Redox Oscillation-Driven Nitrogen and Phosphorus Fluxes Coupled with Carbon Turnover in Glycine max Systems Under Drought-Rewetting Cycles

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Abstract

Drought-rewetting cycles have been identified as one of the most important types of environmental disturbance in agricultural soils and have the potential to produce dramatically large and oscillating changes in soil redox potential (Eh) that reconfigure the biogeochemical environment that controls the supply of nitrogen (N) and phosphorus (P) to Glycine max (soybean) production systems. The objective of the current study is to provide a synthesis of the current scientific understanding of the linkages between the N and P fluxes driven by redox oscillations and carbon (C) turnover in the soybean rhizosphere across disciplines including soil biogeochemistry, microbial ecology, plant physiology and agronomic science. Upon the onset of drought and associated emergence of aerobic soil conditions, oxidative processes such as nitrification, organic matter stabilization, and the adsorption of phosphate to iron (Fe) and manganese (Mn) oxide minerals occur while subsequent rewetting and development of anoxic soil conditions will result in denitrification, fermentation of C, reductive dissolution of Fe oxide bound P, and the Birch effect (an observable transient pulse of dissolved organic C (DOC), ammonium (NH_4^+), and inorganic P occurs following rapid rewettingThese oscillatory dynamics have an intricate and contradictory influence on soybean nutrient acquisition due to transient nutrient pulses both provide short-term benefits to fertility while increasing the potential for gaseous N loss, P leaching, and microbial immobilization. Drought stress disrupts the symbiotic relationship with Bradyrhizobium japonicum and AMF and results in variable recovery from drought after rewetting, which results in complications in BNF and P efficiency. The extracellular enzyme systems that exist, including β-glucosidase, urease, nitrate reductase, acid phosphatase and dehydrogenase, are key biogeochemical regulators that mediate C:N:P transformations and stoichiometric coupling at redox transitions. The microbial community shifts in the abundance of Proteobacteria, Actinobacteria, Acidobacteria, Firmicutes, and functional fungal guilds affect their metabolic capacity as a community and create redundancy at the level of functional redundancy at the community level when exposed to redox stress. Overall, results show that all three redox dynamics; frequency, amplitude, and duration; modulate the N_2O emissions, efficiency of P mobilization, C sequestration potential, soil aggregate stability and ecosystem function, and long-term sustainable soy production. The use of multi-omics methods that are currently being developed, along with stable isotope tracing techniques and machine learning-based biogeochemical modeling, creates a perfect opportunity to better understand how these interconnected processes work. The results of these studies demonstrate that there is an urgent need for drought-adaptive management practices to help maintain nutrient-use efficiency, soil biogeochemical stability, and climate resilience in worldwide soybean production systems. These practices include optimized irrigation scheduling, applying organic amendments (e.g., manure, compost), and the use of bioinoculants (e.g., rhizobacteria).

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1. Introduction

1.1. Global Significance of Glycine max and Nutrient Challenges

Soybean (Glycine max (L.) Merrill) is an important crop with great agricultural and nutritional relevance, accounting for approximately 60 % of global oilseed production and being the primary plant protein source worldwide (Hartman *et al*., 2011) [1]. With annual worldwide production exceeding 370 million metric tons, the soybean is grown in [North America, South America, Asia and Europe] in a variety of different climates and growing conditions, placing it at the confluence of food security, The ability of soybean to fix biological nitrogen (BNF) through a symbiotic relationship with Bradyrhizobium japonicum provides valuable agronomic benefits; BNF has been estimated to provide soybean with 40 - 330 kg N/ha/year under optimal growing conditions (Salvagiotti *et al*., 2008) [3]. Unfortunately, the susceptibility of this symbiotic relationship to environmental perturbations, such as frequent and intense drought-rewetting cycles that are predicted to occur due to climate change (Seneviratne *et al*., 2012) [7], has serious implications for production of soy in the future (Desclaux *et al*., 2000) [4].

Sustainable soybean production requires scientists to understand how nitrogen (N), phosphorus (P), and carbon (C) behave in the rhizosphere (the area immediately surrounding plant roots) so that phosphorous deficiencies do not continue to limit yields throughout much of the tropics and subtropics — where P is very tightly bound (sorbed) to iron (Fe) and aluminum (Al) in the Oxisols and Ultisols that are highly weathered. Phosphorus is one of these. Also, N transformations in the rhizosphere — including: mineralization, nitrification, denitrification, BNF — will be determined by the interaction of four different variables: soil redox potential, the nature of the microbial community in the immediate area around roots, root exudate chemistry, and soil physicochemical properties.

1.2. Drought-Rewetting Cycles as Biogeochemical Drivers

More volatile weather patterns occurring worldwide due to increased precipitation variability as a result of human-caused climate change (Seneviratne *et al*., 2012) [7], have created irregular patterns of wetting and drying throughout the soil in agricultural areas. Soil redox potential (Eh) undergoes intervalic changes associated with DRW cycles. These changes propagate through multiple closely related biogeochemical cycles and affect the transformation of carbon (C), nitrogen (N), phosphorus (P) and the reduction of metals (Fe and Mn) and S (Reddy and DeLaune, 2008; Lovley, 1991) [11, 13]. Dry/wet periods affect microbial metabolic activity by decreasing water availability during dry periods, leading to increased rates of aerobic decomposition (Birch, 1958) [9]. The rapid increase in soil moisture from the rewetting event creates a shift from aerated to anaerobic conditions in large aggregates and small areas within aggregates and increases the activity of fermentation, denitrification, methanogenesis and the reduction of metal oxides (Reddy and DeLaune, 2008; Lovley, 1991) [11, 13]. The effect of rewetting once-a-year will have a greater impact on nutrient fluxes than would normally be expected based on annual nutrient exportation estimates alone (Turner and Haygarth, 2001) [26].

The interplay between the different processes involved in the biogeochemistry of the root zone or rhizosphere of legumes (e.g., soybean) is poorly understood. The management of nutrients that have been transformed by their chemical state through oscillating redox conditions is one way that redox oscillations can affect the growth and overall productivity of plants, as well as their ability to acquire nutrients, contribute to the growth of microorganisms, change the diversity of microbial communities, alter the profiles of exoenzyme activity, and affect the stability of soil aggregates and turnover of soil organic matter (SOM) (Schmidt *et al*., 2011; Lehmann and Kleber, 2015; Nannipieri *et al*., 2003; Sinsabaugh *et al*., 2009) [8, 18, 19, 17]. This creates a major limitation on understanding how the processes of different spatial scales (microenvironmental hot spots within the root-soil interface to field scale nutrient balances) integrate to influence plant productivity and acquisition of nutrients. To address these issues, future research will require the use of a variety of scientific disciplines.

1.3. Objectives and Scope of This Review

The current mechanistic understanding of redox-reactive mechanisms in ecosystem transformations and nutrient cycling (Reddy and DeLaune, 2008; Lovley, 1991; Kuypers *et al*., 2018) [11, 13, 24] will be the basis for this comprehensive synthesis review. In this case, using the cumulative body of work in Rhizosphere Biogeochemistry (Hinsinger *et al*., 2009; Philippot *et al*., 2013; Bais *et al*., 2006) [29, 16, 15], this review aims to achieve the following objectives: (1) To provide an advanced understanding of the thermodynamic/kinetic principles underlying soil redox transitions caused by DRW events; (2) To detail the biogeochemical transformations of C, N, and P across redox gradients via the interaction of soybean roots with soil microbes; (3) To evaluate the responses of microbial communities and their functional roles in an ecosystem to nutrient cycling when subject to a redox stress event; (4) To assess the potential impact of nutrient cycling through redox-reactive processes on the productivity of soybean crop systems and on the efficiency of utilizing soil nutrients; and (5) To summarize potential limitations of existing methodologies and recommended future directions of research for developing drought-resilient soybean production systems. Tables 1-6 and Figures 1-4 are integrated throughout the manuscript to provide a consolidated representation of major results/ data and maps/conceptual frameworks required to complete each objective.

2. Redox Oscillations and Soil Biogeochemical Dynamics

2.1. Fundamental Concepts of Soil Redox Chemistry

Soil Eh which stands for soil redox potential is the tendency for a soil to transfer ions, and is measured in mV (millivolts) as compared to H2. The values typically vary between +700 mV when well aerated down to -300mV under anaerobic flooded conditions (Reddy and DeLaune, 2008) [11]. The relationship and values between Eh and the chemical activities of oxidized and reduced components of soil, are governed by the Nernst equation where pH is an important influencing factor since at equilibrium there is a decrease in Eh of approximately 59 mV when pH is increased by one unit (Prosser and Nicol, 2008) [12]. The driving force for redox chemistry of soils are the microbial respiratory pathways where heterotrophs will deplete their available electron acceptors in the following order of free energy yield: O2 > NO3- > Mn4+ > Fe3+ > SO42- > CO2 (Lovley, 1991) [13]. The fundamental processes controlling chemical transformations of N, P, and C in agroecosystems are also dictated by soil redox (Reddy and DeLaune, 2008; Kuypers *et al*., 2018) [11, 24] (Table 1). There are distinct and predictable sequence of redox reactions and their chemical implications that will occur as soil returns to an aerobic state from an anaerobic state (during flooding or rewetting) that ultimately determine the fate of N, P and C in agroecosystems. Understanding the thermodynamic rules that govern these chemical transformations is necessary in order to explain the complex biogeochemical processes and feedbacks observed in the soybean rhizosphere under DRW (drought-rewetting) stress.

Table 1: Major redox reactions and their ecological significance in agricultural soils under drought-rewetting cycles

Redox Reaction	Eh Range (mV)	Electron Acceptor	Key Microorganism(s)	Ecological Significance
O_2 reduction (aerobic respiration)	+600 to +400	O_2	Heterotrophic bacteria (diverse)	Organic matter decomposition; CO_2 release; sustains plant-available N
NO_3^- reduction (denitrification)	+400 to +200	NO_3^-	Pseudomonas, Paracoccus, Bacillus spp.	N_2O/N_2 emission; N loss from soil; GHG production
Mn^{4+} reduction	+200 to +100	MnO_2	Shewanella, Geobacter spp.	Mn^{2+} mobilization; P desorption from Mn-oxides
Fe^{3+} reduction	+100 to −100	$Fe(OH)_3$	Geobacter, Desulfuromonas spp.	Fe^{2+} release; P mobilization from Fe-mineral surfaces; soil color change
SO_4^{2-} reduction	−100 to −200	SO_4^{2-}	Desulfovibrio, Desulfobacter spp.	H_2S production; metal sulfide precipitation; S cycling
Methanogenesis	< -200	CO_2/acetate	Methanobacterium, Methanosarcina spp.	CH_4 emission; anaerobic C decomposition; GHG production
N_2 fixation (BNF)	+300 to −150 (nodule microaerophilic)	N_2 (atmospheric)	Bradyrhizobium japonicum	Biological N input into soybean system; NH_4^+ supply to plant

2.2. Mechanisms Driving Oxidation–Reduction Fluctuations in Agricultural Soils

In agricultural soils, dynamics of redox potential result from the interaction between O_2 availability (which is affected by diffusion of gas through pores in the soil, moisture level, and physical structure of aggregated soil) and demand for O_2 (which is affected by microbial respiration and chemical oxidation reactions) (Schuur *et al*., 2013) [14]. The amount of moisture in the soil decreases during times of drought, increasing gas-phase diffusion of O_2 in the soil, resulting in greater penetration of O_2 into the soil profile and the persistence of aerobic conditions through the full depth of the profile. Additionally, drying of soil promotes the formation of soil aggregates and stabilization of organic matter within soil aggregates, consequently reducing the availability of substrate to microbial organisms and their metabolic rates, in the short term (Schmidt *et al*., 2011) [8]. In contrast, when the dynamics of soil moisture change from dry to wet, a dramatically different balance is created. Specifically, wet conditions lead to rapid infiltration of water, replacement of gas-phase O_2 with water within pores, generation of water-saturated pores, and release of large quantities of labile organic substrates that accumulated during drought conditions.

The dynamics of redox potential develop based on soil texture, aggregate architecture, organic matter content, and metabolic activity of microbial communities. For example, within the soybean rhizosphere, low molecular weight organic acids, amino acids, and sugars exuded from the plant roots enhance microbial activity and O_2 consumption at the root-soil interface, resulting in the development of a characteristic Eh gradient extending radially from the surface of the root into the surrounding bulk soil (Bais *et al*., 2006) [15]. This effect of the rhizosphere (also called rhizosphere effect) enhances and spatially creates redox dynamics that significantly impact nutrient availability at the root-soil interface.

2.3. Influence of Drought-Rewetting Cycles on Soil Redox Potential

The effects of drought and rewetting cycles on soil physicochemical properties and redox status have been characterized by several field studies that quantitatively measure the changes in soil and plant factors that impact redox conditions (and contribute to the oscillation) during DRW cycles. The two distinct components that contribute to the oscillation are the duration and magnitude of these events. Drought and rewetting events have a variable duration and frequency, which leads to variability in the amount of soil moisture available before rewetting, as well as variability in both the presence and availability of electron donors and electron acceptors during these events. In general, independent studies across diverse systems have demonstrated a strong correlation between changing redox potentials and P availability across time (drought and rewetting) as well as location (upper and lower landscapes) in soils that contain a high percentage of organic matter, have a fine texture, and are rich in microbial biomass (i.e., soybean growing soils) (Frossard *et al*., 2000; Turner and Haygarth, 2001; Pett-Ridge and Firestone, 2005) [23, 26, 21].

Table 2 provides an overview of how the effects associated with drought and rewetting on soil properties and redox status are generally different at the extreme end of the wetting and drying spectrum, especially during the rewetting cycle. Specifically, the way that the redox potential (Eh) behaves during rewetting is different from how it behaved during drought. Within 24 to 72 hours after rewetting, the redox potential in soils with a high organic matter content can fall below the threshold for Fe^{3+} reduction (around +100 mV) and enable the mobilization of P from Fe-oxide surfaces (Lovley, 1991; Frossard *et al*., 2000) [13, 23]. This potentially significant agronomic event occurs when the rewetting cycle creates conditions that enhance the bioavailability of P for soybean uptake (which increases the opportunity for the production of P-rich plant biomass) and allows for increased opportunities for the loss of P through leaching or runoff under certain soil type conditions.

Table 2: Effects of drought-rewetting cycles on soil physicochemical properties and redox conditions

Soil Property	Drought Phase Effect	Rewetting Phase Effect	Net Consequence for Nutrients
Soil moisture content (θ)	Decrease to wilting point ($<0.1\ m^3\ m^{-3}$)	Rapid increase to field capacity or above	Altered diffusion rates; surge in solute transport
Redox potential (Eh)	Increase (+400 to +700 mV); aerobic conditions	Sharp decrease (−100 to +200 mV); transient anoxia	Redox-sensitive element mobilization/immobilization cycles
Soil pH	Slight increase due to proton consumption by oxidation	Decrease due to organic acid release and CO_2 production	Affects P and metal bioavailability; alters enzyme activity
Aggregate stability	Increases due to desiccation and biofilm formation	Decreases rapidly upon rewetting; slaking of macroaggregates	Loss of aggregate-protected organic matter
Bulk density	Increases during desiccation and compaction	Decreases transiently upon swelling	Affects root penetration and water infiltration
Water-holding capacity	Reduced due to shrinkage and hydrophobicity	Temporarily increased post-rewetting	Influences moisture retention for plant uptake
Cation exchange capacity (CEC)	Reduced due to loss of organic matter and clay shrinkage	Partially restored; temporary increase in exchange sites	Affects NH_4^+ and K^+ retention; nutrient buffering capacity
Dissolved organic carbon (DOC)	Accumulation of partially decomposed organic substrates	Pulse release (Birch effect); rapid microbial mineralization	Short-term C, N, P flush drives nutrient cycling surge

2.4. Interactions Among Electron Donors, Electron Acceptors, and Microbial Metabolism

The relationship between the availability of electron donors (organic carbon) and electron acceptors in the soil largely dictate the rate and direction of the transition of soils between oxidizing and reducing conditions during drought-rewetting (DRW) cycles. In the soybean rhizospheres, root exudates, including organic acids (malate, citrate, oxalate), sugars (glucose, fructose) and amino acids, are the primary source of electron donor to support microbial respiration (Bais *et al*., 2006; Philippot *et al*., 2013) [15, 16]. The types and quantities of root exudates produced vary considerably during the vegetative, flowering, and pod fill development stages, with the majority of the root exudate released during the flowering and pod fill development stages. During periods of drought stress, decreased root metabolism limits the release of root exudates, resulting in a short-term depletion of electron donor supplies and the slowing of soil redox transitions. However, during rewetting events that follow drought stress, the rewetting of previously dry soils results in the simultaneous release of accumulated soil organic matter and root exudate, resulting in an immediate surplus of electron donor supplies compared to electron acceptors available for microbial metabolism (Birch, 1958; Kaiser *et al*., 2011) [9, 30].

Microorganisms that can utilize various electron acceptors (i.e., metabolic versatility) thrive under fluctuating redox conditions (Schimel *et al*., 2007; Blagodatskaya and Kuzyakov, 2013) [25, 27]. For example, facultatively anaerobic bacteria such as Pseudomonas and Bacillus can switch their modes of aerobic versus nitrate respiration depending on the changes in the soil redox potential (Eh) to provide functional continuity throughout the soil's redox transition cycle. In contrast, strict anaerobic (i.e., obligate) [e.g., Geobacter and Desulfovibrio] and strict aerobic bacteria [e.g., Nitrosomonas and Nitrospira] are more affected by fluctuations in Eh and suffer population limitations during times of unfavourable redox conditions, which, ultimately, results in reduced rates of denitrification and nitrification (Prosser and Nicol, 2008; Kuypers *et al*., 2018; Lovley, 1991) [12, 24, 13].

2.5. Redox Regulation of Nutrient Transformations and Elemental Cycling

Soil redox chemistry plays a critical role in controlling thermodynamic conditions that determine how some nutrients critical for the growth of soybeans will exist in soils, and, therefore, how much of these nutrients will be available to the plant (Reddy and DeLaune, 2008; Kuypers *et al*., 2018) [11, 24]. For example, redox conditions will define whether nitrogen (N) comes from the oxide pathway (nitrification, where $NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$) — which occurs under high Eh (oxidized) conditions — or from the reduction pathway (denitrification, where $NO_3^- \rightarrow N_2O \rightarrow N_2$) — which occurs under low Eh (reduced) conditions (Prosser and Nicol, 2008; Kuypers *et al*., 2018) [12, 24]. Phosphorus (P) will be liberated from Fe(III) oxide phases, which are the principal minerals involved in P adsorption and retention in soils, due to reductive dissolution of these minerals (Lovley, 1991; Frossard *et al*., 2000) [13, 23]. In the case of C, the availability of electron acceptors will determine if soil organic matter (SOM) will be mineralized to CO_2 (aerobic processes), fermented to CH_4 and CO_2 (anaerobic processes), or stabilized with reduced metal phases (Schmidt *et al*., 2011; Lehmann and Kleber, 2015) [8, 18].

The dynamics of these nutrients are coupled because they are connected with one another through metabolic pathways and competition for thermodynamic energy by different electron acceptors. The microbial biomass has an approximate stoichiometric ratio of C:N:P (about 60:7:1 by mass), therefore limiting the extent to which C, N, and P may uncouple, as microbes must keep their structural (cellular) elemental ratios within a certain target (homeostasis); even if the stoichiometry of the substrates varies (Sinsabaugh *et al*., 2009) [17]. Microbial homeostasis has implications for understanding mineralization and immobilization of N and P in relation to the fluctuation of the C:N:P ratios associated with soil organic matter movement induced by dry river-water (DRW).

2.6. Short-Term Versus Long-Term Ecological Consequences of Redox Oscillations

Scientists actively investigate how redox oscillation affects the biogeochemistry of soils over time. In the short term, (< 2 weeks), the development and subsequent reduction of nutrient-rich pulses; however, during transitional periods such as between DRW cycles in biogeochemical processes; soil ecosystems transition from aerobic to anaerobic conditions, resulting in significant impacts on microbial communities (Schimel *et al*., 2007; Blagodatskaya and Kuzyakov, 2013) [25, 27]. These impacts are usually considered negative for soybean (Glycine max) development through rapid nutrient release, increased N2O emissions and significant shifts in microbial composition affecting the availability of nutrients to plants during critical periods of soybean development (Butterbach-Bahl *et al*., 2013) [6].

Over much longer time scales (e.g., seasons or years), repeated DRW cycles alter the soil structure, amount and quality of SOM, increase the diversity of microbial communities and reduce the ability of soils to hold nutrients against leaching due to their altered, cumulative, properties (Schmidt *et al*., 2011; Luo *et al*., 2016) [8, 31].

Repeated DRW cycles lead to the development of unique microbial communities in soils. Specifically, microbial communities enriched by repeated DRW cycles tend to contain greater numbers of drought-tolerant taxa (such as Actinobacteria and Firmicutes) than moisture-sensitive taxa, resulting in altered functional capabilities for biological nitrogen fixation, N-mineralization and P-solubilization (Fierer and Jackson, 2006; Drenovsky *et al*., 2004; Nannipieri *et al*., 2003) [10, 22, 19].

3. Rhizosphere Ecology and Functional Characteristics of Glycine max Systems

3.1. Morphological and Physiological Characteristics of Glycine max

Glycine max, or soybean, is an annual leguminous herbaceous plant that typically will grow to a height of 0.5–1.5 m. Soybean has a taproot system capable of reaching depths of 1.5–2.0 m in optimum conditions. Its growth habit can be either determinate or indeterminate based on the cultivar type. The reproductive growth stages: R1 and R8 represent the most important nutrient demand and water sensitive stages of soybeans. The peak leaf area index, coinciding with flowering and early pod fill, will occur at the maximum time the crop will demand nitrogen (N), which is obtained primarily through biological nitrogen fixation (BNF) and soil mineralization, as well as phosphorus (P), which is necessary for ATP synthesis, nucleic acid production and function within photosynthetic membranes (Salvagiotti *et al*., 2008; Vance *et al*., 2003) [3, 20]. The physiological architecture of soybeans makes them very susceptible to water deficit and stress during germination, flowering and seed filling, which are all stages with a lot of metabolites produced and consequently a lot of carbon deposited in rhizosphere (Desclaux *et al*., 2000) [4].

3.2. Root System Architecture and Rhizosphere Development

Soybean's root system consists of a primary taproot, lateral roots, and fine root hairs that form a rhizosphere volume that stretches from the root surface to 1–4 mm into the surrounding soil (Bais *et al*., 2006) [15]. The structure of soybean roots is sensitive to the availability of soil moisture. When soil moisture is limited, drought conditions will slow down lateral root growth while facilitating deeper root growth for moisture access in subsoil horizons. The root length density (km of root m^{-2}) of healthy soybean stands is 1.5–4.0 km of root m^{-2} at peak vegetative growth, providing significant surface area for rhizodeposition and root–microbial interactions (Hartman *et al*., 2011) [1]. Due to the volume of root exudates and border cell secretions entering the rhizosphere zone during the growing season, soybean has a strong rhizosphere effect, which is characterized by increased microbial populations, shifts in the structure of microorganisms within the rhizosphere bacterial community, and increased enzyme production in the rhizosphere compared with the surrounding bulk soil (Philippot *et al*., 2013; Kaiser *et al*., 2011) [16, 30].

3.3. Root Exudation and Carbon Allocation Patterns

Soybean plants can modify the biogeochemistry of their rhizosphere through root exudation by introducing about 5-21% of their net photosynthate as either root exudates, border cells or volatile organic compounds, on average, when plants are not under stress (Bais *et al*., 2006) [15]. The components of soybean root exudates consist of predominantly low-molecular-weight organic acids (malate, citrate and fumarate), but there are also amino acids, sugars, phenolic compounds and high-molecular-weight mucilage. The several functions afforded by these components in the rhizosphere include: organic acids chelating (binding) with Fe3+ and Al3+, thus mobilizing P from mineral surfaces and buffering soil pH; amino acids and sugars serving as substrates for microorganisms, thus stimulating both microbial biomass and enzyme activity; and phenolic compounds acting as signalling molecules in the symbiosis between rhizobia and soybean, with phenolic glycosides influencing *Bradyrhizobium* nod gene expression (Salvagiotti *et al*., 2008) [3].

Drought stress greatly reduces both the quantity of root exudates due to reduced photosynthate production as well as decreased permeability of root membranes and leads to increased amounts of osmolytes (e.g. proline and betaines) and stress response compounds (Desclaux *et al*., 2000) [4]. Following rewetting, exudate flux increases rapidly, often with greater rates of release of organic acids that may contribute to enhanced mobilization of P in the rhizosphere. Therefore, the increases in exudates caused by the drought-rewetting phenomenon create dynamic changes in the rates of biogeochemical processes occurring within the rhizosphere, resulting in substantial effects on N and P fluxes.

3.4. Symbiotic Interactions with Rhizobia and Beneficial Microorganisms

Bradyrhizobium and soybean form a symbiotic relationship that is essential in biological fixation of nitrogen for agricultural systems involving soybeans. This symbiotic relationship can provide from 50%-100% of the nitrogen needs of soybean crops when managed properly (Salvagiotti *et al*., 2008) [3]. The process of nodulation begins when signals from flavonoids exuded by soybean roots interact with compatible Nod factors produced by specific strains of Bradyrhizobium. This ultimately leads to the formation of determined nodules which are found in the upper 0-30 cm of the soil profile. In the nodule, the bacteroids utilize the nitrogenase enzyme complex to convert atmospheric N_2 into NH_4^+ and require microaerophilic conditions (pO_2 approximately 3-30 nM). Microaerophilic conditions are maintained through leghemoglobin.

Drought stress affects this symbiotic relationship through several different ways. First, during periods of drought, the lack of soil moisture limits the mobility of Bradyrhizobium and prevents the formation of infection threads. Second, with insufficient water availability, there is decreased diffusion of oxygen into the nodules, thus resulting in their creation of unfavorably anaerobic microenvironments despite having low moisture in the soil; and third, the drought-prevented plants are not able to provide enough photosynthate to meet their carbon requirements needed to fuel the metabolism of the bacteroids (Desclaux *et al*., 2000) [4]. AMF also help make phosphorus available to the soybean plant through hyphal networks. The hyphal networks extend beyond the rhizosphere depletion zone and help provide phosphorus to the plant. However, under drought stress, AMF hyphal survival is compromised. In order to restore the ability of AMF hyphae to uptake phosphorus, it can take days to weeks after rewetting (Richardson *et al*., 2011) [5].

3.5. Nutrient Acquisition Mechanisms Under Water-Limited Conditions

In times of drought, the mass movement of nutrients through the soil and up to soybean roots decreases because of reduced quantity of moisture available in the soil (Richardson *et al*., 2011) [5]. As soil moisture reduces from field capacity, the rate of diffusion of P decreases dramatically and becomes the primary limiting factor for soybean P nutrition. Soybeans adapt to these limiting factors by developing numerous adaptive strategies, such as longer root hairs that create a greater surface area from which to absorb nutrients, producing more acid phosphatase enzymes to convert organic P into available forms of inorganic P, increasing their production of citrate to help mobilize Fe-bound P, and increasing their expression of high-affinity (HAP) P transporter genes (GmPTs) in the root cortical cells (Vance *et al*., 2003) [20]. The type of soil, pH of the soil, and composition of the microbial community in the rhizosphere will all influence how well these adaptations to drought conditions function.

3.6. Rhizosphere Dynamics Across Different Soybean Growth Stages

The soybean rhizosphere is a dynamic biochemical ecosystem that is not a fixed environment but continually changes throughout the year based on the plant's current developmental stage. The microbial communities associated with the soybean rhizosphere during vegetative (V) development are predominantly structured by root exudate composition and the background environmental conditions (e.g., soil type) (Philippot *et al*., 2013; Bais *et al*., 2006) [16, 15]. With the initiation of nodule formation during the first reproductive (R) stages (i.e., R1–R2), biological nitrogen fixation (BNF) rates increase significantly and release an abundance of nitrogen-rich (N-rich) exudates (including amino acids and ureides) into the rhizosphere, thereby also significantly increasing microbial activity associated with mineralization and immobilization for these compounds (Salvagiotti *et al*., 2008) [3]. Peak pod filling (R4–R6) coincides with the highest nutrient (N and P) demand of the plant and the greatest deposition of carbon (C) from root exudates, leading to peak levels of microbial enzyme activity (Kaiser *et al*., 2011; Sinsabaugh *et al*., 2009) [30, 17]. The sequential and stage-dependent nature of these processes is critical for understanding how drought-related weather (DRW) events at different growth stages affect the availability of nutrients to the plant and the resulting formation of soybean yield.

4. Drought-Rewetting Cycles and Soil Environmental Responses

4.1. Principles and Occurrence of Drought-Rewetting Events in Agroecosystems

Drought-rewetting cycles include dry spells when there is insufficient water in the soil to keep it moist enough for crops (usually when the matric potential is less than -0.5 MPa), followed by a rapid influx of water through rainfall or irrigation, returning soil moisture levels to or above field capacity. In soybean-producing areas across the Americas, sub-Saharan Africa, and Southeast Asia, these cycles can occur several times a year in overtly dry tropical climates with convective precipitation patterns, or several times over the course of a year during drought conditions in temperate regions of North America. Climate projections for RCP 8.5 indicate that there will be a 20-40% increase in the frequency of droughts and a 30-50% increase in the intensity of rainfall for all major soybean producing regions by 2100; therefore, should DRW-induced soil disturbances become more frequent, these will have increased agricultural significance.

4.2. Effects on Soil Moisture Distribution and Hydraulic Properties

(dryland research) The soil's moisture distribution during & after a dryland research event is highly heterogeneous, on both a profile & aggregate scale (Drenovsky *et al*., 2004) [22]. In the case of drought conditions moisture loss will occur, in a rapid manner, by the processes of evapotranspiration from the upper horizon, & more slowly by subsoil drainage. Repeated drying will therefore develop areas of hydrophobic SOM which will create non-wetting soils (Schmidt *et al.*, 2011; Lehmann and Kleber, 2015) [8, 18]. Pursuant to the above-mentioned non-wetting conditions, these non-wetting soils could create spatial variability in the rates of biogeochemical processes. After the rewetting of previously hydrophobic soil, water will likely infiltrate along preferential flow paths provided by desiccation fissures, root channels & earthworm burrows. As a result, large quantities of the soil matrix will be bypassed by water & higher rates of biogeochemical activity will be present along those flow paths (Pett-Ridge and Firestone, 2005) [21]. This preferential flow path rewetting will have very large effects on the spatial distribution of hotspots for N_2O production, P mobilization zones, as well as the patterns associated with the reactivation of microbial communities in soybean fields.

4.3. Oxygen Diffusion and Redox Transitions During Drying and Rewetting Phases

The diffusion rate of O_2 gas is 10,000 times higher than that of O_2 in water, which indicates that moisture in the soil is likely to have the greatest effect on the supply of O_2 to respiring microbes (Schuur *et al.*, 2013) [14]. Soil moisture determines the amount of O_2 that reaches soil surfaces. When moisture levels increase from dry to wet through the process of soil rewetting, the volume of WFPS for a given soil will increase until it exceeds 60-80%. At this point, the rate of diffusion of O_2 into the soil becomes limited by the rate of diffusion of water, leading to the formation of anaerobic regions in the soil as microbial respiration continues, even in unsaturated soils. When WFPS > 85-90%, the rate of denitrification in the soil is limited by the availability of NO_3^- as the main electron acceptor for respiration, leading to an exponential increase in the rate of denitrification during wetting (Butterbach-Bahl *et al.*, 2013) [6]. The rate of O_2 consumption will be limited by the amount of O_2 that is available, while the rate of O_2 supply will be limited by the distance to the surface of the soil, moisture content, and temperature during the process of rewetting. This model can be used to predict the emission of N_2O and P in soybean fields following a specific rainfall or irrigation event.

4.4. Impacts on Microbial Habitats and Substrate Availability

The microbial community structure in soil changes dramatically with cycles of dry/wet (DRW) periods (Schimel *et al.*, 2007; Drenovsky *et al.*, 2004) [25, 22]. Under DRW conditions, the available water film for microbial colonization thins and progressively becomes separated from each other, resulting in a lack of connectivity (between microorganisms and from microorganisms to substrates) within the microbial community and limiting diffusive access to organic substrates for microorganisms. Consequently, the majority of microbial communities will be concentrated within the soil aggregates that contain the most moisture. Many types of bacteria will become dormant (through sporulation or some other process) during drought stress periods by either going into dormancy and/or by accumulating compatible solutes to survive the dry conditions.

Fungal hyphal networks will be proportionately more important than bacterial microorganisms during drought-stress conditions to the breakdown of C because of their superior ability to resist drought by maintaining turgor pressure and using various methods to access moisture across disconnected pore spaces (Schimel *et al.*, 2007) [25]. When soil becomes rewetted, simultaneous releases of accumulated osmolites, microbial necromass, and soil organic matter into solution will generate the characteristic "substrate pulse" that initiates the Birch effect, which consists of a labile (rapidly-micro-mineralized) fraction (e.g., soluble organic carbon [DOC], ammonium [NH_4^+], phosphorus [PO_4^{3-}]), as well as less labile (slowly-micro-mineralized) fraction from disrupted soil aggregates, leading to the biphasic mineralization response of each of these substrates, just prior to the initiation of the Birch effect (Birch, 1958; Blagodatskaya and Kuzyakov, 2013) [9, 27].

4.5. Effects on Nutrient Mobility, Transport, and Retention

The movement of nutrients during dry-wet (DRW) cycles depends on a combination of: 1) the interactions between soil moisture movement, speciation of nutrients, charge characteristics of the soil, and physicochemical properties of the solid phase. Water-soluble nitrate (NO_3^-) is a nutrient that is very mobile in the soil and is easily leached from it during periods of high intensity rewetting, especially in sandy soils and those with a predominance of macropores (Butterbach-Bahl *et al.*, 2013) [6]. Cation exchange sites of ammonium (NH_4^+) retain NH_4^+ as an exchangeable form and thus make it less liable to leach out. However, NH_4^+ will be subject to rapid nitrification after rewetting under aerobic conditions (Prosser and Nicol, 2008) [12]. The retention of phosphate in soils is highly affected by how much Fe^{3+} and Al^{3+} are present. The reductive dissolution of Fe-oxides that occurs as a result of wetting the soil is one of the main ways that phosphate becomes mobilized from iron-rich tropical soils (Richardson *et al.*, 2011; Frossard *et al.*, 2000) [5, 23].

4.6. Long-Term Implications Under Climate Change Scenarios

Repeated cycle accumulation of DRW repeated cycle creation has resulted in long-term or "legacy" effects on the soil's biological and physicochemical properties that exist beyond the immediate biogeochemical effects of the individual DRW events (Lehmann and Kleber, 2015) [18]. Long-term exposure to DRW negatively impacts soil aggregate stability, macropore connectivity, drought-tolerant microbial communities, and labile SOM depletion—all reducing the soil's ability to retain nutrients, sequester C and buffer biology against climate fluctuations (Schmidt *et al.*, 2011; Lehmann and Kleber, 2015) [8, 18]. Therefore, climate adaptation strategies for producing soybeans will need to factor in not only the immediate nutrient management difficulties associated with DRW events but also the cumulative impact on soil health resulting from more frequent climate extremes.

5. Nitrogen Fluxes Under Redox Oscillation Regimes

5.1. Nitrogen Cycling Pathways Affected by Redox Fluctuations

It's a complicated system. The nitrogen cycle in soybean soils in their root zone has a number of mechanisms for transforming nitrogen in multiple pathways. Pathways include BNF (biological nitrogen fixation), mineralization, immobilization, nitrification, denitrification, anammox (anaerobic ammonium oxidation), and DNRA (dissimilatory nitrate reduction to ammonium) (Kuypers *et al.*, 2018) [24]. Each pathway is governed by different ranges of redox potential and microbial populations as well as the amount of substrates available for that pathway.

The presence of redox oscillations throughout the drying and rewetting (DRW) cycles will disrupt these pathways in ways that depend on the context of each environment. Each environment has its own unique set of conditions (e.g., soil texture, temperature, quantity of organic matter, community composition), so it would be difficult to identify a clear generalization that would apply to all cases.

Table 3 shows the major nitrogen (N) and phosphorus (P) transformation pathways that are influenced by redox oscillations, and collectively, they provide a mechanism for understanding how the redox dynamics caused by DRW cycles impact the availability of nutrients in a soybean system.

Table 3: Nitrogen and phosphorus transformation pathways influenced by redox oscillations

Transformation Pathway	Element	Redox Condition	Key Enzyme/Mechanism	Direction Under Rewetting
Nitrification	N	Aerobic (Eh > +350 mV)	Ammonia monooxygenase (AMO); nitrite oxidoreductase	Inhibited post-rewetting; resumes during re-oxidation
Denitrification	N	Anoxic (Eh < +200 mV)	Nitrate reductase; nitrous oxide reductase (nosZ)	Stimulated during rewetting; N_2O and N_2 production surge
Ammonification (N mineralization)	N	Broad range (aerobic to mildly anaerobic)	Urease; proteases; aminidases	Enhanced by Birch effect; flush of NH_4^+ post-rewetting
Biological N fixation (BNF)	N	Microaerophilic (Eh −50 to +150 mV)	Nitrogenase (nifH gene products)	Inhibited during severe drought; restored upon rewetting
N immobilization	N	Aerobic (C:N ratio > 25)	Microbial assimilation; no specific enzyme	Stimulated by DOC flush; competes with plant N uptake
Fe^{3+} reduction → P release	P	Anoxic (Eh < +100 mV)	Dissimilatory iron reducers; ferredoxin-linked reductases	P mobilized into soil solution during rewetting anoxia
Mn^{4+} reduction → P release	P	Mildly reducing (+100 to +200 mV)	Manganese reductases; indirect microbial reduction	P released from MnO_2 surfaces during early anoxia
P mineralization (organic P)	P	Aerobic and slightly anaerobic	Acid/alkaline phosphatase; phytase	Stimulated post-rewetting; converts organic-P to inorganic-P
P immobilization (sorption)	P	Aerobic (Eh > +300 mV)	Adsorption to Fe/Al-oxides; abiotic	Enhanced upon re-oxidation as Fe^{2+} re-oxidizes to $Fe(OH)_3$
Methanogenesis	C	Strictly anaerobic (Eh < −200 mV)	Methyl-CoM reductase (mcrA gene)	Stimulated in prolonged anaerobiosis post-rewetting

5.2. Biological Nitrogen Fixation in Soybean Systems

Soybeans can fix nitrogen through their symbiotic relationship with the bacterium *Rhizobium japonicum* which means that the amount of nitrogen put into a soy crop has not been changed since the introduction of chemical fertilizers. According to Richards and Hamissors, "on average, under optimal conditions, nitrogen fixation by soybeans may be expected to range from 100–200 kg N ha^{-1} season^{-1}" for unfertilized or moderately fertilized fields (Salvagiotti *et al.*, 2008) [3]. However, the nitrogenase enzyme complex that Soybeans use to fix nitrogen is very sensitive to high levels of oxygen (>20 nM) and requires specific conditions for functioning (i.e., microaerophilic) during biochemical reactions in order to perform nitrogen fixation. Soybeans experience four ways that drought stress will affect their biological nitrogen fixation (BNF) ability: (i) if soil moisture levels continue to decrease, the soybeans will not be able to produce infection threads and initiate nodule development; (ii) as soil moisture is depleted, oxygen permeability through nodule cortex will be altered or lost which will have a negative impact on nitrogenase activity because an appropriate microaerophilic environment cannot be maintained; (iii) as soil moisture continues to decrease, the availability of carbohydrates (primarily malate and succinate) will be reduced or diminished which are required by the soybean bacteria for BNF; and (iv) there is a possibility that there could be a negative impact on the ability to fix nitrogen as a result of increased levels of abscisic acid (ABA) that can inhibit the induction of nod genes responsible for initiating symbiotic relationships with rhiobactoria and developing nodules (Desclaux *et al.*, 2000) [4]. After rewetting, BNF rates are reportedly delayed for 7–21 days which indicates that when rewetting occurs, the soybeans will need to rely on soil nitrogen mineralization to satisfy their nitrogen requirements. This lag time is indicative of how important it is to conserve soil organic nitrogen levels in soybeans that experience drought and rewetting cycles.

5.3. Mineralization and Immobilization Processes

Microbial mineralization of organic sources of nitrogen including amino acids and proteins, as well as nucleic acids; into ammonium occurs via a range of extracellular enzymes (urease, protease, and aminidase) that are produced by fungi and bacteria representing diverse taxonomic groups

(Philippot *et al*., 2013) [16]. Following rewetting events, there is a sharp increase in the mineralization of nitrogen, the Birch effect for nitrogen, that can release between 5 and 50 kg of nitrogen per hectare within a few days after rewetting. This represents a significant proportion of the amount of nitrogen consumed by crops throughout the year (Birch, 1958) [9]. It is important to note that mineralized nitrogen is quickly immobilized by metabolic processes occurring in microbial cells—particularly where dissolved organic carbon (DOC) released through rewetting creates high C:N ratios that preferentially support microbial nitrogen assimilation compared to net mineralization. The C:N ratio of available substrates will dictate if net nitrogen mineralization occurring (C:N 2025), or nitrogen immobilization (C:N 2530); as well as the current metabolic state of the microbial community (Sinsabaugh *et al*., 2009) [17]. Because the soil in the soybean rhizosphere typically contains large amounts of rootderived, organic carbon (i.e., C:N ratios of 4080), immobilization of nitrogen that has been released from rewetting will reduce the availability of ammonium to the plant for a short period of time.

5.4. Nitrification and Denitrification Dynamics During Drought-Rewetting Cycles

Nitrification, the aerobic oxidation of NH_4^+ to NO_3^- through NO_2^-, involves NH_4^+-oxidizing bacteria (e.g. Nitrosomonas) and archaea (e.g. Nitrososphaera) co-existing with nitrite-oxidizing bacteria (e.g. Nitrospira) (Prosser and Nicol, 2008) [12]. During drought conditions, nitrification rates are limited by accumulating substrate (NH_4^+) and low enzyme activity due to the effects of water stress on nitrifier populations. Following rewetting, synchronous availability of accumulated NH_4^+, restored enzyme activity and increased concentrations of O_2 (during the initial aerobic post-rewetting phase) can create high rates of nitrification, resulting in large amounts of NH_4^+ being converted to NO_3^-. Subsequent to this pulse of NO_3^- being produced, it becomes substrate for denitrification as anaerobic microsites formed by continual water saturation expand, leading to a sequential nitrification-denitrification cascade occurring in a single rewetting event—the process known as coupled nitrification-denitrification (Kuypers *et al*., 2018) [24].

The rates at which denitrification occurs in rewetted soils are particularly affected by temporal changes in redox potential declines, nitrate (NO3-) availability, and dissolved organic carbon (DOC) supply (Lovley, 1991) [13]. The incomplete conversion of nitrate to dinitrogen gas (N2) and the role of nitrous oxide (N2O) as an intermediary contribute to greenhouse gas emissions that impact climate change and create a loss of agronomically beneficial nitrogen. The N2O:N2 ratio associated with denitrification is influenced by redox potential, pH, and the amount of nitrous oxide reductase available (encoded by the nosZ gene). The N2O:N2 ratio tends to be increased when redox potential is high (the soil is in a more oxidized state) and when pH is low (Butterbach-Bahl *et al*., 2013) [6].

5.5. Nitrous Oxide Production and Greenhouse Gas Implications

With a global warming potential (GWP) of about 265 times CO2 over the next 100 years, nitrous oxide (N2O) is one of the most powerful greenhouse gases. Nitrous oxide is emitted from agricultural soils and particularly from soils that have experienced cycles of drying and rewetting (DRW) (Butterbach-Bahl *et al*., 2013) [6]. In soybean production systems, emissions of N2O occur from both the nitrification pathway, through oxidation of hydroxylamine, and the denitrification pathway; however, peak emissions for both pathways occur in the early rewetting period when both processes are simultaneously stimulated. In addition, biological nitrogen fixation (BNF) in soybean nodules may also result in N2O emissions through inhibition of N2O reductase by O2 in the bacteroid as nodule temperature and moisture levels are suboptimal. Cumulative emissions can be increased from 30–200% by experiencing DRW cycles compared to continuously wet soils, resulting in substantial climate and agronomic trade-offs for producers using DRW management practices.

5.6. Redox-Mediated Controls on Nitrogen Availability and Losses

Through the integration of multiple pathways for the N transformation during a drum-type cycle, a very complex N mass balance has been developed that will determine: 1) the net amount of available N to soybean. There are many losses in the form of N2 and N2O through denitrification, as well as losses from NH3 volatilization due to rewetting of calcareous soils, and NO3- leaching. There are also gains via biological N fixation, through atmospheric N deposition, and via net N mineralization from SOM when the nodules are functioning (Kuypers *et al*., 2018) [24].

The extent of N losses during DRW cycles is a concern for intensively managed soybean systems where N fertilizer is applied to supplement biological N fixation. Therefore, the N losses from fertilizer coincident with the potential for denitrification as a result of DRW can greatly reduce fertilizer-N use efficiency. A number of types of conservation management practices (e.g., cover crops, addition of organic mater, deficit irrigation strategies) could provide valuable opportunities to reduce the N losses resulting from DRW events.

6. Phosphorus Fluxes and Mobilization Mechanisms

6.1. Forms and Fractions of Phosphorus in Agricultural Soils

Various forms of phosphorus can be found naturally occurring in soil at different levels of availability for plants. Inorganic orthophosphate ($H_2PO_4^-/HPO_4^{2-}$), which is present in soil solution, is the only source of phosphorus that plants can use directly; however, phosphorus can be found in other forms (primarily due to interactions with iron and aluminum oxides) since it is also found in very strongly sorbed ionic states (e.g. iron, aluminum, or manganese oxide), very slightly sorbed ionic states (e.g. organic phosphates), and mineral states (e.g. apatite, fluorapatite) (Vance *et al*., 2003; Frossard *et al*., 2000) [20, 23]. Hedley fractionation/ sequential extraction methods show that labile inorganic and microbial biomass P usually account for only 3 to 15% of total soil P, with the other 85 % being present in three different types of sites: moderately to strongly sorbed, organically bound, or mineral occluded. The quantity of total P in soils that is available to plants is greatly influenced by several factors (e.g., soil redox status, pH, contents of iron or aluminum oxides, quantity of organic matter, activity level of microbes) that can all be altered tremendously by repeated cycles of defoliation, root wooling, and winter-summer growth associated with soybean rhizosphere soils (Richardson *et al*., 2011; Nannipieri *et al*., 2003) [5, 19].

6.2. Redox-Sensitive Phosphorus Release and Retention Processes

Soil anoxia causes the reduction of crystalline and amorphous Fe(III) oxyhydroxides (ferrihydrite, goethite, hematite), resulting in the release of phosphorus (P) due to the reduction of Fe(III) to soluble Fe(II) by dissimilatory iron-reducing bacteria (Geobacter, Shewanella spp.) (Lovley, 1991) [13]. The release of phosphorus co-precipitated or sorbed when trivalent iron was originally precipitated will differ significantly across soils because the molar ratio of the total amount of phosphorus and total amount of iron in individual Fe-oxide fractions can vary substantially between soil types; the degree of crystallinity of the phosphorus in Fe-oxide fractions will also vary among different soil types (thus affecting phosphorus solubility). In addition, the presence of competing anions, e.g. silicate and carbonate, will result in variable amounts of phosphorus being released relative to the number of Fe ions reduced across different soil types (Frossard *et al*., 2000) [23]. In tropical soybean-growing soils containing high amounts of Fe oxides (5–20% by weight), the use of this reductive mechanism for phosphorus release following rewet of the soil can rapidly increase phosphorus bioavailability to plants, potentially providing significant amounts of plant-available phosphorus to support critical phases of soybean growth (Richardson *et al*., 2011) [5].

In the opposite manner, the dried out or aerated soil rewinding creates fresh Fe-oxides that have a much larger surface area for P sorption than the pre-reduction condition with the Fe2+ irons being oxidized to form Fe(OH)3. Thus, through oxidation of Fe2+ to Fe(OH)3, P will be scavenged from the soil solution and less will be available than before the soil was reduced through wetting (Frossard *et al*., 2000) [23]. Thus, the net result of one complete DRW event cycle to P availability is determined by the interplay of reductive release of P (during re-wetting) and oxidative sorption of P (during drying) with the net results being very different between soil types and DRW event characteristics.

6.3. Interactions Among Phosphorus, Iron, Manganese, and Organic Matter

The biogeochemical processes associated with P in soils around soybean roots are closely intertwined with the cycling of Fe, Mn, and organic matter as they share mineral surface chemistry and undergo microbially mediated reduction-oxidation processes (Reddy and DeLaune, 2008) [11]. Organic matter serves two main functions: it is an electron donor that supports the microbial reduction of Fe and Mn, which releases P; and it is a ligand that competes for binding sites on Fe-oxides (to reduce P sorption to these surfaces, while maintaining more P in solution, even under aerobic conditions). In addition, humic and fulvic acid molecules form stable complexes with Fe and Al ions, which reduces the potential for the formation of crystalline Fe-oxides that can sorb P, and maintains more P in solution. Organic matter is a primary mechanism in P mobilization in the rhizosphere of soybeans that have high levels of root-derived organic acids and microbial byproducts (Lehmann and Kleber, 2015; Bais *et al*., 2006) [18, 15]. The microbial reduction of Mn (at Eh values of +100 to +200 mV) will also contribute to P mobilization early in the wetting process and release P from sorption to MnO_2 surfaces, prior to the time at which reduction of Fe^{3+} becomes thermodynamically favourable (Lovley, 1991) [13].

6.4. Microbial Phosphorus Solubilization and Mineralization Mechanisms

Microbes solubilize phosphorous through several mechanisms that occur in aerobic and anaerobic environments: (1) by producing organic acids (gluconic, citric, and oxalic) which act to acidify the rhizosphere and to chelate Fe^{3+} and Ca^{2+} ions from inorganic phosphorous minerals, (2) by producing protons and exopolysaccharides, which displace phosphorus from mineral surfaces, and (3) by producing siderophores, which chelate Fe^{3+} and facilitate the dissolution of iron oxides and the concomitant release of phosphorous (Richardson *et al*., 2011) [5]. The most frequently occurring strains of phosphorus-solubilizing bacteria (PSB) found in the rhizosphere of soybean include *Pseudomonas fluorescens*, *Bacillus megaterium*, and *Aspergillus niger*; these are active during the rewetting phase due to their metabolic versatility and rapid substrate utilization rate (Philippot *et al*., 2013) [16]. Phosphorous that is originally in the organic form can be mineralized from organic phosphorous by the action of the enzymes acid phosphatase and phytase secreted by both microorganisms and soybean roots, which convert esterified organic phosphorous (phosphate monoester and diester) to inorganic orthophosphate; this is of considerable importance considering that in some soils up to 80% of the total phosphorous exists as organic phosphorous (Vance *et al*., 2003; Richardson *et al*., 2011) [20, 5].

6.5. Influence of Drought-Rewetting Cycles on Phosphorus Bioavailability

P bioavailability in soybean systems is impacted by the timing and balance of various mechanisms of P release and retention, as detailed in the previous sections. The overall sequence of events in response to moderately severe drought followed by rapid rewetting (conditions anticipated to be more frequent due to climate change) proceeds in the following manner: drought conditions create very concentrated soil solutions containing P, which promotes P sorption to drying mineral surfaces; rewetting events will trigger mineralization from organic sources simultaneously with periods of P release from iron/manganese oxides due to reductive dissolution and pulse release of microbial-derived P from lysed (i.e., dead) cells; the combination of these P pulses dramatically increases the concentration of P in soil solution for short periods of time (i.e. before being re-adsorbed, leached, or taken up by microbes) (Birch, 1958) [9]. The duration of the opportunities to take up P during these pulses is very short (hours to days) and highlights the critical roles of actively growing roots and mycorrhizal infections for the utilization of short-term available P.

6.6. Coupling Between Phosphorus Transformations and Redox Dynamics

In Figure 1, we see a diagram that shows the connection between C turnover with N and P fluxes in the Glycine max rhizosphere during drought and rewetting cycles, via redox oscillation. This diagram highlight soil redox potential's importance as a linking variable between microbial metabolism, mineral surface chemistry, and plant nutrient acquisition throughout the DRW disturbance cycle. The shifting relationship between P transformations and redox dynamics is primarily mediated by the biogeochemical shuttle formed by Fe cycling; Fe^{3+} sorbs and sequesters P during oxidized phases, while Fe^{2+} releases P during reduced phases (thus creating oscillating P availabilities between oxidized and reduced states), which are phase-locked to the DRW cycle (Reddy and DeLaune, 2008) [11]. In addition to this coupling (Fe-P) between redox and P, there are also other processes (microbial mineralization of P, organic-acid mediated solubilization of P, mycorrhizal uptake of P) that occur in the soybean rhizosphere and contribute to a multi-mechanisms P dynamics model.

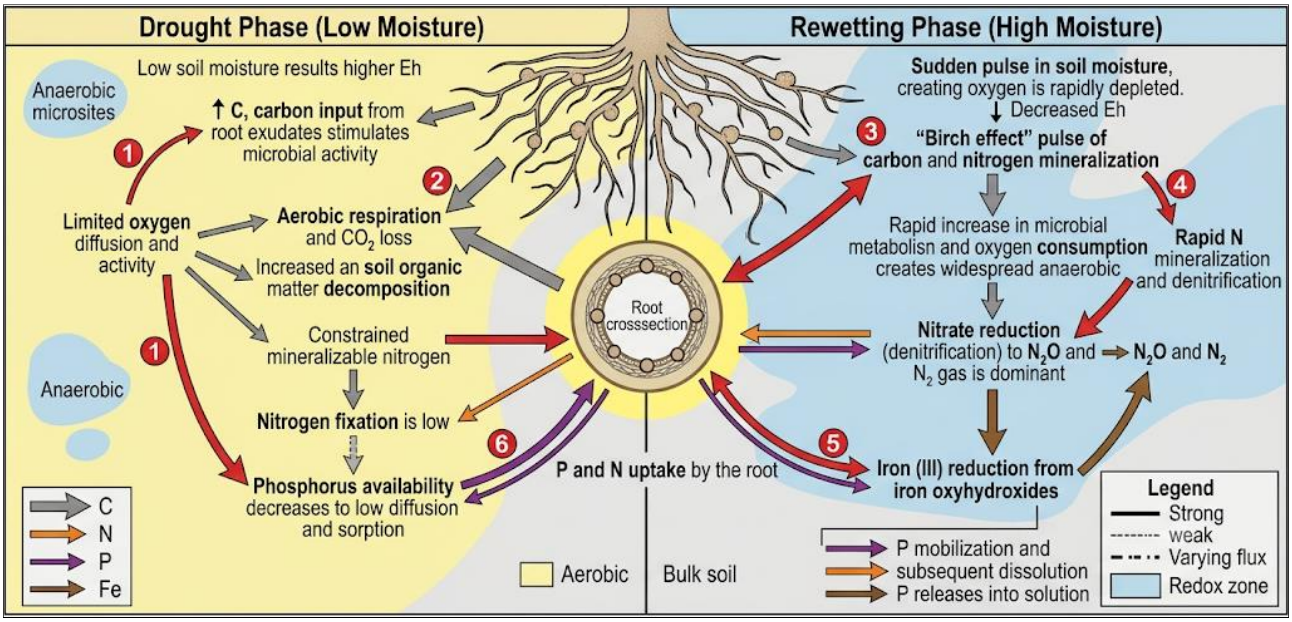

Fig 1: Conceptual diagram illustrating redox oscillation-driven coupling of carbon turnover with nitrogen and phosphorus fluxes in Glycine max rhizosphere under drought-rewetting cycles

7. Carbon Turnover and Soil Organic Matter Dynamics

7.1. Carbon Cycling Processes in Soybean Rhizosphere Systems

Carbon cycling in soybean rhizosphere soils consists of a series of processes ranging from the rapid utilization of root exudates by microorganisms in the rhizosphere to the long-term stabilization of recalcitrant materials in association with minerals (Bais *et al*., 2006) [15]. The rhizosphere of soybean has a high rate of carbon turnover (microbial respiration rates in the rhizosphere are 2-5 times greater than rates in bulk soil), largely as a result of a constant availability of labile carbon originating from roots. Carbon inputs to the rhizosphere mainly come from the following sources: root exudates (e.g., low molecular weight organic acids, sugars, amino acids), mucilages produced by roots (e.g., polysaccharides), sloughing of border cell and root cap cell materials, and the turnover of fine roots providing particulate organic matter sources. The combination of these carbon inputs support diverse food webs of microorganisms in the rhizosphere who utilize carbon at multiple levels of the food web before either releasing it in the form of CO_2 or becoming incorporated into either microbial biomass or microbial necromass fractions, both of which contribute to soil organic matter (Schmidt *et al*., 2011) [8].

7.2. Soil Organic Matter Decomposition and Stabilization Mechanisms

The decomposition of organic matter in soybean fields occurs in stages and can be divided into three categories based on [8]: (i) highly labile (amino acids, simple sugars), (ii) moderately labile (cellulose, hemicellulose), and (iii) various types of recalcitrant materials (lignin, suberin, lipids, aromatic compounds). Different types of organic materials will decompose at different rates, which can range from a few hours to thousands of years. There are three main ways that organic matter is stabilized: (i) chemical structure (biochemical recalcitrance); (ii) physical stabilization (aggregate-occluded organic matter) and (iii) formation of organo-mineral complexes with metals (Fe and Al oxides) and clay minerals or Ca-bridged structures/bases. The cycling of drought and wet conditions disrupts one or more of these stabilization mechanisms: (i) the disruption of soil aggregates results in the release of occluded organic matter, (ii) the reductive dissolution of iron oxides releases organic material from bound iron; (iii) the physical and chemical stresses of soil wetting and drying causes some recalcitrant materials to hydrolyze at an increased rate (Lehmann and Kleber, 2015) [18].

7.3. Rhizosphere Priming Effects Under Fluctuating Moisture Conditions

The rhizosphere priming effect, which can involve the stimulation (positive priming) or repression (negative priming) of the breakdown of stable soil organic matter (SOM) by adding fresh organic materials with roots, is an important but not well-understood process in soybean carbon (C) cycles (Bais *et al.*, 2006) [15]. The addition of root exudates to the soil stimulates the microbial metabolism, where microorganisms use both fresh and stable SOM as an energy and nutrient source. This increase in microbial activity can lead to an increase in the degradation of stable SO by using it for co-metabolism. In agriculture, this is thought to be a means of losing C from agricultural soils. Drought will decrease the effects of priming on the degradation of SOM by decreasing the metabolic activity of microorganisms; however, following a rehydration event, positive priming can briefly occur as the microorganisms are able to use both fresh and stable SOM in parallel. The spatial and temporal magnitudes and directions of priming effects in soybean rhizospheres under different Drought-Rewetting (DRW) regimes continues to be a subject of research, with some studies suggesting that there is a greater amount of C loss (Birch, 1958) [9], while other studies suggest that there is more C stored in soil under moderate frequencies of DRW (Lehmann and Kleber, 2015) [18].

7.4. Dissolved Organic Carbon Dynamics During Drying and Rewetting Events

Soil moisture, redox processes, and nutrient transformations associated with dry-wet cycles are summarized in one diagram (Figure 2) which clearly shows how dynamics in dissolved organic carbon (DOC) are central to the biogeochemical cascade of events that occur when soils are re-wetted. During drought conditions, DOC concentrations in soil pore-water are reduced due to decreased microbial activity, while increasing moisture loss from soils causes DOC to sorb onto mineral surfaces. When soils are re-wetted, there is a large pulse of DOC (microbial necromass, desorbed humic material, and fresh root exudates) that leads to the mineralization of nitrogen (N) and phosphorus (P) through the Birch effect (Birch, 1958) [9]. This DOC pulse serves as a source of carbon (C), N, and P for several processes including heterotrophic respiration, denitrification (providing electron donors for reducing nitrate ions to N_2 gas), and synthesis of new microbial biomass. The size of the pulse is positively correlated with both drought severity and the length of time soils have been desiccated, as extended periods of drought provide for accumulation of microbial biomass that has been killed by desiccation and of partially decomposed organic matter.

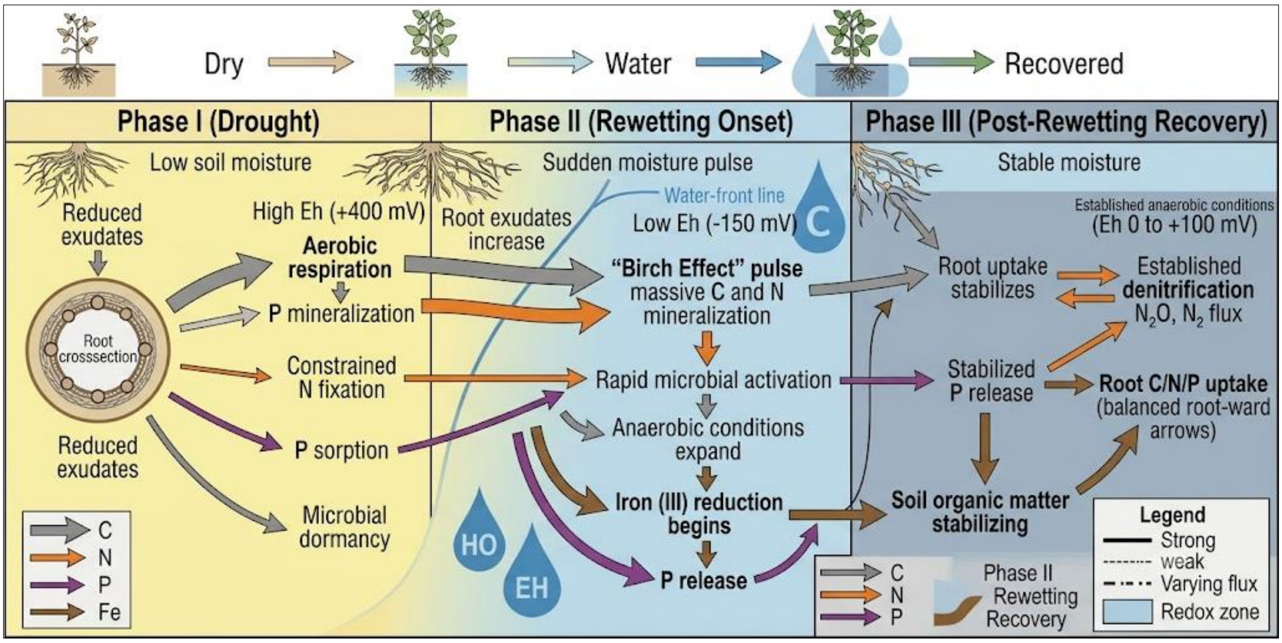

Fig 2: Flowchart showing soil moisture fluctuations, redox transitions, and associated nutrient transformation pathways

7.5. Microbial Carbon-Use Efficiency and Carbon Sequestration Potential

The key factor that determines whether the microbial decomposition of carbon is going to contribute to soil organic matter or the loss of carbon from the ecosystem is through microbial carbon-use efficiency (CUE), which is defined as the ratio of carbon that has been incorporated into microbial biomass versus carbon that has been respired as CO_2. CUE values in agricultural soils typically range from 0.1 to 0.6 with greater CUE being associated with good quality substrates (low C:N ratios), suitable temperature and moisture conditions, and higher levels of fungi compared to bacteria present in a specific microbial community (Schimel *et al*., 2007) [26]. CUE is reduced under drought conditions as carbon is allocated to the development of compatible solutes or for maintenance of respiration in an organism; while the presence of water after a drought will introduce a pulse of available substrate that can lower CUE because the microorganisms will be prioritizing rapid growth over effectively incorporating the carbon into their biomass (Blagodatskaya and Kuzyakov, 2013) [28]. The long-term potential for carbon sequestration within the soybean rhizosphere soils under dry and wet conditions is therefore dependent not only on the quantity of carbon that is applied as an input but also on the ratio of CUE to microbial necromass production and if the necromass-derived soil organic matter is kept from subsequent decomposition.

7.6. Interactions Between Carbon Turnover and Nutrient Fluxes

Microbial stoichiometric relationships and enzyme activity are the main ways that relationships between carbon (C) cycling and nitrogen (N) and phosphorus (P) cycling for soybean rhizosphere systems are mediated (Sinsabaugh *et al*., 2009) [17]. When labile C is more abundant than either of the nutrients N or P (i.e., the substrate has a high C:nutrient ratio), microbes sequester mineral forms of soil N and P to meet cellular demand leading to lower short-term tissue nutrient availability to plants. On the other hand, when substrates rich in the nutrients N and P are mineralized (fertilizing substrates - e.g., microbial necromass or root debris with low C:N:P ratios), both N and P are released as nutrients are mineralized via C mineralization. Regulatory enzyme systems responsible for the cycling of C, N, and P (i.e., processes all related to the biogeochemical cycles) will be co-produced and co-regulated through environmental sensing pathways that connect redox signals, nutrient supply limits, and substrate availability. Together with each of these components, the entire system will be tightly coordinated to produce a biogeochemical response to DRW (drought-rewetting) disturbances.

8. Microbial Community Responses to Redox Oscillations

8.1. Changes in Bacterial and Fungal Diversity Under Drought-Rewetting Conditions

The communities of soil microorganisms that make up the roots of soybeans are among the most diverse ecosystems found on Earth, with 10^4-10^5 varieties of bacteria and hundreds of types of fungi present in just 1 g of rhizosphere soil (Fierer and Jackson, 2006) [10]. The repeated cycles of dry and wet (drought wetting) conditions naturally produce different pressures on both bacterial and fungal populations due to differences in gene expression. While drought conditions favours organisms that are drought tolerant by being able to survive in a dormant state, form spores, and accumulate compatible solutes - rewetting will favour fast growing opportunistic organisms that are able to take advantage of the pore spatiotemporally during times of heavy moisture release. The overall impact of successive DRW cycles on soil microbial biodiversity is highly influenced by context; moderate levels of DRW stress may promote biodiversity through the increased availability of nutrients over time, while extreme or extended periods of drought tend to decrease the available amount of moisture and, therefore, eliminate moisture sensitive species (Philippot *et al*., 2013) [16]. 16S rRNA amplicon type sequencing studies have shown that bacterial community composition changes dramatically from dry to wet during the DRW cycle, with Actinobacteria and Firmicutes generally increasing in relative abundance from one DRW cycle to the next; while Proteobacteria (specifically, Gammaproteobacteria) increase almost immediately when drying to rewet.

8.2. Major Microbial Groups Involved in Carbon, Nitrogen, and Phosphorus Cycling

The major microbial taxa associated with the cycles of C in Glycine max rhizosphere systems are summarized in Table 4. The inclusion of a variety of functional role information for C, N, and P cycling of each taxon allows for integrated representations of each taxon's response to drought-rewetting. The results from this table demonstrate the functional complementary and partial redundancy of different taxonomic groups, which are critical for understanding the ecosystem's resilience to drought-rewetting stress.

Table 4: Major microbial taxa involved in carbon turnover and nutrient cycling in Glycine max rhizosphere

Microbial Group	Phylum/Class	Role in C Cycling	Role in N Cycling	Role in P Cycling	Drought-Rewetting Response
Bradyrhizobium japonicum	Proteobacteria (Alphaproteobacteria)	Minimal direct C cycling	BNF; provides fixed N to soybean	Phosphate solubilization (limited)	Drought-sensitive; nodule function disrupted under severe drought
Pseudomonas spp.	Proteobacteria (Gammaproteobacteria)	DOC utilization; siderophore production	Denitrification; N_2O production	Phosphate solubilization; siderophore-mediated P mobilization	r-strategist; rapid responder to rewetting pulses
Streptomyces spp.	Actinobacteria	Lignocellulose decomposition; humus formation	N mineralization via extracellular proteases	Organic P mineralization; phosphatase production	Drought-tolerant; spore-forming; resumes activity upon rewetting
Acidobacteria (RB41, etc.)	Acidobacteria	Recalcitrant SOM decomposition; slow turnover	Minimal direct N cycling	Limited P cycling	K-strategist; slow response; dominate stable environments
Bacillus spp.	Firmicutes	Endospore formation; resilient C decomposition	N mineralization; some denitrification	Phytase production; inorganic P solubilization	Highly drought-tolerant; rapid activation upon rewetting
Archaea (Nitrososphaera spp.)	Thaumarchaeota	Minimal C cycling	Ammonia oxidation; nitrification	Minimal direct role	Drought-tolerant; important nitrifiers in water-limited conditions
Geobacter spp.	Proteobacteria (Deltaproteobacteria)	Anaerobic C oxidation via Fe^{3+} reduction	Minimal N cycling	P release via Fe^{3+} reductive dissolution	Stimulated under rewetting-induced anoxia
AMF (Glomus, Rhizophagus)	Glomeromycota (Fungi)	Hyphal C allocation; glomalin production	N uptake facilitation	P acquisition via hyphal networks; phosphatase secretion	Hyphae damaged by drought; recover slowly post-rewetting
Trichoderma spp.	Ascomycota (Fungi)	Lignocellulose degradation; enzyme production	N mineralization (secondary)	Organic P solubilization; phosphatase activity	Moderate drought tolerance; resurgence post-rewetting

The Alphaproteobacteria, which includes Bradyrhizobium japonicum - a BNF symbiont that is critical to the soybeans' N nutrition, as well as two free-living nitrogen fixing genera (Azospirillum and Mesorhizobium), are much more important contributors to the soybeans' N nutrition compared to many other groups of Proteobacteria (Gammaproteobacteria AND Actinobacteria). Gammaproteobacteria are well known for their ability to grow under many different conditions. An example of this versatility is demonstrated by Pseudomonas spp., which have the potential to carry out aerobic or anaerobic respiration, solubilize phosphorous, and produce siderophores (all traits that support the ability to thrive under changing redox potential). Actinobacteria (e.g. Streptomyces and Micromonospora) thrive in dry conditions through the production of spores as well as variety of extracellular enzymes related to the decomposition of lignocellulose; thus, they can significantly contribute to SOM turnover when moisture is limited. Acidobacteria are typically slower growing (initially) and exhibit K strategy to growth and reproduction; however, they are present in large numbers in stable rhizosphere systems and have the potential to contribute to the slow degradation of SOM over an extended period of time (i.e. as K strategists) (Fierer and Jackson, 2006) [10].

The genera Bacillus and Paenibacillus form spores; both genera are capable of producing numerous hydrolytic enzymes (such as cellulases, proteases, and phytases) after being rewet. They have been identified as drought-surviving species, and when they are rehydrated, they contribute to the Birch effect of mineralizing soil with moisture by adding hydrolytic enzymes to it. In the absence of oxygen, methane-producing Archaea become metabolically active in poorly-drained soybean fields after they have been rehydrated, competing with both sulfate-reducing bacteria and iron-reducing bacteria for electron donors. While doing so, the archaeans are also generating the greenhouse gas methane (Prosser and Nicol, 2008) [12]. There is a growing body of evidence suggesting that ammonium-oxidizing Archaea (primarily Nitrososphaera viennensis) are important nitrifiers in acidic and water-stressed agricultural soils, especially since the populations of ammonium-oxidizing bacteria are declining in these environments (Prosser and Nicol, 2008) [12].

8.3. Community Succession and Adaptive Mechanisms Under Redox Stress

Microbial communities are known to exhibit unique temporal patterns during dry to wet cycles based upon the sequential availability of both electron acceptors and labile carbon sources. Immediately following the re-wetting of those environments, the dominant groups of organisms are aerobic heterotrophs and r-strategists (e.g., Pseudomonas and Flavobacterium) that are using the pulse of dissolved organic carbon and oxygen. As oxygen becomes depleted from the re-wetted soil and as C and O are being consumed, the relative abundance of denitrifying (e.g., Pseudomonas, Paracoccus) and ferrous (Below, 2010) reducing (e.g., Geobacter) and sulfate-reducing (e.g., Desulfovibrio) microbes increases as the sequential redox transitions (see

Table 1) occur (Lovley, 1991) [13]. The re-assembly of the microbial community after a drought is characterized by the reactivation of dormant endospores (from Firmicutes), germination of drought resistant actinomycete spores, and regrowth of moisture adapted Proteobacteria which results in a community succession pattern that may take weeks to months to return to a pre-drought community structure.

8.4. Functional Redundancy and Ecosystem Resilience

Functional redundancy (i.e., the number of different taxa (species) that can carry out the same biogeochemical process) is frequently believed to influence an ecosystem's ability to recover after being disturbed (Nannipieri *et al*, 2003) [19]. In soybean rhizosphere microbial communities, some processes, e.g., aerobic carbon (C) mineralization, show a high degree of functional redundancy over hundreds of taxa of microorganisms, making those processes more resistant to DRW-induced shifts in microorganism populations and functional capabilities. Other processes, e.g., nosZ-mediated N_2O reduction, biological nitrogen fixation (BNF), and methane oxidation (methanotrophy), are performed by fewer taxa of microorganisms, thus they are more vulnerable to DRW-induced reductions in biodiversity. Therefore, if repeated severe drought events result in large reductions in the population of nosZ-type I denitrifying microorganisms, during rewetting periods there may be particularly large increases in the proportion of N_2O:N_2, with corresponding greenhouse gas effects. Improving the preservation and enhancement of microbial functional redundancy in DRW-impacted soybean systems through appropriate organic matter management practices, reducing tillage, and using microbial inoculants provides a viable pathway to sustain biogeochemical stability.

8.5. Microbial Interaction Networks and Keystone Taxa

The analysis of co-occurrence networks associated with the microbial community associated with the rhizosphere of soybeans has created a complex network of connection or interaction among the various microbial taxa represented. It is believed some of the most highly connected taxa (key or hub taxa) in the network exert an influence that is not in proportion to their abundance or would dominate community structure and functions under drought stress (i.e. DRW) conditions. The keystone taxa found in soybean rhizosphere networks generally include Bradyrhizobium spp. (function as central BNFs) Pseudomonas spp (metabolically versatile and P solubilizers), Streptomyces spp. (produce anti-biotics and degrade SOM), and specific AMF taxa (hyphal networks and P acquisition). The effects of the potential disruption of the keystone taxa due to extreme drought stress, or their protection and enhancement due to management interventions have potential cascading or indirect effects on the functional capacity of all of the taxa within the network beyond those directly impacted (through the disruption of individual taxa). SEM approaches have begun to evaluate indirect network effects, and suggest that almost 40-60% of the variance in the relationship between DRW intensity and N_2O emission rates could be explained by microbial diversity (Butterbach-Bahl *et al*, 2013) [6].

9. Coupling of Carbon Turnover with Nitrogen and Phosphorus Fluxes

9.1. Stoichiometric Relationships Among Carbon, Nitrogen, and Phosphorus Cycling

The ecological stoichiometry framework provides an understanding of how C, N, and P cycling is coupled between the soybean rhizosphere (Sinsabaugh *et al*, 2009) [17]. Microbial homeostasis (the ability of microorganisms to maintain relatively constant cellular C:N:P ratios (~60:7:1 by mass) despite different substrate stoichiometries) acts as a constraint on the rates of nutrient mineralization and immobilization. When C-rich substrates (root exudates, plant residues) with high C:N and C:P ratios are mineralized by microorganisms, the excess C is respired as CO_2 while N and P are immobilized into cellular mass from the soil solution to meet the demands of the microbes cellular. In contrast, when N- or P-rich substrates (microbial necromass or legume residues) with low C:N and C:P ratios are mineralized by microorganisms, then the result is a net release of N and P in conjunction with the mineralization of C. The stoichiometric dynamics create predictable coupling patterns among the fluxes of C, N, and P that change in relation to the redox-induced changes in the quality of the substrates available and to the community composition of the microorganisms present during dry-rewet cycles. Figure 3 presents a mechanistic model depicting microbial-mediated interactions among C cycling, N fluxes, P mobilization, and redox dynamics in the soybean rhizosphere. The model highlights how microbial stoichiometric homeostasis integrates multiple biogeochemical cycles and how DRW-induced redox oscillations propagate through the system to produce the observed patterns of coupled nutrient fluxes.

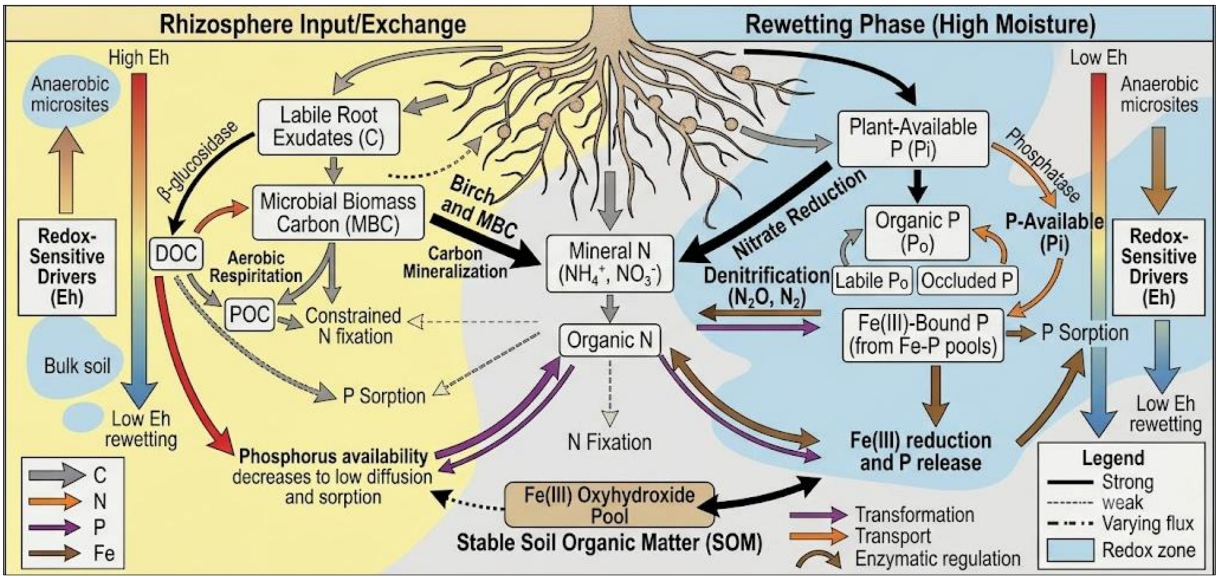

Fig 3: Mechanistic model depicting microbial-mediated interactions among carbon cycling, nitrogen fluxes, phosphorus mobilization, and redox dynamics

9.2. Carbon-Driven Regulation of Nitrogen Transformations

The primary factors determining all the N transformation processes occurring in soybean rhizosphere soils are the C being present in the soil and the NO_3^- present in the soil, since denitrification requires some C to supply electrons for the reduction of NO_3^- to N_2. Additionally, one of the primary factors impacting denitrification rates and the reduction of NO_3^- to either N_2 or N_2O is the amount of C available relative to the amount of NO_3^- in the soil (i.e.C:NO_3^- ratio). The Birch effect DOC pulse that occurs as the soil warms after rewetting typically coincides with the transient peak NO_3^- produced by the nitrification of NH_4^+ that is released by rewetted soils, creating a time period where nitrification and denitrification are coupled, thereby increasing the likelihood that N_2O emissions will occur. In order for BNF to occur in soybean plants, energy from photosynthesis (e.g. malate and succinate) will serve as the C source for BNF through the use of bacteria in a plant's rhizosphere to fix N_2 to form ammonia, so any limiting effect of drought stress on photosynthesis or on respiration losses due to rewetted dry soils will negatively impact the ability for soybean plants to BNF and also reduce the leguminous N advantage associated with soybean.

9.3. Carbon-Mediated Phosphorus Mobilization Mechanisms

The release of citrate, malate, and oxalate by soybean roots is one of the ways that plants can mobilize phosphorus (P) from soil. By chelating with ferric (Fe3+) and aluminum (Al3+) ions, root-derived organic acids remove these ions as barriers to P recovery, as well as displacing P from where it adsorbs to soil (Vance *et al*, 2003) [21]. The amount and diversity of organic acids released from soybean roots are affected by carbon (C): maximum organic acid release occurs when root growth is most active and the plant has enough photosynthate, while if there is no C available due to drought conditions, less overall organic acids are released and there will be less diversity in organic acids released. The generation of organic acids under anaerobic conditions from decayed organic matter (DOC) represents an additional method of C-driven P mobilization when resaturating soil following a wet dry cycle and can thus be viewed as an additional route of P availability mediated by microbes (rather than solely by plants). As such, the regulation of P availability by the allocation of C by plants and the metabolism of C by microbes creates a feedback loop between the dynamics of C, the redox status of the soil, and the availability of P that vary throughout the course of a dry and wet cycle.

9.4. Enzymatic Controls Governing Coupled Biogeochemical Cycles

he enzymes responsible for regulating coupled carbon, nitrogen, and phosphorus cycling in soybean rhizosphere soils are displayed along with their substrates, their connection to the nutrient cycle, their sensitivity to redox conditions and their response to fluctuations in moisture (table 5). The enzyme activities found in rhizosphere soil types represent the combined metabolic activity of the roots, free-living microorganisms, and mycorrhizal fungi, thus providing a functional fingerprint for rates of biogeochemical processes that are much more related to in situ nutrient fluxes than community composition alone (Sinsabaugh *et al*, 2009) [17].

Table 5: Key enzymes regulating coupled carbon, nitrogen, and phosphorus cycling processes

Enzyme	Primary Substrate	Nutrient Cycle	Redox Sensitivity	Drought-Rewetting Response
β-glucosidase	Cellobiose → glucose	C cycling (cellulose degradation)	Inhibited under anoxia; optimal at Eh > +200 mV	Activity depressed during drought; pulse increase post-rewetting (Birch effect)
Cellulase (endoglucanase)	Cellulose polysaccharides	C cycling (plant residue decomposition)	Aerobic; reduced under reducing conditions	Rapid activity surge upon rewetting; key driver of DOC flush
Urease	Urea → $NH_4^+ + CO_2$	N cycling (urea hydrolysis, mineralization)	Broad; active under aerobic and mildly anaerobic conditions	Stimulated post-rewetting; contributes to NH_4^+ flush; substrate accumulation during drought
Nitrate reductase	$NO_3^- \rightarrow NO_2^-$	N cycling (denitrification initiation)	Induced under anoxia (Eh < +200 mV)	Rapidly induced upon rewetting; key enzyme for N_2O production surge
Acid phosphatase	Organic P esters → inorganic P	P cycling (organic P mineralization)	Active under acidic and moderately reducing conditions	Activity pulse post-rewetting; enhanced by root exudation and microbial necromass turnover
Alkaline phosphatase	Organic P esters → inorganic P	P cycling (rhizosphere P mobilization)	Active under aerobic, alkaline conditions	Suppressed during drought; partial recovery upon rewetting
Dehydrogenase	Diverse organic substrates → electrons	Overall microbial metabolic activity indicator	Strictly anaerobic activity at very low Eh	Depressed during drought; surge post-rewetting indicating microbial resurgence
Leucine aminopeptidase	Peptides → amino acids	N cycling (protein mineralization)	Broad range; aerobic optimal	Activity enhanced by proteinaceous substrate accumulation during drought

Beta-glucosidase levels will typically decrease (20-70%) under dry conditions and then return and increase (50-300%) after rewetting. This occurs at the same time as the Birch effect, where dissolved organic carbon (DOC) is flushed from soils after rewetting. Urease activity differs substantially; it accumulates and becomes stabilised during dry conditions as a soil enzyme, then catalyses the rapid mineralisation of accumulated urea-N following rewetting, creating a peak in NH_4^+ following rewetting. A lack of available phosphorous during dry conditions causes phosphatase activity (the enzyme produced jointly at the floor by soya bean roots and by prokaryotic organisms around the roots of soybean plants) to decline, while subsequent rewetting leads to a rapid return of phosphatisation activity from both the prokaryotic organisms around the roots and from the microbial activity in general and from the availability of organic P substrates. Dehydrogenase activity showed the greatest suppression during drought conditions (60-90% reduction) and had an overall dramatic recovery following rewetting, which supports using this enzyme as a biomarker for microbial (prokaryotic) stress from rewetting and the recovery dynamics of all prokaryotes following rewetting.

9.5. Microbial Nutrient Allocation and Metabolic Trade-offs

Microbial communities trade-off their ability to produce (1) growth, (2) maintenance, (3) enzyme production and (4) synthesise compatible solutes when they are under DRW-induced nutrient limitation or dry to wet conditions, which will affect the function of biogeochemical coupling. Fast-growing r-strategists (e.g. Pseudomonas and Bacillus) that rapidly take up resources after being rewetted will have a greater proportion of their carbon allocated to growth and enzyme secretion (i.e. producing and secreting enzymes to mineralise carbon) than they would under nutrient-limited conditions; thus, triggering rapid carbon mineralisation and nutrient release. K-strategists (some Acidobacteria and Actinobacteria) will optimise their carbon use efficiency and the amount they invest in producing enzymes; therefore, they will contribute to a larger proportion of organic matter being stable than for carbon mineralisation (Schimel *et al.*, 2007) [26]. These trade-offs in the life-history strategies of microbial communities in the rhizosphere are a major factor that affect whether a DRW event results in net carbon sequestration or carbon loss and whether nitrogen and phosphorus will be mineralised into plant-available forms or retained in the microbial biomass.

9.6. Feedback Mechanisms Linking Nutrient Fluxes and Carbon Dynamics

The interaction of C, N, and P cycling in soybean rhizosphere systems creates several feedback loops, which interact through biological variation between levels. At the microorganisms level, microbial nutrient limitations enhance the production of extracellular hydrolase enzymes at a C cost, in order to obtain N or P from soil organic matter (Sinsabaugh *et al.*, 2009) [17]. This, in turn, provides a positive feedback loop between C use and demand for nutrients. In addition to this, the presence of N and P limitations at the plant level, due to either microbial immobilization or DRW-driven volatilization of N and/or P, stimulates an increase in C allocation to roots and to mycorrhizal symbionts to further enhance rhizosphere C inputs and associated microbial activity (Bais *et al.*, 2006) [15]; (Philippot *et al.*, 2013) [16]. At the ecosystem level, the coupling of N and P mineralization to C mineralization creates stoichiometric controls on net primary productivity and C sequestration potential that will guide the trajectory of long-term soil fertility under the DRW climate scenario (Luo *et al.*, 2016) [31].

10. Soil Physicochemical Responses and Soybean Productivity

10.1. Soil pH, Aggregate Stability, and Physical Property Changes

Repeated cycles of drought and rewetting have differing impacts on soils and their chemical and physical properties. These soil properties combine to impact overall habitat quality for the soybean root systems and the soil-dwelling microorganisms in the rhizosphere. Soil pH will often increase slightly during dry periods due to proton consumption by oxidative processes being predominant, but will then typically decrease temporarily during rewetting when there's an increase in CO_2 released by microbial activity and root exudates enhance the availability of organic acids to the soil as well as increasing the relative PCO_2 of the soil's atmosphere [11]. Although these pH oscillations are typically of low amplitude (0.3–1.0 pH units), they greatly affect the availability of various nutrients to the soybean plants—e.g., P is optimally available to the soybean roots when the soil has a pH of 6.0–7.0 (Vance *et al*., 2003) [20]; thus, the solubility of Mn and Fe occurs with the increasing concentrations of Mn and Fe in soils as the soil pH decreases during reducing conditions (Lovley, 1991) [13]; conversely, the solubility of Zn dramatically decreases with the pH increases. The stability of the aggregate structure of soils also plays an important role in determining how easily water can infiltrate into the soil, how freely gases can move into and out of the soil, and how the soil organic matter is protected from decomposition (Lehmann and Kleber, 2015) [18]. Repeated drought-rewetting cycles compromise aggregate stability by slaking (the rapid disruption of aggregates by soaking) and by disrupting the fungal hyphae and microbial biofilms that stabilize soil aggregates during prolonged dry periods [18]. Loss of aggregate stability also results in progressively less physical buffering of the soil from future Drought-Rewetting Disturbances, creating a progressive cycle of deterioration in soybean lands subjected to repeated extreme weather events.

10.2. Consequences for Nutrient Availability and Microbial Functioning

Mechanisms by which DRW-induced physicochemical changes affect nutrient availability and the functioning of the microbiome, will primarily affect yield stability in soybeans under global climate change conditions. The decreased stability of soil aggregates reduces the degree of protection provided by aggregate-occluded SOM, leading to accelerated rate of C and N loss, with an immediate increase in soluble nutrients; this acts as a net negative factor for the long-term productivity of the soil even though there may have been an immediate increase in soluble nutrients (Lehmann and Kleber, 2015) [18]. The loss of SOM decreases CEC of the soil, which translates into a decreased ability of the soil to hold cationic nutrients (NH_4^+, K^+, Ca^{2+}, and Mg^{2+}) and therefore, to retain these nutrients against leaching, further decreasing soil fertility. The change in pore size distribution associated with the transition from aggregated to macropore-dominated structures will enhance drainage of water from the rooting zone and will decrease the time that water (and dissolved nutrients) remain in the rooting zone; this decreases the capacity for biological nitrogen fixation (BNF) because BNF requires a continuous supply of moisture to the root nodules and for mycorrhizal P uptake to occur over a longer period of time compared to the interval between single rainfall events.

10.3. Impacts on Soybean Growth and Productivity

Soybean productivity and growth may be affected by DRW-induced biogeochemical disturbance accumulation via N nutrition, P availability, water supply, and root-microbiome relationships. Soil physical compactness from drought (e.g., higher bulk density, more penetration resistance) and root dieback or hypoxia-induced aerenchyma development during extreme rewetting events reduce root establishment as well as cause reduced nodulation function; i.e., drought-based constraints on the number of bradyrhizobia in the soil also inhibit the leghemoglobin function of nodules in the post-rewetting environment (Salvagiotti *et al*., 2008; Bais *et al*., 2006; Philippot *et al*., 2013) [3, 15, 16]. Biomass accumulation has a nonlinear relationship with DRW stress severity (i.e., moderate DRW cycles might be likely to enhance compensatory growth responses, such as increased root branching and higher P transporter expression), whereas either severe or poorly timed DRW events during flowering and pod fill can result in substantial yield losses—20-60% decrease under severe drought during R1-R4 growth stages (Desclaux *et al*., 2000; Hartman *et al*., 2011) [4, 1].

The framework presented in Figure 4 integrates the effects of drought-rewetting induced redox oscillations on nutrient-use efficiency, ecosystem function, and soybean yield. It is a synthesis of the mechanistic pathways discussed throughout this review (redox transitions through biogeochemical events through plant physiological events to yield) that provides a systems level approach to understanding the relationship between DRW and soybean, and therefore provides the basis for optimizing management strategies appropriate for these systems.

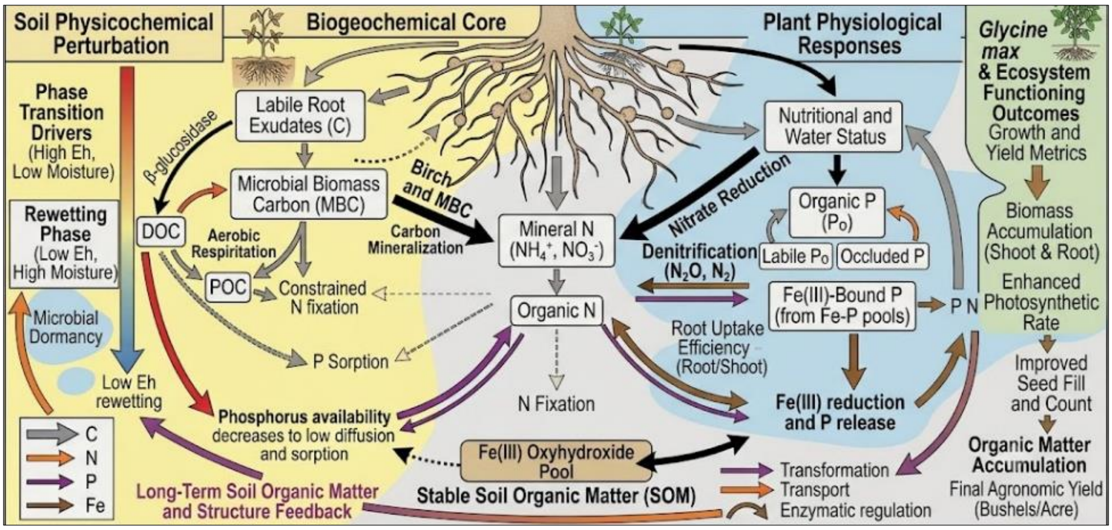

Fig 4: Integrated framework illustrating impacts of drought-rewetting-induced redox oscillations on nutrient-use efficiency, ecosystem functioning, and soybean productivity

10.4. Implications for Sustainable Crop Management and Climate Resilience

Agricultural scientists face a major challenge when converting fundamental knowledge regarding DRW (drought) to practical management strategies that enhance sustainability of soybean production due to the climate-driven increase in frequency of drought (Hartman *et al*., 2011; Seneviratne *et al*., 2012) [1, 7]. Numerous management strategies have been shown to be effective in enhancing nutrient-use efficiency and soil health even as the frequency of DRW continues to increase (Richardson *et al*., 2011; Lehmann and Kleber, 2015) [5, 18]. (i) Proper irrigation scheduling based upon crop water-use monitoring with the primary goal of maintaining WFPS (water-filled pore space) between 50% and 75%, where only aerobic processes (C mineralization, nitrification) occur while minimizing anaerobic losses (N gases) and minimizing N2O emissions due to anaerobic (methane producing) conditions at these WFPS (Butterbach-Bahl *et al*., 2013; Prosser and Nicol, 2008) [6, 12]; (ii) biochar application to increase soil water-holding capacity, CEC (cation exchange capacity), aggregate stability as an effective buffer against the physically and chemically damaging effects of DRW on soils (Lehmann and Kleber, 2015; Schmidt *et al*., 2011) [18, 8]; (iii) co-inoculation of soybeans with drought-tolerant Bradyrhizobium strains, and AMF (arbuscular-mycorrhizal fungi) to support BNF (biological N fixation) and N-acquisition under conditions of DRW-induced abiotic stress (Salvagiotti *et al*., 2008; Philippot *et al*., 2013) [3, 16]; and (iv) organic matter management (cover crops, reduced tillage) to maintain SOM (soil organic matter) levels, functional diversity of soil organisms, and aggregate stability (Nannipieri *et al*., 2003; Schmidt *et al*., 2011) [19, 8].

11. Emerging Technologies and Future Perspectives

11.1. Multi-Omics Approaches for Resolving Biogeochemical Coupling

There is a high level of mechanistic complexity in redox oscillation mediated biogeochemical coupling in the soybean rhizosphere, which requires the application of advanced molecular and analytical technologies to properly capture functional responses at an appropriate spatiotemporal resolution. Routine use of 16S rRNA amplicon sequencing to characterize the bacterial communities will provide taxonomic information; however it will not provide a means of making direct connections between taxonomic data and functional activity (Fierer and Jackson, 2006) [10]. ITS-based fungal profiling can provide a picture of the diversity of fungi, but provides no information about their function. Additionally, metagenomics—complete shotgun DNA sequencing of total community DNA—provides an inventory of functional genes that can be used to link the potential for biogeochemical processes, enabling the identification of denitrification functional genes (e.g., nirS, nirK, nosZ), N_2 fixation functional genes (e.g., nifH), and phosphate solubilization functional genes (pqqC) in rhizosphere communities (Philippot *et al*., 2013; Kuypers *et al*., 2018) [16, 24]. Conversely, metatranscriptomics—sequencing total community RNA—provides direct evidence of active gene expression under specific in situ conditions and will yield the most functionally relevant data on a community level in order to fully understand biogeochemical processes during DRW events (Blagodatskaya and Kuzyakov, 2013) [28].

Soil pore water and root exudates metabolomics may provide a more comprehensive and quantitative understanding of the availability of the C substrates that fuel microbial metabolism during dry-rewetting cycles and the temporal variability in the availability of those substrates than soluble organic carbon alone (Bais *et al*., 2006; Kaiser *et al*., 2011) [15, 30]. The use of isotope tracing with ^{13}C, ^{15}N, ^{18}O, and ^{31}P allows for tracking of specific C, N, and P compounds through biogeochemical pathways, through microbial (isotope probing) or plant (plant uptake studies) groups, allowing for a mechanistic understanding of the biogeochemical process that is not typically possible through pool size measurements (Nannipieri *et al*., 2003) [19]. The incorporation of these multi-omic approaches into coordinated experimental designs to understand dry-rewetting events in soybean rhizosphere systems is a new frontier in research with the ability to transform our understanding of mechanistic biogeochemistry (Luo *et al*., 2016; Blagodatskaya and Kuzyakov, 2013) [31, 28].

11.2. Statistical and Ecological Analytical Approaches

The high-dimensional multi-omics data require complex statistical and ecological analytical methods to find biologically significant patterns. Methods such as PCA and other ordination methods (such as NMDS) are used to create the process of dimensionality reduction to visualize changes in community composition from the DRW cycles. RDA and CCA give an explicit measurement of the proportion of variance in community composition that can be explained through environmental variables (Eh, pH, moisture, DOC), which assists in determining what the key drivers of community structure changes are during DRW events (Drenovsky *et al*., 2004; Pett-Ridge and Firestone, 2005) [22, 21]. SEM is a very powerful analysis tool that can test hypothesized causal paths between redox dynamics, community composition, enzyme activity and nutrient flux outcomes as part of the overall multi-factor integrated framework that includes indirect effects and feedback loops (Butterbach-Bahl *et al*., 2013) [6].Through network analysis of fish rhizosphere communities, Co-occurrence Network Analysis shows microbial interaction network structure and allows for discovery of keystone taxa, interaction hubs and network properties (modularity, connectance) with predictable changes throughout DRW cycles, and the potential to be used as a forecast for ecosystem functional responses to stress (Philippot *et al*., 2013; Fierer and Jackson, 2006) [16, 10]. An increasing number of machine learning techniques (e.g. random forests, neural networks and gradient boosting algorithms) are being applied to high-dimensional community and environmental data to predict rates of biogeochemical processes (e.g. N_2O emissions, P mobilization and C mineralization) (Bouskill *et al*., 2012; Luo *et al*., 2016) [29, 31].

11.3. Methodological Limitations and Uncertainties

Several methodological limitations hinder the understanding of how DRW has changed biogeochemical cycling in soybean systems despite considerable progress made in recent years; most of the mechanistic evidence is derived from laboratory and mesocosm studies, so the various complexities associated with the field (i.e., root architecture, soil heterogeneity, management history, drought variability, etc.) are always simplified (Hinsinger *et al*., 2009; Seneviratne *et al*., 2012) [29, 7]. In situ measurement of soil redox potential using conventional Pt electrodes results in spatially coarse resolution and subject to equilibration time (which could result in missing rapid redox transitions following rewetting) (Pett-Ridge and Firestone, 2005; Reddy and DeLaune, 2008) [21, 11]. Additionally, assays of extracellular enzyme activity using substrate analogs may overestimate activity because there may be differences in environmental conditions (i.e., pH, temperature, substrate concentration) between earth and assay sites (Sinsabaugh *et al*., 2009; Schimel *et al*., 2007) [17, 25]. Attributing specific biogeochemical functions within microbial communities based on 16S rRNA data is limited due to variation in genetic diversity of taxa and horizontal gene transfer of functional genes from one line of evolutionarily distant to another (Fierer and Jackson, 2006; Kuypers *et al*., 2018) [10, 24]. A comprehensive summary of research gaps, methodological limitations, and future research needs related to redox-driven nutrient cycling in soybean systems can be found in Table 6.

Table 6: Research gaps, methodological limitations, and future research priorities in redox-driven nutrient cycling studies

Research Gap / Limitation	Current Methodology	Methodological Challenge	Proposed Future Approach	Priority Level
Mechanistic links between real-time Eh fluctuations and specific N_2O production pathways in soybean rhizosphere	Static incubation experiments; isotope dilution	Inability to capture dynamic redox transitions at fine temporal scales	In situ Eh microsensors combined with $15N_2O$ tracing and metatranscriptomics	High
Fe-P interactions under cyclic drought-rewetting in field soybean systems	Batch extraction; sequential P fractionation	Inadequate temporal resolution; destructive sampling	Synchrotron X-ray fluorescence (XRF) mapping + pore-water sampling at high frequency	High
Contribution of distinct microbial guilds to Birch effect C and N flush	Community-level enzyme assays; PLFA	Low taxonomic resolution; no activity linkage	DNA-SIP (stable isotope probing) + metatranscriptomics during rewetting	High
Role of Archaea in ammonia oxidation under drought-rewetting in soybean fields	qPCR for amoA gene	Gene abundance ≠ activity; lacks functional confirmation	Protein-SIP + metatranscriptomic profiling of archaeal amoA transcripts	Medium
Long-term legacy effects of repeated drought-rewetting cycles on soil C sequestration	Short-term incubation (weeks to months)	Cannot capture multi-year dynamics; lacks ecosystem context	Long-term field mesocosms with real-time soil C monitoring (NDIR sensors)	High
AMF hyphal recovery after drought and role in P acquisition during rewetting	Root colonization assessment; PLFA 16:1ω5	Incomplete hyphal network assessment; 2D visualization only	X-ray computed tomography (CT) of intact soil cores + AMF-specific transcriptomics	Medium
Integration of redox dynamics with plant N and P uptake physiology in soybean	Pot experiments with destructive sampling	Isolated systems; lack field relevance; no real-time plant monitoring	Isotope-labeled nutrient tracing in field conditions with non-destructive plant sensors	High
Predictive modeling of N_2O emissions from soybean fields under climate change	DNDC and CENTURY models	Poor representation of fine-scale rhizosphere redox dynamics	Process-based model integration with machine learning; rhizosphere-explicit sub-models	Medium

11.4. Future Research Directions and Technological Innovations

From this review's synthesis, several priority research directions emerge. The first priority is developing and deploying in situ multi-sensor arrays that can measure many chemicals (examples: soil Eh, pH, O_2 concentration, DOC, NH_4^+, NO_3^-, and Fe^{2+}) at the aggregate level simultaneously. This technology will provide insights into the spatiotemporal patterns of redox-driven nutrient fluxes in soybean rhizospheres (Reddy and DeLaune, 2008; Pett-Ridge and Firestone, 2005) [11, 21]. A second priority is enabling the use of isotope-based techniques (DNA-SIP and protein-SIP) to connect specific metabolic activities to the taxa responsible for those metabolic activities. This linkage will greatly enhance our understanding of the mechanistic nature of community responses during DRW events (Blagodatskaya and Kuzyakov, 2013; Philippot *et al*., 2013) [28, 16]. The third priority is to initiate long-term (greater than five years) field trials using multiple frequency and intensity DRW treatments along with continuous soil monitoring and biogeochemical evaluations. These studies will allow us to determine both legacy effects and trajectory dependency within soybean soil biogeochemistry due to global climate change (Seneviratne *et al*., 2012; Luo *et al*., 2016) [7, 31].

12. Conclusion

This summary of the evidence of the relationship between redox oscillation-driven soil biogeochemistry and the fluxes of nitrogen and phosphorus associated with carbon turnover in the rhizosphere of Glycine max using drought-rewetting cycles has resulted in a conclusion that the Eh oscillations caused by DRW are not simply a physical disruption of soil moisture; they also represent transformative biogeochemical forcing events that are transmitted through the interconnected cycles of C, N, P, Fe and Mn associated with Glycine max rhizosphere, which will all influence nutrient availability, microbial community composition, enzyme catalysis, GHG emissions and crop yield through cascading effects.

Under Dry to Wet (DRW) conditions, there are competing pressures from BNF (Biological Nitrogen Fixation) disruption, denitrification-induced N losses, N_2O emission pulses, and the timing of mineralization and immobilization occurring during re-wetting processes. Phosphorus (P) is made available through a combination of reductive oxide (Fe) dissolution and microbial P solubilization and mycorrhizal P uptake; all of these processes are influenced by DRW cycles, in both stimulating and disrupting ways, this influence varies greatly between soil types and the severity of the DRW cycle. Carbon (C) turnover connects these N and P dynamics because C turnover affects the allocation of microbial nutrients (N and P) based on stoichiometric ratios, the profiles of enzymatic activity and the supply of electron donors (DOC) for denitrification; this connection between the three macronutrient cycles is strong and cannot be understood separately.

The huge changes our world will go through due to climate change and how many new ways people are going to need to control their environments means that we will likely see a huge increase in the variability of soil moisture conditions. Research shows that higher rates of DRW event occurrence and severity over time will lead to a loss of SOM that is more rapid than previously anticipated, leading to reduced aggregate stability, reduced amounts of functional diversity in soil microorganisms, and a reduced ability of soybean production systems to maintain proper levels of N and P nutrition without the use of fertilizers. Additionally, it has also been shown that DRW-induced destabilization of organic matter will substantially undermine the current CO2 sequestration potential of soils and that using effective soil water management strategies to maintain moderate soil moisture levels will be critical in mitigating the most disruptive redox transitions. Four important areas for future research have been identified through this review as follows: (i) mechanistic characterizing of the effects of DRW on aggregate-level redox dynamics using multiple in situ sensors; (ii) multi-omicly investigating microbial community functional responses during and post during DRW events; (iii) conducting long-term field experiments by quantifying the cumulative impacts of DRW on soil fertility and carbon stock in soybean farms; (iv) Building process-based, computer-generated models of redox dynamics, plant growth physiology, and microorganism ecology to support precision nutrient management decision-making. By interconnecting molecular microbiology with soil physics, plant physiology, and computer-modeling techniques, we will ultimately create what may be one of the most advanced ecological systems for growing soybeans and maintaining our territory in order to feed the world with a sustainable food source.

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