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Biological Transfer Capacity:

A Practical Diagnostic Framework for Assessing Soil Nutrient Delivery in Agricultural Systems

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Abstract

Conventional soil health assessments distinguish between nutrient availability and biological activity but rarely integrates them into a single diagnostic question: Is the soil food web actually delivering nutrients to the crop at the rates and in the forms that plant demand requires? This paper introduces Biological Transfer Capacity (BTC) as a conceptual diagnostic framework to address that question. A critical distinction underlies the framework: processing capacity — the ability of the microbial community to transform organic substrates — is not the same as transfer capacity, the ability to release nutrients in plant-available forms at times and places that match crop demand. Soils with high processing capacity do not always exhibit high transfer capacity, and this discrepancy explains many observed cases in which biologically active soils fail to translate their activity into yield response.

BTC proposes that nutrient delivery depends on five interdependent elements organized as a diagnostic chain: substrate availability, microbial biomass and community character, metabolic activity and efficiency, predator-prey dynamics and the microbial loop, and nutritional receptivity. Each element has an established theoretical basis in soil ecology and rhizosphere science; what is novel is their integration into a sequential diagnostic chain applicable to agricultural field assessment. The paper describes the theoretical foundation of each element, identifies failure modes that interrupt delivery at each link, and outlines a research agenda for testing BTC as an applied framework in agronomic settings. BTC is positioned as a complementary diagnostic layer to existing soil health frameworks, designed to explain why biological scores and soil amendment responses — including mineral fertilizers — do not always predict agronomic outcomes, and to direct investigation toward the specific link in the delivery chain that is limiting. The goal is to give agronomists and extension professionals a coherent conceptual tool for diagnosing where and why nutrient delivery is failing, and to foster the coordinated field research needed to validate the framework.

1. Introduction: The Diagnostic Gap in Soil Biological Assessment

Interest in soil biological health has grown substantially over the past two decades. Soil organic matter, microbial biomass carbon, and basal respiration are now routinely measured by agronomic consultants and progressive farmers as proxies for soil vitality. The implicit assumption behind these measurements is straightforward: more biological activity means more nutrient cycling, which means better crop nutrition and higher yield.

This assumption is often correct. However, it is not always correct, and the exceptions are agronomically important. Yield responses to biological inputs — compost, cover crops, and microbial inoculants — are highly variable across soils and management contexts, and the sources of this variation are not well explained by conventional biological metrics. The inconsistency of microbial inoculant yield responses is extensively documented across inoculant types — including plant growth-promoting rhizobacteria, phosphate-solubilizing organisms, and arbuscular mycorrhizal fungi — with responses varying substantially by soil condition, management context, and the biological state of the receiving community (O’Callaghan, 2022; Kaminsky et al., 2019). A meta-analysis of maize trials across the United States reported yield increases of only 1.8–3.5% on average, with statistically significant effects in only two of six years (O’Callaghan, 2022). This diagnostic gap extends equally to mineral fertilizer amendments. A nutrient-balanced soil with adequate supply in chemically available form can still show depressed nutrient uptake efficiency when the biological transfer mechanisms connecting the nutrient pool to the root surface are not functioning — the same failure mode the BTC chain is designed to detect and address. The sources of this variability are not well captured by standard biological or chemical indicators alone, suggesting that a more mechanistic diagnostic framework — one that assesses the delivery chain rather than its individual components in isolation — is needed to explain and predict amendment responses across soil and management contexts.

The diagnostic gap lies in a distinction the current toolkit does not make explicit: the difference between processing capacity and transfer capacity. While not previously formalized in these terms, this distinction is implicit in the mechanistic literature on microbial loop dynamics, food web structure, and inoculant response variability. This paper makes it explicit as a diagnostic framing. Processing capacity describes the ability of the microbial community to transform organic substrates and mineral-bound nutrients — to decompose, mineralize, solubilize, and cycle nutrients within and beyond the biological fraction. Transfer capacity describes something more specific: whether those transformed nutrients are being released in plant-available chemical forms, at the right time in the crop’s growth cycle, and in spatial proximity to root surfaces where uptake can occur. A soil can have high processing capacity and low transfer capacity simultaneously, and when this happens, the biological activity measured by standard metrics does not translate into plant nutrition or yield.

Biological Transfer Capacity (BTC) is proposed as a framework for addressing this gap. It defines nutrient delivery from the soil food web to the plant as a chain of five linked elements, each of which must be functional for delivery to occur. Failure at any single link reduces or eliminates the delivery outcome regardless of the status of the other links. The framework draws on established theoretical foundations in soil ecology, rhizosphere science, and plant-microbe interactions. Its practical contribution is to organize those foundations into a sequential diagnostic logic that extension professionals and agronomists can apply to identify where delivery is failing and why.

BTC is not proposed as a replacement for existing soil health assessment frameworks. The Cornell Comprehensive Assessment of Soil Health, the NRCS Soil Health Scoring system, and similar tools provide valuable summary measures of soil condition. BTC operates as a complementary diagnostic layer beneath these frameworks — a tool for explaining why a soil that scores well on standard biological indicators may still fail to deliver agronomic benefit, and equally why soil amendments such as compost, cover crop residues, microbial inoculants, or mineral fertilizers may not produce the expected yield response or input reduction efficiency even when applied correctly. This applies with particular force to mineral fertilization: a nutrient-balanced soil can still show depressed nutrient uptake efficiency when the biological transfer mechanisms connecting the nutrient pool to the root surface are not functioning. Both biological and mineral amendment failures have the same underlying cause: the delivery chain is interrupted at one or more links. BTC directs investigation toward identifying which link that is.

2. Conceptual Foundation: From Soil Food Web Theory to Nutrient Delivery

The theoretical lineage of BTC runs through three interconnected bodies of work: the microbial loop, the soil food web energy channel concept, and nematode faunal analysis.

The microbial loop was articulated by Clarholm (1985), who demonstrated that bacterial-feeding protozoa release plant-available nitrogen through grazing. When protozoa consume bacteria, nitrogen immobilized in bacterial biomass is mineralized and released as ammonium in quantities that exceed the nitrogen needs of the protozoa themselves. This overflow nitrogen enters the soil solution and becomes available for plant uptake. The critical insight is that nutrient release is not simply a function of microbial activity but of the trophic interaction between bacteria and their predators. Without predation, nutrients remain locked in microbial tissue regardless of how active the community is — a direct expression of the processing capacity versus transfer capacity distinction.

Hunt et al. (1987) formalized the soil food web energy channel concept, integrating bacteria, fungi, protozoa, nematodes, microarthropods, and their trophic relationships into a quantitative model of nitrogen transfer across the detrital food web. This work demonstrated that the magnitude and timing of nitrogen release to the plant are determined not by any single trophic level but by the structure and activity of the entire food web simultaneously.

Ferris, Bongers, and de Goede (2001) extended this tradition by developing nematode faunal analysis as a practical diagnostic tool. By characterizing nematode communities according to their colonizer-persister (cp) scale life history position, they derived three diagnostic indices — the Enrichment Index (EI), the Structure Index (SI), and the Channel Index (CI) — reflecting enrichment state, structural complexity, and decomposition channel dominance respectively. This work demonstrated that community composition, not biomass alone, encodes diagnostic information about food web function and nutrient cycling status.

A parallel and practically significant contribution came from Elaine Ingham and colleagues, whose foundational research on trophic interactions and nitrogen cycling in soil food webs (Ingham et al., 1986a, 1986b) demonstrated how bacterial and fungal biomass levels, and the organisms that graze them, together determine nutrient cycling rates and plant productivity. Ingham subsequently synthesized this body of work into the Soil Biology Primer (Ingham, 1999), which introduced the fungal-to-bacterial ratio framework and the succession-state concept to a generation of agronomists, soil consultants, and farmers. For many extension professionals, this synthesis remains the primary conceptual entry point into soil food web thinking. The BTC framework builds directly on the ecological logic that Ingham's research and communication work helped establish in agronomic practice.

In parallel, research on rhizosphere ecology has established that plant roots actively modulate the microbial communities in their immediate vicinity through exudate release. Plants release a significant fraction of their photosynthate through roots, and exudate composition shifts with plant developmental stage and nutrient status (Badri & Vivanco, 2009). Specific signaling compounds recruit specific functional organisms: strigolactones stimulate arbuscular mycorrhizal fungi (AMF) colonization under phosphorus deficiency (Akiyama et al., 2005), while flavonoids mediate rhizobial nodulation under nitrogen deficiency (Cooper, 2004). These rhizosphere interactions represent one regulatory layer within the broader food web system.

BTC integrates these theoretical traditions into a single diagnostic question: given the state of the soil food web, is biological nutrient transfer to the plant actually occurring, at what rate, and where is it being interrupted? The five-element chain proposed here provides the structure for answering that question systematically.

3. The Five Elements of the BTC Chain

BTC proposes that soil nutrient delivery depends on five elements that must each be adequately functional for delivery to occur. The elements are presented in a logical sequence reflecting how substrate supports community development, which in turn enables metabolic activity and predator-prey dynamics, all of which must operate within permissive soil chemistry conditions. However, these elements are not strictly sequential prerequisites — they interact, operate in parallel, and constrain each other bidirectionally. Failure at any single link reduces or eliminates the delivery outcome regardless of the status of the others, and compound failures involving multiple links simultaneously are common in practice. Figure 1 presents the chain schematically.

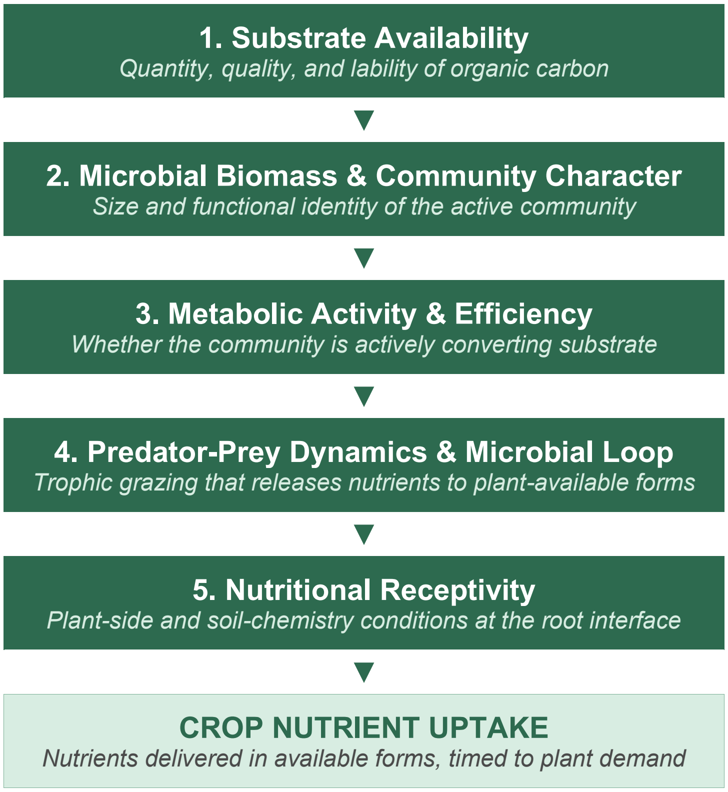

Figure 1. The BTC chain: five interdependent elements whose adequate function is required for biological nutrient delivery to the crop. The elements interact and operate in parallel as well as in sequence; failure at any single link reduces or eliminates the delivery outcome regardless of the status of the others.

3.1 Substrate Availability

Substrate availability describes the pool of organic carbon and nutrients accessible to drive microbial activity. It is the entry point of the chain and its most fundamental prerequisite: without adequate substrate, microbial community development cannot proceed regardless of other conditions.

Substrate quantity is important, but substrate quality and temporal accessibility are equally so. Organic matter in soil exists on a humification continuum from fresh, partially decomposed material through fulvic acid fractions to humic acids and stable organo-mineral complexes (Doran & Parkin, 1994). Fresh, labile material releases carbon and nutrients rapidly and drives enrichment-phase microbial activity — the rapid proliferation of fast-reproducing, stress-tolerant organisms that follow a resource pulse such as fresh organic matter addition, tillage, or high nitrogen inputs. This enrichment phase is ecologically distinct from the mature or structural phase of community development, in which slower-reproducing, stress-sensitive organisms have established across multiple trophic levels under conditions of greater stability and lower disturbance. Stabilized humus releases carbon slowly and feeds long-term structural community development rather than enrichment-phase activity. The enrichment pulse that initiates rapid nutrient cycling comes from labile fractions, not from stabilized humus — an important counter-intuitive point for practitioners accustomed to equating high organic matter with high biological availability.

The C:N ratio of the substrate pool determines whether microbial activity generates net nitrogen mineralization or net nitrogen immobilization. Substrates with C:N ratios above approximately 25:1 drive immobilization — the microbial community draws down plant-available nitrogen to process the carbon rather than releasing it. Substrates with C:N ratios below 20:1 release nitrogen in excess of microbial demand, driving mineralization and increasing plant availability (Paul & Clark, 1996). The timing of this release relative to crop demand is critical: a large mineralization pulse occurring before or after peak crop demand delivers less agronomic benefit than a moderate, sustained release aligned with the crop's growth curve.

The ratio of labile to stable carbon fractions determines how much substrate is biologically accessible on seasonal timescales relevant to crop nutrition. Lavallee et al. (2020) formalized this distinction by defining particulate organic matter — physically recognizable plant fragments that are fast-cycling and biologically accessible — versus mineral-associated organic matter, which is chemically stabilized through binding to mineral surfaces and largely inaccessible to microbial processing on seasonal timescales. Cotrufo et al. (2013) further demonstrated through the MEMS framework that labile, low-molecular-weight inputs are preferentially incorporated into mineral-associated fractions through microbial processing, meaning that repeated additions of easily decomposable material paradoxically build the stable rather than the labile pool over time. Together these frameworks establish that a soil with high total soil organic carbon (SOC) but dominated by mineral-associated fractions may have a small biologically accessible pool inadequate to sustain the nutrient delivery needed during critical crop demand periods — a distinction invisible to total SOC measurement alone.

3.2 Microbial Biomass and Community Character

The active microbial community is the primary agent of nutrient transformation. BTC depends not only on how much microbial biomass is present but on what kind of community is doing the processing — what has been called community character.

The fungal-to-bacterial (F:B) ratio is the most diagnostically informative single expression of community character. Bacterial-dominated communities cycle nitrogen rapidly and produce inorganic nitrogen in forms prone to leaching. Fungal-dominated communities cycle more slowly, retain nutrients within hyphal biomass for longer periods, and release nutrients in a more spatially proximate, temporally distributed manner near root surfaces (Wardle et al., 1995; Ingham, 1999). The F:B ratio also reflects the decomposition pathway and the succession state of the community: low F:B is characteristic of disturbed, enrichment-phase soils — those recently tilled, fertilized, or receiving fresh organic inputs — while high F:B is characteristic of mature, stable food webs under lower disturbance regimes.

Total microbial biomass carbon (MBC) provides a measure of the size of the processing engine but must be interpreted in the context of F:B ratio and in relation to total soil organic carbon. The ratio of MBC to total organic carbon — the microbial quotient or qMIC — indicates how efficiently the substrate pool is being biologically occupied. A low qMIC in a high-organic-matter soil is particularly diagnostic — and counter-intuitive — because it indicates that the substrate pool is predominantly stabilized and biologically inaccessible rather than genuinely available to the microbial community; the soil appears biologically rich by the most common metrics while the community is in fact carbon-limited at the functional level (Anderson & Domsch, 1989). This is precisely the condition in which standard organic matter measurements most thoroughly mislead the practitioner, and it is a condition the BTC framework is designed to detect.

An important practical implication follows: two soils with identical MBC can have radically different BTC if their community character differs. Community character, not biomass alone, determines the quality of the potential transfer.

3.3 Metabolic Activity and Efficiency

Metabolic activity addresses whether the microbial community is actively converting substrate — not merely present. A large, well-composed community will have reduced BTC if it is metabolically suppressed by moisture stress, pH extremes, compaction, anaerobiosis, or chemical inhibition.

Two metabolic indicators are particularly diagnostic for BTC. The specific respiration rate, or qCO_2 — defined as basal respiration per unit of microbial biomass — reflects the metabolic efficiency of the community (Anderson & Domsch, 1985). A high qCO_2 indicates a stressed, early-successional community — one in enrichment phase, dominated by fast-reproducing organisms burning carbon rapidly to sustain rapid growth and reproduction — consuming carbon in maintenance rather than efficient biomass production. A low qCO_2 indicates a mature, efficient community incorporating a higher fraction of consumed carbon into new biomass — a condition associated with greater carbon use efficiency (CUE) and more conservative, temporally buffered nutrient cycling (Manzoni et al., 2012).

The temporal dimension of metabolic efficiency is directly relevant to crop nutrition. A low-CUE community burning carbon inefficiently releases nutrients in large, poorly timed pulses that may not align with crop demand windows. A high-CUE community cycling carbon efficiently generates smaller but more sustained nutrient releases across the growing season. This distinction between pulse release and sustained release is one of the primary mechanisms through which community maturity translates into agronomic outcomes that total microbial biomass alone cannot predict. Carbon use efficiency — the fraction of consumed carbon retained in biomass rather than respired — is a key expression of this maturity, with higher CUE associated with more conservative, sustained nutrient cycling (Manzoni et al., 2012); qCO_2 provides a field-accessible proxy for the same dimension of community state, with higher qCO_2 indicating a stressed or early-successional community burning carbon at high maintenance cost and lower qCO_2 indicating a mature, efficient community (Anderson & Domsch, 1985).

Metabolic activity is also the element most sensitive to short-term conditions. A soil with strong long-term community structure can temporarily exhibit low metabolic activity during drought, cold, or waterlogging without having lost its underlying food web architecture. Distinguishing temporary metabolic suppression from structural community decline is an important diagnostic distinction.

3.4 Predator-Prey Dynamics and the Microbial Loop

The predator-prey element is the most conceptually distinctive link in the BTC chain for agronomic diagnostic practice — it is the point at which the distinction between processing capacity and transfer capacity becomes most visible, and it is the mechanism least commonly incorporated into standard soil health assessment frameworks. Microbial processing alone does not transfer nutrients to plant roots. The actual transfer mechanism is the microbial loop — the grazing of bacteria and fungi by protozoa and nematodes, which releases nutrients immobilized in microbial biomass into plant-available mineral forms in the rhizosphere.

When protozoa consume bacteria, nitrogen immobilized in bacterial protein is released as ammonium at a rate that exceeds protozoan nitrogen demand. This surplus ammonium enters the soil solution adjacent to roots and is directly available for plant uptake. Nematode bacterivores perform an analogous function at a larger scale, and fungivorous nematodes release nutrients from the fungal channel. Importantly, this nutrient release occurs in the rhizosphere — spatially proximate to root surfaces — because protozoa and bacterivorous nematodes concentrate their activity where bacterial prey is most abundant, which is precisely where root exudates are most concentrated (Clarholm, 1985; Bonkowski, 2004).

The ecological maturity of the predator-prey community is therefore a direct determinant of nutrient delivery rate. A community in early enrichment phase — the condition characterized by rapid bacterial proliferation following disturbance or resource addition, dominated by flagellate protozoa and cp-1/cp-2 bacterivore nematodes that are the first colonizers of a disturbed or enriched system — performs the grazing function but does so without the trophic complexity that characterizes a structured food web. As protozoan succession advances through amoebae to ciliates, and as nematode communities develop higher-guild fungivores, omnivores, and carnivores — organisms that require greater ecological stability and time to establish — the food web acquires greater regulatory capacity over the timing and magnitude of nutrient release (Ferris et al., 2001; Foissner, 1999).

A high-MBC, high-activity community with no functional predator-prey loop has high processing capacity but low transfer capacity. In practical terms, this can occur after soil sterilization followed by bacterial recolonization, in soils treated with nematicides, or in soils so disturbed by tillage that higher-guild organisms have not yet recolonized. In all of these cases, nutrients may be cycling actively within the microbial fraction while remaining inaccessible to the plant.

The plant participates in this process through rhizosphere exudates. Specific exudate compounds selectively recruit microbial functional groups: strigolactones stimulate AMF colonization (Akiyama et al., 2005), flavonoids influence rhizobial nodulation and phosphorus solubilization (Cooper, 2004; Hassan & Mathesius, 2012), and organic acids such as malate, citrate, and oxalate attract specific bacterial communities through chemotaxis (Bais et al., 2006). Exudate composition and quantity shift substantially with plant developmental stage: a direct field study with maize across four growth stages from early vegetative through early grain fill found that developmental stage was the primary driver of both exudate quality and quantity, with carbon exudation per plant increasing with biomass production but exudation rate per unit root surface declining with maturity, indicating a dynamic and stage-specific allocation strategy rather than a constant signal (Santangeli et al., 2023). However, this plant-mediated recruitment can only function if the community with the capacity to respond is already present in the soil. BTC is a prerequisite for the rhizosphere signaling model to operate as described.

A second and distinct nutrient delivery mechanism operates in parallel with the grazing-driven microbial loop: biological solubilization. Where the microbial loop releases nutrients by breaking open microbial biomass through predation — liberating nutrients that have already passed through biological processing — solubilization acts upstream, converting nutrients that are chemically bound in mineral or organic forms directly into dissolved, plant-available forms through biochemical action. The two mechanisms are additive contributors to the plant-available nutrient pool and together constitute the full biological transfer pathway.

Four solubilization mechanisms are agronomically significant. First, phosphorus solubilization: bacteria including Pseudomonas and Bacillus species, and many soil fungi, produce organic acids — citric, gluconic, and oxalic among others — that acidify the immediate microenvironment around soil particles and chelate the calcium, iron, and aluminum that hold phosphate in insoluble mineral forms, releasing orthophosphate into solution (Richardson & Simpson, 2011). Second, mineral weathering: fungal hyphal exudates and ectomycorrhizal activity physically penetrate mineral surfaces and release potassium, calcium, magnesium, and trace elements through a combination of acidification and chelation. Third, siderophore production: specific bacterial groups produce iron-chelating compounds that maintain iron in plant-available form in alkaline soils where iron would otherwise precipitate as ferric hydroxide (Lemanceau et al., 2009). Fourth, enzyme-mediated organic nutrient release: phosphatases, proteases, and glucosidases produced by both bacteria and fungi cleave organically bound phosphorus, nitrogen, and sulfur from humic and fulvic acid fractions without requiring predation — particularly important in high-organic-matter soils where a significant fraction of nutrients is held in organic rather than mineral form (Nannipieri et al., 2011).

Solubilization capacity is closely tied to community character. Phosphate-solubilizing bacteria are themselves prey for protozoa and nematodes, meaning the grazing loop and solubilization are coupled rather than independent — a more active predator-prey community stimulates greater bacterial turnover and, through it, greater solubilization activity. Fungal-dominated communities contribute disproportionately to mineral weathering and enzyme-mediated organic nutrient release. The community character element (Section 3.2) therefore determines not only the pathway and timing of nutrient cycling but also the identity and magnitude of the solubilization mechanisms available.

3.5 Nutritional Receptivity

Nutritional receptivity is the demand side of the transfer relationship. It addresses whether plant and soil chemistry conditions allow nutrient reception at the point of root uptake. Even when the first four elements are functioning well, delivery can fail if chemical or physiological conditions at the plant-soil interface prevent uptake. It is worth noting that biological solubilization — described at the close of Section 3.4 — can partially compensate for some chemical immobilization constraints: phosphate-solubilizing organisms lower local pH and chelate competing cations (Richardson & Simpson, 2011), and siderophore producers maintain iron availability in alkaline conditions (Lemanceau et al., 2009). The effectiveness of this biological compensation diminishes as chemical constraints intensify. Where pH falls within the range of microbial tolerance, where cation imbalances are moderate, and where P levels have not yet suppressed AMF colonization, biological solubilization can make a meaningful contribution to nutrient delivery. Where these conditions become severe — pH severely outside microbial tolerance (Paul & Clark, 1996), mineral antagonisms driven by gross cation imbalance (Marschner, 2012), or P saturation suppressing the AMF community (Treseder, 2004) — biological solubilization alone cannot restore adequate delivery and chemical correction becomes necessary. Nutritional receptivity therefore represents a constraint that operates both on the delivery pathway and on the biological community performing the delivery, across a continuum from partial compensation to full chemical intervention depending on severity.

Mineral antagonisms are a primary mechanism of disrupted nutritional receptivity. These are competitive interactions at the root surface in which excess of one nutrient suppresses the uptake of another. Excess iron suppresses manganese uptake. High potassium competes with magnesium at root transporters. Excess phosphorus can suppress zinc and iron uptake. Calcium-to-magnesium imbalance affects cell membrane function and can impair the uptake of multiple nutrients simultaneously. These antagonisms operate at the physiological level — biologically released nutrients in plant-available forms may be present in adequate concentrations in the soil solution but remain effectively unavailable because uptake is blocked at the root transporter (Marschner, 2012).

Phosphorus saturation presents a specific and important constraint. Soils with chronically high phosphorus inputs reach saturation conditions that suppress arbuscular mycorrhizal colonization, because the plant-AMF carbon-for-phosphorus exchange becomes economically unfavorable from the plant's perspective when soil P is already high (Treseder, 2004). Since AMF are the primary biological vector for phosphorus delivery and extend the effective root uptake surface substantially, P saturation effectively closes the fungal transfer channel even when hyphal networks are otherwise well-developed.

Soil pH affects nutritional receptivity through two simultaneous mechanisms: it shifts nutrient speciation between plant-available and plant-unavailable chemical forms, and it directly affects microbial community composition and activity. Low pH causes aluminum and manganese to move into forms that are both toxic to roots and competitive with other nutrient uptake pathways. High pH precipitates iron, manganese, zinc, and boron into forms that may be biologically released but immediately re-immobilized before reaching the root transporter.

Nutritional receptivity is the element of the BTC chain most dependent on soil chemistry and least remediable through biological management alone. It represents the final gate through which all upstream biological work must pass.

4. When the Chain Functions: The Integrated Delivery State

Before examining where the chain fails it is worth establishing what the chain looks like when it is functioning — the integrated delivery state that represents the positive reference condition against which failure is measured. This state is not theoretical. It has observable biological, chemical, and agronomic signatures that a trained agronomist can recognize in the field and confirm analytically.

At the substrate level, the soil contains a meaningful labile carbon fraction alongside stabilized humus, with organic inputs entering at a C:N ratio that drives net nitrogen mineralization rather than immobilization. The organic matter pool is actively replenished — by root exudates, cover crop residues, or compost additions — at a rate sufficient to sustain microbial activity across the growing season rather than only during the period immediately following incorporation.

At the community level, MBC is adequate and the F:B ratio reflects a mixed or fungal-trending community appropriate to the cropping system. Crucially, the community is not dominated by a single functional guild. Active fungal hyphae are visible microscopically — containing cytoplasm and physically associated with soil aggregates and organic matter particles — indicating that the structural and mycorrhizal channels are operating alongside the bacterial decomposition pathway. The qMIC indicates that a meaningful fraction of total organic carbon is in active biological use rather than stored in chemically stabilized forms inaccessible on seasonal timescales.

Metabolically, the community is active and efficient. Respiration is elevated relative to a biologically depleted soil but qCO_2 is moderate or declining — the community is incorporating carbon into biomass at a reasonable efficiency rather than burning it rapidly in a high-maintenance stress state. This metabolic efficiency translates directly into a more sustained and temporally distributed nutrient release pattern: rather than a large mineralization pulse following substrate addition that rapidly exceeds crop uptake capacity and is lost to leaching, nutrients are released in smaller, more continuous increments as predator-prey dynamics operate across the growing season.

The predator-prey loop is operating at a level of trophic complexity above the enrichment baseline. Protozoan assessment reveals amoebae alongside flagellates — not a fully mature ciliate-dominated community necessarily, but one in which the primary nutrient release mechanism is active in the rhizosphere. Nematode community composition shows at least early fungivores (cp-3) alongside bacterivores, indicating that the food web has sufficient trophic depth to regulate microbial biomass turnover across both the bacterial and fungal channels. Solubilizing bacteria are present and active, measurable through enzyme assays or inferred from organic acid profiles in rhizosphere soil. The combined effect of grazing-driven mineralization and biological solubilization is that plant-available nitrogen, phosphorus, and micronutrients are released in spatial proximity to root surfaces at rates that track, rather than precede or lag, the crop’s demand curve.

At the nutritional receptivity level, the soil pH is within the range that keeps macronutrients and micronutrients in plant-available speciation, cation balance does not impose significant antagonism at root uptake sites, and phosphorus levels are adequate without approaching saturation. AMF colonization of root tissue is detectable and the mycorrhizal network extends the effective root uptake surface, providing both phosphorus delivery and access to water and micronutrients beyond the depletion zone immediately surrounding the root.

The agronomic signatures of the integrated delivery state are characteristic and recognizable. Yield is responsive to biological inputs and shows a positive trajectory season over season without requiring escalating external nutrient applications. Tissue analysis at peak demand shows macro and micronutrient concentrations within or approaching sufficiency ranges across the elemental profile, not merely for nitrogen and phosphorus in isolation. Crop canopy development tracks the expected growth curve without the mid-season plateaus or deficiency symptoms that indicate nutrient delivery has fallen behind demand. Soil aggregate stability is good and improves with management, reflecting the active fungal networks and humic accumulation that are the physical expression of a functioning BTC chain over time (Tisdall & Oades, 1982; Six et al., 2004).

It is equally important to be clear about what the integrated delivery state is not. It is not the highest possible biological activity as measured by total MBC or respiration rate. It is not a maximally enriched food web with abundant early-successional organisms. It is not dependent on exotic inoculants or intensive biological inputs. It is a condition of functional adequacy at each link — sufficient substrate quality, appropriate community character, adequate metabolic activity, an operational predator-prey loop, and permissive soil chemistry — that produces reliable, temporally matched nutrient delivery as an emergent property of the whole system. The goal of BTC diagnosis is not to maximize any individual element but to identify which link is preventing the system from reaching this functional state, and to address it with the minimum intervention necessary to restore chain continuity.

5. The Chain as a Diagnostic Tool: Where Delivery Fails

The BTC framework is most useful as a diagnostic tool when yield response to biological management is absent or inconsistent. The following plausible scenarios, grounded in mechanisms documented in the soil ecology literature, illustrate how failure at each link produces distinct field outcomes that standard biological indicators — total microbial biomass carbon, basal respiration rate, and total organic matter — would not identify as delivery chain failures, even when those indicators appear adequate or elevated.

It is important to acknowledge that compound failures — in which two or more links are simultaneously limiting — are common in practice, particularly in soils with long management histories or significant chemical modification. The four scenarios below are presented with a single failing link each for diagnostic clarity, but real field situations rarely isolate so cleanly. A soil with high-C:N substrate inputs may simultaneously have a disrupted predator-prey loop and a marginal P saturation issue, with each constraint partially masking the others. The BTC framework is therefore best applied iteratively rather than as a single-pass diagnosis: the most constraining link is identified and addressed first, and the soil is reassessed to determine whether a secondary constraint becomes apparent once the primary one is resolved. This iterative logic reflects the biological reality that food web succession is a sequential process in which resolving one bottleneck opens the pathway to the next.

To make the iterative process concrete, consider the following consultation sequence. An agronomist assessing a transitioning vegetable farm finds high MBC and vigorous respiration but flat yield response to compost additions over two seasons. A BTC assessment identifies the predator-prey link as the primary failure: microscopy shows flagellate-dominant protozoa with no amoebae and a sparse nematode community of cp-1 bacterivores only. The recommendation is to introduce diverse mature compost as an inoculant and reduce tillage frequency. At reassessment — conducted after sufficient time for measurable biological succession to occur, typically several weeks to months depending on the organisms being assessed and the season — amoebae are now present and nematode diversity has increased to include early fungivores. Yield response at mid-season improves modestly. However, tissue analysis at this point reveals that while nitrogen delivery has improved, zinc and iron concentrations are marginal — a nutritional receptivity signal that was previously masked by the more severe predator-prey failure. Soil chemistry review finds soil pH has drifted to 7.4 from repeated lime applications. The second intervention targets pH correction and temporarily reduces compost P inputs. This two-step sequence — first resolving the biological delivery failure, then uncovering and addressing the chemical reception failure — is the practical expression of iterative BTC diagnosis.

Scenario A: High-Carbon Soil with Nitrogen Immobilization (Substrate Link)

A market vegetable farm incorporates large volumes of wood chip compost with a C:N ratio of approximately 35:1 and measures a substantial increase in soil organic matter over two seasons. Despite the biological investment and improved soil structure, crop nitrogen response is weaker than expected, and tissue nitrogen concentrations remain below optimum during peak vegetative growth. MBC measurements show adequate microbial biomass is present.

The BTC diagnosis points to the substrate link. High-C:N material drives net nitrogen immobilization — the microbial community is consuming available nitrogen to decompose the carbon rather than releasing it. The biological engine is running, but it is drawing nitrogen toward the microbial fraction rather than releasing it toward the plant during the crop's peak demand window. A correction in organic input C:N ratio — blending wood chips with lower-C:N materials or allowing pre-composting to reduce C:N before field incorporation — addresses the diagnosis directly (Paul & Clark, 1996).

Scenario B: Active but Bacterially Dominated Community (Community Character Link)

A conventionally managed annual crop field is transitioned to reduced tillage and cover cropping. After two seasons, total MBC increases substantially and basal respiration is elevated. However, yield response to reduced synthetic nitrogen inputs is modest and nitrogen use efficiency remains low. F:B ratio measurement shows the community remains strongly bacterial-dominated despite the management change.

The BTC diagnosis points to the community character link. A bacterial-dominated community cycles nitrogen rapidly but produces inorganic nitrogen predominantly in nitrate form, which is highly mobile and leaches readily in wet conditions. The community has high processing capacity but low transfer capacity — nutrients are released in a form and at rates that are poorly matched to crop demand timing. The management response — extending cover cropping diversity to include species producing high-C:N residues that preferentially stimulate fungal decomposers (Wardle et al., 1995), and continuing to reduce tillage frequency to protect hyphal network integrity and allow community succession toward more K-selected, slow-cycling life strategies (Schmidt et al., 2018) — addresses community character specifically rather than total biological activity.

Scenario C: Food Web Activity Without a Functional Predator-Prey Loop (Loop Link)

A soil receiving annual compost applications for five years has high organic matter, high MBC, and vigorous microbial activity as measured by CO2 burst. Microscopic observation reveals abundant bacterial colonies and fungal hyphae. However, nematode Baermann extraction shows only a sparse community of cp-1 bacterivores with no fungivores or higher-guild organisms, and protozoan assessment shows flagellate dominance with no amoebae or ciliates.

The BTC diagnosis points to the predator-prey link. The microbial processing engine is large and active but the transfer mechanism — grazing-driven nutrient release in the rhizosphere — is not operating at the trophic complexity needed for efficient delivery. Nutrients are cycling within the microbial fraction without being released into plant-available forms at rates and locations matching crop demand. The management response is to reduce disturbance frequency to allow the trophic succession that K-selected predator and fungivore guilds require to establish (Ferris et al., 2001), and to consider introducing mature compost as a source of diverse soil organisms — including active protozoa and early fungivore nematodes — to accelerate recolonization of depleted communities (Ingham, 1999; Bonkowski, 2004).

Scenario D: Developed Food Web in a P-Saturated Soil (Nutritional Receptivity Link)

A long-term organic vegetable farm with a fifteen-year history of compost application has excellent soil biological indicators across all measured parameters: high MBC, high F:B ratio, diverse nematode community including fungivores, and active protozoan community with amoebae and ciliates. Despite this biological richness, yield response to biological inputs has been flat for several seasons, and plant tissue analysis shows adequate phosphorus but marginal zinc and iron.

The BTC diagnosis points to the nutritional receptivity link. Long-term compost inputs have driven soil phosphorus to saturation levels that suppress AMF colonization, closing the primary fungal delivery channel for phosphorus and associated micronutrients. The food web is structurally mature with high processing capacity, but the chemical conditions at the plant-soil interface are blocking the final transfer step. The management response requires soil chemistry intervention before biological management can translate into improved yield response. Where P saturation has suppressed AMF colonization (Treseder, 2004), a multi-year reduction in phosphorus inputs is needed to allow mycorrhizal community recovery; where pH is driving nutrient immobilization or speciation into unavailable forms (Marschner, 2012), targeted pH adjustment is required. Both interventions address the conditions blocking the final transfer step, and neither can be substituted by biological inputs alone.

Table 1 summarizes the BTC chain elements, their observable indicators, their primary failure modes, and the management implications of each.

Element	What It Represents	Observable Indicators	Failure Mode	Management Implication
Substrate Availability	Organic carbon and nutrient pool accessible to drive microbial activity	OM quantity and humification state; C:N ratio; labile vs stable C fractions	Depleted or over-stabilized substrate; high C:N driving N immobilization	Adjust input C:N ratio; increase labile carbon fraction
Microbial Biomass & Community Character	Size and functional identity of the active microbial community	MBC; F:B ratio; microbial quotient (qMIC)	Wrong community type; bacterially dominated when fungal channel is needed	Increase high-C:N inputs; reduce tillage; diversify cover crops
Metabolic Activity & Efficiency	Whether the community is actively converting substrate and at what efficiency	Basal respiration; qCO2; carbon use efficiency (CUE)	Metabolic suppression by moisture, pH, compaction, or chemical stress	Address suppression cause; improve aeration, moisture management, pH
Predator-Prey Dynamics & Microbial Loop	Trophic grazing interactions that release nutrients from microbial biomass to plant-available forms	Protozoan community succession state; nematode guild composition; EI and SI indices	Absent or early-successional predator community; nutrients locked in microbial tissue	Introduce diverse mature compost inoculant; reduce disturbance frequency
Nutritional Receptivity	Plant-side and soil-chemistry conditions that allow or block nutrient uptake at the root interface	Tissue elemental ratios and antagonism pairs; soil pH; P saturation; cation balance	Mineral antagonisms; P saturation closing AMF channel; pH-driven immobilization	Soil chemistry correction; multi-year P management; pH adjustment

Table 1. BTC chain elements, indicators, failure modes, and management implications.

6. A Research Agenda for BTC in Agriculture

The individual elements of the BTC chain are grounded in established theoretical frameworks and have each been the subject of substantial scientific investigation. What is largely absent is research that tracks all five elements simultaneously in field agricultural conditions and connects their combined state to yield outcomes. Three research priorities are proposed.

6.1 Simultaneous Multi-Element Field Assessment Protocols

No existing agronomic field protocol assesses all five BTC elements in a single coordinated study design. Research in substrate availability typically occurs independently of research in predator-prey dynamics. Rhizosphere exudate research is rarely connected to field yield outcomes.

Nematode faunal analysis studies do not routinely include paired nutritional receptivity measurements.

The first research priority is the development of a coordinated field protocol in which all five elements are measured simultaneously within the same plots, at multiple points during the growing season, with yield as the outcome variable. Existing tools can be assembled into such a protocol without requiring new laboratory methods. Table 2 presents a schematic of the assessment elements, recommended measurements, sampling timing, and indicative decision thresholds. These thresholds are provisional and literature-derived; establishing empirically validated thresholds is itself a key objective of the research agenda.

BTC Element	Recommended Measurement	Sampling Timing	Decision Threshold (Indicative)
Substrate Availability	Labile C fraction (permanganate oxidizable C or particulate OM); C:N ratio of primary inputs	Pre-season and mid-season	C:N < 25:1 for net mineralization; labile C fraction > 15% of total SOC
Microbial Biomass & Community Character	MBC (chloroform fumigation or Microbiometer); F:B ratio (PLFA or Microbiometer)	Pre-season; peak vegetative growth	F:B ratio trending toward 0.3 or above for annual crops (literature-derived, not validated threshold); qMIC above 1% as indicative of biologically accessible substrate — both require local calibration
Metabolic Activity & Efficiency	Basal respiration; qCO2 (respiration/MBC); Solvita CO2 burst as field proxy	Peak vegetative growth; after stress events	qCO2 declining season-over-season suggests improving efficiency; no validated absolute threshold — trend direction is more informative than single-point values
Predator-Prey Dynamics	Protozoan succession state (microscopy); nematode guild composition (Baermann extraction)	Pre-season; mid-season	Amoebae detectable in protozoan community; cp-3 nematodes present in Baermann extract — minimum indicative thresholds; community trajectory over time more diagnostic than single-point presence
Nutritional Receptivity	Mehlich-3 full panel; base saturation; soil pH; tissue analysis at peak demand	Pre-season (soil); peak demand (tissue)	pH 6.0–7.0 as a general working range; P saturation below site-specific threshold (varies by soil type and P sorption capacity); tissue ratios within crop-specific sufficiency ranges — all require site-level interpretation

Table 2. Schematic BTC field assessment protocol. Measurements, timing, and thresholds are indicative and drawn from existing literature. Empirical validation across soil types and cropping systems is the primary research need.

Developing an integrated sampling design and a shared analytical framework is a prerequisite for BTC field testing. Such a protocol would require multiple sampling events across the growing season to capture temporal variation in element states, with timing guided by crop growth stage and the succession dynamics of the organisms being assessed. The specific sampling design, number of events, and resource requirements would need to be established through initial protocol development work — itself, a component of the proposed research agenda — before a formal multi-site validation study could be designed.

6.2 Identifying the Most Constraining Link Across Management Systems

A second research priority is systematic investigation of which BTC element is most constraining — in the sense that addressing it would produce the greatest improvement in delivery outcome, while addressing other elements in isolation would not — under different management systems, soil types, and cropping contexts. This concept of the most constraining element is analogous to the rate-limiting step in biochemistry: just as the slowest reaction in a pathway determines the overall rate regardless of how fast the other steps proceed, the most constraining BTC element determines delivery capacity regardless of how well the other elements are functioning. Based on the theoretical framework and the mechanisms documented for each BTC element, the most constraining link is expected to differ substantially between systems — an expectation that itself constitutes a testable prediction of the BTC framework. In conventionally managed annual crop soils with low organic matter, substrate availability may be the primary constraint. In long-term organic systems with high organic matter accumulation, nutritional receptivity — particularly P saturation and associated mineral antagonisms — may be the primary constraint. In recently disturbed soils recovering from tillage or fumigation, the predator-prey loop may be the constraining element even when substrate and biomass metrics are adequate. None of these predictions has been tested prospectively using a simultaneous multi-element assessment design, which is precisely what this research priority proposes.

Identifying which link is most constraining across a range of systems would allow the BTC framework to generate differentiated management recommendations rather than uniform prescriptions. This differentiation is precisely the diagnostic capability that conventional metrics lack and that BTC is designed to provide.

6.3 Threshold and Trend Research Connecting Element States to Yield Outcomes

The third research priority is empirical threshold and trend research. For BTC to function as a practical diagnostic framework, it needs to be accompanied by decision thresholds — quantitative or semi-quantitative criteria that distinguish functional from non-functional states at each link. What F:B ratio is associated with functional fungal channel delivery for a given crop type? What protozoan succession state is the minimum necessary for adequate microbial loop activity? At what P saturation level does AMF suppression become practically significant for crop nutrition?

These thresholds do not currently exist in a form that is usable for agronomic decision-making. Developing them requires longitudinal field studies that track BTC element states across multiple growing seasons and connect changes in element states to changes in nutrient delivery efficiency and crop yield. Trend data — not just cross-sectional snapshots — are needed because the food web is a succession system in which the current state reflects management history as much as current conditions. Such research would also allow the BTC framework to be used prospectively: not only to diagnose current delivery failure but to predict which management practices are likely to move the food web toward functional delivery over a defined time horizon.

7. Limitations of the Framework

BTC is a conceptual framework, and its limitations should be stated explicitly before it is applied in research or extension contexts.

Most importantly, the five-element chain has not been tested as an integrated whole in field agricultural conditions. Each element has theoretical and empirical support in the literature, and the chain logic is consistent with established soil food web theory. However, whether the five elements, assessed simultaneously, reliably predict nutrient delivery outcomes across a range of soils, crops, and management systems is not yet known. The framework generates hypotheses; it does not yet constitute a validated predictive model.

The element weights implied by the chain structure — specifically, the assumption that each element is a prerequisite for the next — may oversimplify the actual biological relationships. In reality, partial function at one link may partially compensate for weakness at another. A strongly developed predator-prey community may sustain some nutrient delivery even when substrate quality is suboptimal. The strict sequential logic of the chain is a diagnostic simplification; the underlying biology is more continuous and interactive.

The indicative decision thresholds presented in Table 2 are drawn from the mechanistic literature cited in this paper and are presented as provisional starting points for research design rather than validated agronomic standards. They have not been tested against field outcomes within the BTC framework itself and should be treated as hypotheses to be refined rather than established decision criteria. Different soil types, climate zones, and cropping systems will likely require threshold calibration before the framework can be applied with confidence in specific local contexts.

Finally, the framework currently focuses on nutrient delivery and does not explicitly address other soil food web services — disease suppression, aggregate stability, water infiltration, and carbon sequestration — that are also agronomically important and that emerge from similar food web succession dynamics. Extending BTC to encompass these services is a direction for future development rather than a feature of the current framework.

8. Conclusion

Biological Transfer Capacity offers a reframing of the central soil health question — from how much biological activity is present to whether the food web is delivering nutrients to the crop at the rates, in the forms, and at the times that plant demand requires. The distinction between processing capacity and transfer capacity is the conceptual core of this reframing, and it explains a category of agronomic outcomes — biologically active soils that fail to produce yield response, and mineral adequate soils that fail to translate nutrient supply into crop uptake — that conventional biological and chemical metrics, considered in isolation, cannot account for.

The theoretical justification is that the five elements of the chain each have strong independent support in the soil ecology literature, and their sequential logic is consistent with the foundational energy channel and microbial loop models developed over four decades of soil food web research. The integration of these elements into a single diagnostic chain is conceptually novel, but the building blocks are established.

The practical urgency is that agronomists and extension professionals regularly encounter situations in which biologically active soils do not translate their activity into crop response. BTC provides a structured way to ask why — and to direct investigation and intervention to the specific link in the delivery chain that is limiting. It is proposed as a complement to existing soil health frameworks, not a replacement for them.

The scenarios presented in this paper are illustrative, not empirical. Validating BTC as a framework requires the multi-element field research outlined in Section 6. That research does not require new laboratory methods — the tools exist. What is needed is a coordinated study design that brings those tools together within a single chain-of-evidence logic, applied to real soils across a range of management contexts.

Extension professionals and agronomists willing to apply BTC thinking to their diagnostic work can begin by asking, for any soil showing discrepancy between biological activity and crop response: which link in the chain is most likely failing here, and what evidence would confirm that diagnosis? That question, applied systematically and iteratively, is the practical starting point for the research agenda proposed in this paper.

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