While the agricultural N problem is widely recognized and better placement and timing of fertilizer application and release have made inroads in addressing it (IFA, 2009), solutions focused on N fertilizer management alone have arguably begun to stagnate (Zhang et al., 2015), and to maintain or improve global N use efficiency (NUE) will require an acceleration of management practice innovations (Vishwakarma et al., 2022). Management approaches informed by soil health concepts show promise to boost agroecosystem N use efficiency, but first require advances in our conceptual understanding and assessment of N cycling and bioavailability to be effective (Wade et al., 2020).

The cycling of bioavailable N (e.g. inorganic N plus dissolved low molecular weight organic compounds such as amino acids and nucleosides that are potentially available to plants and microbes) is an emergent property of the terrestrial biogeochemical system (e.g. Jilling et al.,

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2018; Legay et al., 2020), as it is in other ecosystems (e.g. aquatic; Covino et al., 2018). Plants are not just passive players in the N cycle but actively shape intricate three-way interactions with microbes and minerals. However, no single measurement captures these complex non-linear drivers of bioavailable N, and the usefulness of common measurements is limited because they assess only short-term dynamics (e.g. net N mineralization) and exclude roots (e.g. buried bags or cores). Many leading management approaches continue to focus narrowly on manipulating fertilizer (Dimpka et al., 2020) alone or in combination with breeding more N-efficient plants (Anas et al., 2020; Ciampitti et al., 2022; Ciampitti and Lemaire, 2022) and largely overlook *in situ* bioavailable N cycling as a powerful leverage point to optimize soil bioavailable N, enhance NUE, and minimize environmental N losses.

Many functionally distinct N pools with different cycling dynamics are components of soil organic matter (SOM), which is foundational to the soil health framework, an increasingly prominent holistic approach to soil assessment and management that focuses on soil physical, chemical, and especially biological functions (Doran and Zeiss, 2000; Lehmann et al., 2020). However, there is currently a disconnect between carbon (C) and N in soil health frameworks due to a lack of integration across disparate lines of research from plant science, soil science, and ecology. Incorporating bioavailable N cycling into soil health frameworks is likely to have multiple benefits. For example, Wade et al. (2020) found that investments in building soil biological health in rainfed systems boost the effect of N fertilizer on yields. Other research shows that the resilience of N supply to plants under adverse conditions can be improved by enhancing soil health, likely because it increases the number of potential avenues for N mobilization of bioavailable N (Bowles et al., 2022). In short, soil health increases the ecological complexity and interactions that we expect to produce a better-functioning and more resilient system (e.g. Bullock et al., 2022).

Here we revisit our conceptual understanding of how and from where plants obtain N in agroecosystems, using a framework that predicts the dominant pathways for N mobilization and access will shift as soils shift along the soil health gradient. By extension, we assert that building soil health should be an effective strategy to increase the number and diversity of these pathways. However, while diversified N acquisition pathways promote system resilience, they also make quantifying bioavailable N difficult. In the context of soils that vary in soil health, we consider the source(s) of bioavailable N, links between soil health and the resilience of soil N supply, limitations of current methods to accurately capture N availability across soil health gradients, and challenges in balancing internal and external N sources. This framework is meant to supplement and build upon previous soil fertility research that has contributed to our understanding of N use efficiency, crop yield responses to N, and how to optimize regional N management using local knowledge and practices. We intend this framework to help hasten a future in which improved scientific knowledge, advances in soil N monitoring and assessment, new biogeochemical models, and locally adapted management practices optimize crop bioavailable N use.

2. N is an emergent soil property

For over a century, how to characterize soil bioavailable N has been the target of much soil research because N often limits or co-limits crop productivity. Early experiments relating soil nutrient status to plant growth, including many of those that formed the basis for Liebig's Law (Liebig, 1855), were carried out in simplified greenhouse systems with sandy soil media, and neatly demonstrated a direct link between inorganic N pool sizes and plant productivity. However, they also laid the foundation for our dominant view that vast amounts of standing dissolved N must be available to plants to satisfy high N demand during short windows of exponential plant growth. The narrow focus on inorganic N pool sizes and simple net changes in inorganic N pool sizes over time (i.e. net N mineralization rates) could be an unintended legacy of Liebig's Law. This notion of inorganic N pools persisted through the mid-1990s and conceptualized plant N availability more or less as the net balance of microbial mineralization and immobilization of inorganic N (Binkley and Hart, 1989; Jarvis et al., 1996). Microbes and plants were viewed primarily as competitors for N and immobilization an obstacle to plant N uptake (Kaye and Hart, 1997).

In recent decades, our understanding of N cycling and availability has evolved to a paradigm that centers the N cycle on the breakdown of organic N. This model identifies the upstream step of depolymerization as the rate-limiter for plant available N (Schimel and Bennett, 2004). As soon as complex organic N is transformed into a bioavailable form, three sinks compete for it: plant uptake, microbial uptake, and abiotic uptake through sorption or chemical association on soil particle surfaces such as minerals (Daly et al., 2021). Each of these sinks and flows are themselves regulated by an array of physical, chemical, and biological factors. We therefore posit that bioavailable N is best viewed as an emergent property of the plant-microbe-soil system whereby the "… whole cannot (not even in theory) be deduced from the most complete knowledge of the components, taken separately or in other partial combinations" (Mayr, 1982; Broad, 1925).

Because plants, microbes, and minerals all immobilize dissolved N, soils could experience very high rates of N turnover yet never accrue substantial standing pools of bioavailable N. Crop N demands can be intense, as during early maize growth when uptake can exceed 3 kg N ha^{-1} d^{-1} (Bender et al., 2013), but it is probable that large standing pools of inorganic N are not the only way to fulfill this requirement (Bowles et al., 2015a), especially given the multitude of avenues for plant N uptake arising from the interactions between growing plants, the soil environment, microbes, and various organic N pools (Moreau et al., 2019; Henneron et al., 2020; Zhao et al., 2021, Fig. 1). Plant N uptake is the result of the steady accumulation of small amounts of bioavailable N that plant roots capture from these pools of rapidly cycling dissolved N (Kaye and Hart, 1997), suggesting that plant N availability should be more related to gross N turnover rates and transfer of N between forms than to the net result of N turnover on the equilibrium size of dissolved N pools. Although additional quantitative estimates of the significance of these pools are needed (Näsholm et al., 2009), recent findings suggest that microbial mineralization of SOM can provide substantial bioavailable N to plants (Osterholz et al., 2017); for example, Carter and Schipanski (2022) found that rapeseed crops acquired 64–89% of their total N from SOM even under high inorganic N fertilization. We anticipate that healthier soils provide more avenues for accessing this actively cycling bioavailable N (Fig. 1 and discussion below).

Nitrogen "immobilized" by microbes is not permanently inaccessible. Microbes excrete as waste any N in excess of their stoichiometric needs, and microbial biomass itself turns over giving opportunities for plants to capture fleetingly available dissolved N (Fig. 1). Soil organisms that feed on microbes excrete additional N since C limitation increases with trophic level, and inefficiencies in feeding can cause soil micro- and mesofauna to release more microbial contents than they can consume (Bonkowski et al., 2009). This release of N by predation is known as the microbial loop (see Fig. 1C; Bonkowski, 2004; Geisen et al., 2018; Moreau et al., 2019) and, alongside phage-induced lysis (e.g. Sokol et al., 2022; Wu et al., 2022) and microbial turnover, could provide a sustained source of bioavailable N for plants without necessarily enlarging standing dissolved N pools. Researchers have begun to develop microbially-explicit models of soil N cycling (Sulman et al., 2017; Kyker-Snowman et al., 2019) but, despite the wealth of research documenting the microbial loop, soil organisms are perennially overlooked in broader-scale accounting of soil N cycling (Grandy et al., 2016).

We also suspect that the underestimated role of the mineral-associated organic matter pool (MAOM, a SOM component <53 μm isolated by physical fractionation of whole soils; Cambardella and Elliott, 1992) has hindered our ability to understand soil N bioavailability (Jilling et al., 2018, 2021). Historically, much focus on N from SOM was on the breakdown of organic N in particulate organic matter

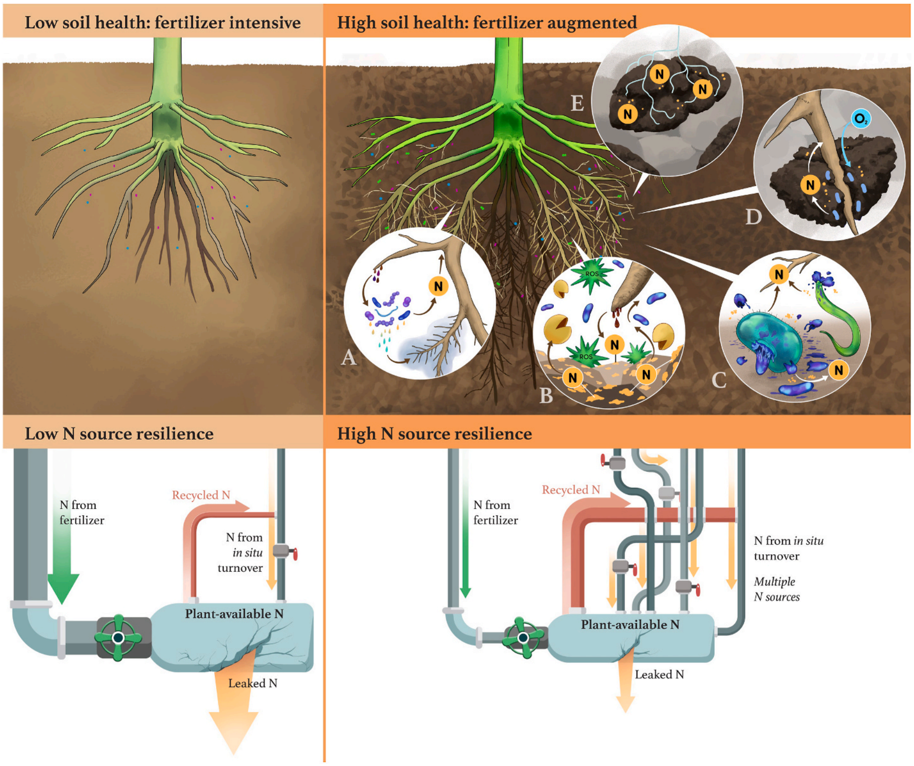

Fig. 1. Top. Healthy soil promotes emergent N cycling arising from root growth, SOM accumulation, and microbial activity, providing multiple pathways for plants to access bioavailable N. **A**) Root exudates stimulate microbes to produce auxin and other plant growth promoting hormones that stimulate fine root production. **B**) Root exudates increase microbial activity and produce or stimulate the production of organic acids and enzymes that enable mobilization of MAOM-N. **C)** Protists, nematodes, and other predators feed on microbes, releasing N in the "microbial loop." **D)** In healthy soils that have good structure, fine roots can grow into aggregates and open microsites where oxygen stimulates microbial activity and N release. **E)** Mycorrhizae can penetrate aggregates to access otherwise occluded pockets of N. **Bottom.** Healthy soils strengthen multiple internal pathways for accessing N, increasing the resilience of N delivery under variable climate and other disturbances. The unhealthy soil is almost entirely dependent on N fertilizer, which cycles very little through organic pools but rather remains as a large standing inorganic N pool that is vulnerable to leaching. Disruptions to the delivery of fertilizer N (e.g. water limitation) will lead to N limitation. The healthy soil is augmented by fertilizer N, which cycles through organic pools, with a smaller standing pool of bioavailable N. The multiple pathways for plants to access N provide more resilient N supply under variable conditions: if one "pipe" is shut off, many others may still provide N.

(POM, here discussed as the SOM component >53 μm). This is understandable given that crop tissues are the primary source of organic inputs in most large-scale agricultural production systems, and because POM turns over faster than MAOM on average. However, some MAOM components do have high turnover rates and MAOM is rich in proteins and amino acids, with MAOM-N often accounting for the majority of total soil N (Jilling et al., 2018). Bowles et al. (2022) show that complex crop rotations, a management strategy to increase biodiversity in agroecosystems, increase MAOM-N and that this N can boost maize productivity, especially under drought. Thus, MAOM is gaining recognition as not only a storage reserve but also an important source of bioavailable N (Lavallee et al., 2020; Jilling et al., 2021). How N enters and exits the MAOM pool still needs research attention, but the most likely mechanisms of MAOM-N mobilization involve complex interactions between soil health management, mineral surfaces, microbes and their enzymes, and plant roots.

3. Plants shape the complex soil function networks that generate bioavailable N

Plants are now recognized as the heart of many soil function networks that produce emergent properties: they are active participants, even drivers, of the bioavailable N cycle (Galindo-Casteñada et al., 2022, Fig. 1). Plant traits are thus central to improving crop N uptake (Abalos et al., 2019; Freschet et al., 2021) and can directly influence the soil N cycle by mediating N mining (especially from MAOM), N foraging, and the rate and timing of N uptake from soils. Plant architectural, morphological, and physiological root traits determine their spatial distribution and N uptake capacity. For example, high growth rates of metabolically cheap fine roots and root hairs, steep root growth angles, and high root N content are considered indicative of high capture of inorganic N (Lynch, 2019; Legay et al., 2020; Saengwilai et al., 2021). Selection pressure for improved grain yield can select for plants with higher per-root-length N uptake efficiency (Aziz et al., 2017). Root biomass and traits can affect soil properties such as porosity and water infiltration, thereby regulating bioavailable N and the prominence of various N loss pathways (Gould et al., 2016; Rabbi et al., 2018). MAOM-N may be more readily mined by plants with long, dense root hairs and high mucilage production that improves root–soil contact (Ahmed et al., 2014; Koebernick et al., 2017).

Plant traits that regulate beneficial interactions with soil microorganisms are particularly relevant to understanding N availability. One of the best-known examples of this interaction is the symbiosis between leguminous roots and N-fixing rhizobial bacteria, which can reduce fertilizer N input needs and promote organic N accumulation over time (Drinkwater et al., 1998; Herridge et al., 2008; Schipanski et al., 2010). Arbuscular mycorrhizal fungi (AMF) can access inorganic and organic N sources through their vast network of fine hyphae and transfer it over long distances to the host plant (Govindarajulu et al., 2005; Veresoglou et al., 2012; Cavagnaro et al., 2015; Hodge and Storer, 2015). Plant-AMF associations can significantly increase plant N uptake while reducing environmental N losses (Asghari and Cavagnaro, 2012; Bender et al., 2015). However, the specific abilities of AMF to access N in MAOM versus other soil N pools across variable environments, as well as the partitioning of acquired N between hyphae and plants, requires further investigation (Hodge and Fitter, 2010; Lazcano et al., 2014; Bender et al., 2015).

Most of the interactions between plants and soil microorganisms relevant to N availability are controlled by rhizodeposits (Fig. 1), which also serve as signaling molecules (Oldroyd, 2013; Venturi and Keel, 2016), and their specific effects on N cycling include complex feedbacks between N availability, root morphology, root exudation, and soil microorganisms. For example Yu et al. (2021) show that N-deficient maize increased root exudation of flavones, leading to a shift in soil microbial community composition and increased production of auxin, which appeared to promote lateral root growth and N uptake (Fig. 1A; Finkel et al., 2020). Root exudates influence soil N availability by altering the activity and structure of the microbial community (Moreau et al., 2019). Compared to aboveground litter inputs, exudation and root biomass disproportionately contribute to stabilized SOM, thereby enhancing long term N storage and availability (Austin et al., 2017; Angst et al., 2021; Cotrufo et al., 2022). Conversely, root exudates also chemically destabilize and solubilize MAOM-N (Keiluweit et al., 2015; Jilling et al., 2018).

A growing number of studies show that SOM mineralized by microbes stimulated with root exudates, i.e. priming, can significantly contribute to the plant-available N supply (Phillips et al., 2011; Rousk et al., 2016; Meier et al., 2017; Yin et al., 2018). The distribution of N across SOM pools and the specific nature and chemistry of mineral-organic associations may influence the amount of N that can be primed by root-soil interactions (Jilling et al., 2018, 2021; Chen et al., 2019). Soils containing highly reactive minerals may limit the potential magnitude of priming (Chen et al., 2019) while particulate SOM fractions may be more vulnerable to priming (Olayemi et al., 2022). However, plants and microbes are equipped with strategies to overcome even the strongest organo-mineral associations. Root-derived organic acids may stimulate the abiotic mobilization of N from Fe-bound SOM (Jiang et al., 2021; Jilling et al., 2021), releasing some of the most persistent forms of SOM into labile, bioavailable pools. Through direct and indirect mining efforts, plants both compete and cooperate with microbes for soil organic N (Fig. 1B,D,E; Tegeder and Masclaux-Daubresse, 2018). Understanding plant traits regulating this competition-cooperation spectrum is therefore critical to shift plant-microbe interactions towards higher NUE and retention of the various N forms present in healthy soil ecosystems.

From the interactions of plants, microbes, and minerals arise many pathways for plants to access bioavailable N. We hypothesize that some of these pathways for accessing N are weak to non-existent in unhealthy soils (Fig. 1) because potential N acquisition from OM is limited by poor soil structure; low SOM concentrations; and small, modular, sparse, niche-specialized, and inactive microbial communities (Ortiz-Álvarez et al., 2021). In contrast, we expect healthy soils to have multiple pathways for plants to access mobilized organic N because of interactions between active microbial communities, well-adapted root systems, and mineral surfaces. These pathways include the production of plant growth promoting hormones by rhizosphere microbes (Fig. 1A), accelerated activities of microbially-produced exoenzymes and reactive oxygen species that mobilize MAOM-N (Fig. 1B), trophic interactions including faunal predation of microbes that release spillover nitrogen (the microbial loop, Fig. 1C), and accessing intra-aggregate and other occluded N by more vigorous root (Fig. 1D) and hyphal (Fig. 1E) penetration.

These potential pathways for plants to access bioavailable N still need to be quantified across a range of ecosystems. However, we will briefly refer to the Marsden Farm Research Experiment (Ames, Iowa, USA) which provides one example of a system where internal N cycling supplies substantial amounts of bioavailable N (Liebman et al., 2008). Since 2002 this agroecosystem has been managed holistically with animal manure inputs and extended crop rotations which have increased soil organic N concentrations and microbial activity (King and Hofmockel, 2017) and enhanced other soil ecosystem services that impact N cycling (Baldwin-Kordick et al., 2022). Relative to a conventional inorganic fertilizer-based system, this diversified system increased maize and soybean yields by 5% and 21%, respectively, while substantially reducing inorganic N pool sizes and nitrate-N loss (Tomer and Liebman, 2014). This site is more ideal than many, having naturally rich soils and excellent access to organic N inputs, but nevertheless provides proof-of-concept that management can enhance internal N cycling, reduce inorganic N application, and attain better environmental outcomes while remaining productive.

In addition to improving the efficiency of internal N cycling, building soil health to open multiple avenues for bioavailable N acquisition should also increase the resilience of the N supply under variable conditions as some pathways can provide N even when others are blocked (Fig. 1, bottom panel). Soils whose fertility is entirely dependent on a single N source (e.g. fertilizer) are defenseless against fertilizer shortages caused by economic, environmental, or management limitations. While we can be confident that complex N supply pathways will improve soil resilience, this very complexity is inherently difficult to characterize, let alone manage, and presents real challenges to soil health assessments. Further compounding these challenges is the need to develop tools that are useful in soils with both high and low N pathway complexity, i.e. in soils that are healthy or unhealthy alike.

4. More potential N sources confer system resilience in variable climate but strain N assessment

While climate change has and will increasingly impact many environmental conditions, impacts on water are the most significant for N dynamics (Bowles et al., 2018). Water influences all processes in the plant-soil-microbe N cycle. For instance, mass flow and diffusion of N to roots decreases dramatically as soils dry, and low soil water potential spatially limits the availability of N to plants (Darrouzet-Nardi and Weintraub, 2014). Soil water content controls the coupling of reduced and oxidized constituents and thus the processes of nitrogen mineralization, nitrification, and denitrification. Fertilizer-centric approaches to reducing N losses during drought are largely ineffective because fertilizer management guidelines are based on expectations of optimal weather and yield potential, and fertilizer decision-making mainly occurs well in advance of weather impacts (Nkebiwe et al., 2016; Eagle et al., 2017; Bowles et al., 2018).

Building soil health may be an effective management approach to improving the climate resilience of the plant-soil-microbe N cycling system. Healthy soils allow for plants to continue accessing pockets of bioavailable N even as mass flow decreases with soil drying. Soils with well-developed structure and a greater abundance of meso- and macro-sized pores create a sponge-like and tortuous pore system that reduces system water and nutrient losses (de Jonge et al., 2009). Furthermore, improved porosity can allow for more root proliferation (Nunes et al., 2019) and interactions with microbes which can expand plant access to bioavailable N. As soil dries, water remains in smaller and smaller pore spaces, including inside aggregates, which can be difficult for roots to access. If healthier soils support a more abundant and active mycorrhizal community, roots can form more associations with hyphae that can extend into small, N-containing pore spaces (Fig. 1E), which effectively extends the plant root system into the spaces in soil where water and thus nitrogen remain for uptake.

Soil health management can increase SOM fractions that may provide more N during periods of water stress, particularly MAOM-N (Bowles et al., 2022). This large and N-rich fraction is bound to the same mineral surfaces that retain a thin film of water in most conditions (i.e. clays). Even in very dry soils, microbial activity and sorption-desorption processes persist on mineral surfaces, so MAOM-N pools built under soil health management could supply plants with N in such conditions (Schimel et al., 2007; Dannenmann et al., 2016). Furthermore, maintaining high organic matter levels can help supply reduced, energy-rich dissolved organic matter (DOM) to the soil solution within pores, increasing microbial N demand and building microbial biomass; this could help mitigate the procession (as in soils with C-limited microbes and low microbial biomass) toward a soil solution dominated by nitrate.

At the agroecosystem scale, cropping systems applying soil health principles are more resilient to droughts. Although the precise mechanisms remain unclear, a growing number of studies show that crop yields are higher in more diversified systems with healthier soils during stressful growing conditions—including droughts and heat waves—compared to very simplified systems (Bowles et al., 2020; Gaudin et al., 2015; Renwick et al., 2020, 2021). This may result in part from the types of changes in N access and supply that benefit plants during stress, as well as other positive plant-soil-microbe feedbacks (Ortiz-Álvarez et al., 2021). Increasing the complexity of microbial community and plant-microbe interactions will promote emergent N cycling that is more resilient to drought (Bullock et al., 2022). Limiting yield losses during droughts also means more plant N uptake, leaving less residual bioavailable N and reducing potential N loss to the environment, compared to systems in which productivity suffers more with drought.

Soil health increases should enhance the resilience of soil bioavailable N supply. Yet, it remains difficult to accurately estimate these changes in soil N supply, and differences in the controls on bioavailable N across soil health gradients make assessment challenging. Measurements of pool sizes may be useful in low fertility soils with limited inherent N-supplying capacity and weak root-microbe-soil interactions. In contrast, pool sizes will not reflect potential bioavailable N in healthy soils with dynamic rhizosphere nutrient cycling. Gross N fluxes are more integrative than pool sizes but generally require using ^{15}N isotopes as tracers, are time consuming and expensive, and because they are conducted in the absence of roots do not fully capture the potential for roots to intercept newly mineralized N or to prime N mineralization. Indeed, after nearly a century of work on N bioavailability, few measurements provide better and more reliable predictions of N bioavailability than soil total N content, which itself does not have high predictive power (Fraps, 1908; Allison and Sterling, 1949; Ros et al., 2011). Thus, approaches to N bioavailability that expand on the soil-centric perspective of pools and fluxes are long overdue. Novel approaches could incorporate the “plant’s eye view” of soil N cycling, such as through micro-lysimeters (Riedl et al., 2022), microdialysis (Buckley et al., 2020), and levels of expression of root genes involved in N uptake and assimilation (Zebarth et al., 2011; Bowles et al., 2015a, 2015b; Anas et al., 2020). There is room to investigate strategies that are low--tech—even a simple combination of two basic tests, the 5-min tetraphenyl borate extraction of ammonium and the 14-d aerobic incubation for net N mineralization, greatly improved the quality of N fertilizer recommendations—as well as high-tech, like new field sensors to quantify soil N availability in real time (McDaniel et al., 2020).

If it is the N cycle’s emergent features that frustrate our ability to accurately measure bioavailable N, we hypothesize soils that are neither very poor nor very healthy will offer the greatest measurement challenges (Fig. 2). In unhealthy, nutrient-depleted soils, relatively simple N measurements should reveal a strong need for external N. In healthy soils with very high levels of potential soil N supply capacity, independent microbial mineralization dynamics will likely dominate (Schomberg, 2009) and overpower other N sources, rendering plant-microbe-soil feedbacks relatively inconsequential to plant N uptake and productivity. In these N-rich soils any of a number of extant measurements, especially ones that reflect organic N content and microbial activity, should reasonably capture high levels of N bioavailability. Between these extremes lie moderately healthy soils; that most of the world’s crops are likely produced in such soils may help to explain why quantifying the supply of soil bioavailable N has frustrated scientists for decades (Mariano et al. 2017; Franzluebbers, 2018). Here, the full suite of biogeochemical interactions regulating bioavailable N become important: soil properties including the mineral characteristics, microbial community structure and physiology, chemistry of organic N, and plant identity could have a meaningful impact on internal bioavailable N supply and thus also necessary external N application rates. This complexity has so far made it so no one measurement can adequately reflect bioavailable N.

As a demonstration of the particular difficulty in predicting N bioavailability at middling levels of soil health, we present a small illustrative dataset from three sites using the CO_2 burst test, a short-term measurement of C mineralization (1 or 3 d; Haney et al., 2001; Franzluebbers, 2018; Franzluebbers and Pershing, 2018; Franzluebbers et al., 2018). Across 113 site-years the CO_2 burst explains just over 30% of the variation in maize economic optimum N rate. At low CO_2 burst levels, the economic optimum for N application is high; this is consistent with our hypothesis that less healthy soils will have little plant-soil-microbe-driven bioavailable N cycling. A high test result seems to capture the elevated microbial activity and access to SOM we expect in very healthy soils, where we found that low to zero N inputs are needed. Interestingly, variability in the relationship between CO_2 burst and optimal N application rate appears to be greatest at intermediate levels of C mineralization potential. At these intermediate levels, the N supply in the field may be strongly influenced by factors that cannot be captured by this simple test. This underscores the need for a special focus on moderately-healthy soils as we design research and methods to untangle the complex system that is soil bioavailable N cycling.

Most agroecosystems cannot rely solely on *in situ* N cycling, so we must also consider external N fertilizer applications during our assessments of bioavailable N across soil health gradients. The ideal nutrient economy would be circular, obviating the need for inorganic fertilizers by continually cycling N between humans and agroecosystems. Realistically, though, N exported in agricultural products must be replaced by external inputs, which in many systems will take the form of inorganic N. Internal N cycling varies greatly in its response to N fertilization across soils, but typically inorganic N has a neutral to positive effect on soil C (Grandy et al., 2013; Jian et al., 2016; Chen et al., 2018), with increased POM accounting for much of the observed SOC increases (Rocci et al., 2021). This could be due to direct (i.e. decreased losses of older soil C) and/or indirect effects (i.e. increased crop biomass inputs) effects of N fertilization (Huang et al., 2020). Microbes may even convert crop inputs to SOM more efficiently in the presence of mineral fertilizers (Spohn et al., 2016; Li et al., 2018). Indeed, cycling through crop residue and soil pools could account for the finding that crop

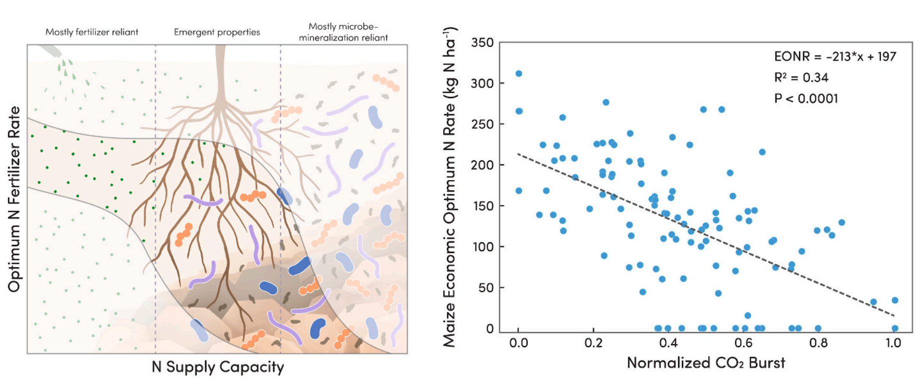

Fig. 2. *Left panel.* Hypothesized relationship between *in situ* N supply capacity and optimum N fertilizer rate suggesting that the variance is highest in intermediate regions where the specific interactions between plant roots, microbes, and minerals will have the strongest impact and be most difficult to predict. *Right panel.* Relationship between normalized CO_2 burst (1-, 3-, or 4-d CO_2 released when dry soil is re-wetted) and N fertilizer needed for economic optimum maize production across three studies (N = 113). Data were normalized by using Maximum-Minimum normalization, where $(X_{raw\ data} - X_{min})/(X_{max} - X_{min})$. Data are from Franzluebbers (2018), Yost et al. (2018), and Bean et al. (2020) and were collected in the following US states: NC, VA, IA, IL, IN, MO, MN, ND, NE, WI. The CO_2 burst is interpreted as a proxy for both soil health and N availability, and shows variation in the relationship with the optimum N rate that is generally similar to our hypothesis.

recovery of fertilizer N in the first year is only 43.8% (±11%) but increases by ~ 22%–66% (±15%) over the long term (Vonk et al., 2022). This increase in long-term recovery illustrates the internal N cycling abilities of healthy soils and the potential role of fertilizer N in building soil health (Wade et al., 2020).

However, inorganic N applied in excess of the agronomic optimum rate likely reverses any gains from conservative fertilization, instead causing greater losses of older SOC (Huang et al., 2020), decreased gross N ammonification (Mahal et al., 2019), and potentially less vigorous root growth and exudation (Ordóñez et al., 2021; Prescott et al., 2021). N fertilizer suppresses the production of oxidase enzymes that are needed to depolymerize large, non-repeating molecules such as lignin (Matocha et al., 2004; Jian et al., 2016; Chen et al., 2018; Morrison et al., 2019). This can slow decomposition rates and increase new SOM accumulation but potentially reduce internal N supply. Indeed, Breza et al. (in review) found that N application rates of 180 kg N ha^{-1} y^{-1} suppress the breakdown of proteins to amino acids in farming systems with dedicated use of cover crops and otherwise high quality soil. High inorganic N fertilization is also likely to reduce rates of both MAOM-N formation and MAOM-N desorption (Jilling et al., 2018). Oxidases such as peroxidase generate highly reactive species including Mn^{3+} and hydroxyl free radicals (Jones et al., 2020), whose small size and reactivity allow them greater access to MAOM compared to lock-and-key enzymes that may not be able to properly contact substrates in tight spaces. Thus, suppression of oxidase production, as with inorganic fertilization, is likely to slow the release of MAOM-N.

Excessive applications of inorganic N will also increase environmental N losses to water and the atmosphere, promote issues with pathogenic bacteria and fungi (e.g. Lekberg et al., 2021), and reduce mycorrhization and N fixation (Egerton-Warburton et al., 2007; Bahulikar et al., 2021), which can play key roles in generating internal N supplies (Xie et al., 2022). When external N applications are necessary, combining inorganic nutrients with organic fertilizers such as compost or manure that also supply C could optimize microbial diversity and enzymatic activity as much as possible given the constraints of production requirements (Kramer et al., 2002; Francioli et al., 2016). Moreover, microbial and mineral uptake of fertilizer N may be optimized when it is applied with careful consideration to type, placement, and timing (IFA, 2009). Because N fertilizer affects so many disparate components of the plant-mineral-microbe-soil system, it will be particularly challenging to assess the sources of bioavailable N to crops that depend on fertilizer N to supplement *in situ* N cycling.

5. Future directions

Efficient N management should rise to the top of our priority list in soil health management. We suggest pursuing efforts in several areas. We should link N cycle resilience to agroecosystem complexity established by management practices including plant diversity, grazing, tillage, and inputs of fertilizer and organic matter. Then, we can investigate how such agroecosystem complexity impacts N cycling and its climate resiliency across ecological scales—geochemical, microbial, and plant. We propose focusing substantial effort on assessing N availability in soils that are neither exceptionally poor nor exceptionally fertile, and using multiple approaches that integrate *in situ* measurements with process- and pool-based measurements. Findings should be translated for producers to evaluate the impact of soil health building practices on N, adjust fertilizer regimes in season, and make better use of organic fertilizers to increase soil health and improve NUE. These efforts may enable us to classify soils by their potential bioavailable N supply for use in tailoring management practices to specific soil health regions (Devine et al., 2021). Finally, we should focus research effort to advance newly restructured terrestrial biogeochemistry models that explicitly represent microbial communities. These new microbially-explicit models capture unexpected non-linear impacts of variation in both microbial community and plant traits on C and bioavailable N (e.g. Wieder et al., 2015; Abramoff et al., 2018; Kyker-Snowman et al., 2019). For example, new models can estimate the rhizosphere priming effect (Henneron et al., 2020), a key non-linear interaction between plants and microbes in the rhizosphere that mobilizes bioavailable soil N from SOM. A specific effort to parameterize these models with new data from agroecosystems provides a promising avenue for predicting management and climate change impacts on bioavailable N.

To continue pushing the frontiers of our understanding of soil bioavailable N cycling, improve management, and alleviate the N crisis, we will need a portfolio of approaches. Combining fundamental knowledge, assessment techniques, local soil health classification, and models will be key to harnessing the potential of *in situ* bioavailable N to supply crops with N while minimizing environmental N losses. Centering N alongside C in soil health concepts should lead to better outcomes in agroecosystems.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability

Data will be made available on request.

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