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Review Article

Biochar-Mediated Microbial Mechanisms in Saline–Alkali Soils: Insights from Functional Genes and Multi-Omics Evidence

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ABSTRACT: Saline–alkali stress is a growing constraint on agricultural productivity and the ecological recovery of degraded lands worldwide. Biochar has attracted sustained interest as a soil amendment because it can improve soil structure and ionic conditions while reshaping microbial habitats that underpin key ecosystem processes. However, mechanistic understanding remains fragmented, particularly regarding how biochar-driven changes in the soil microenvironment translate into predictable shifts in microbial communities, functional genes, and the recovery of carbon, nitrogen, and phosphorus cycling. This review synthesizes current knowledge on the multidimensional mechanisms by which biochar alleviates saline–alkali stress, with a particular focus on microbial community succession and functional reprogramming. Drawing on multi-omics evidence reported in the literature, we integrate insights from metagenomic, transcriptomic, and metabolomic studies to identify convergent molecular signatures associated with biochar amendment and to relate these signals to changes in enzyme activities, nutrient availability, greenhouse-gas dynamics, and crop performance across saline–alkali settings. By connecting biochar properties and soil physicochemical amelioration with microbe-mediated biogeochemical outcomes, we propose an integrated mechanistic framework that helps explain when biochar promotes a transition from stress-adapted, low-function microbial states to more resilient and metabolically efficient communities. Finally, we highlight priorities for future research, including long-term field validation across contrasting saline–alkali soil types, harmonized multi-omics workflows and metadata standards that enable robust cross-study synthesis, and experimental strategies that move beyond correlation to causal testing of key taxa, pathways, and gene networks to improve predictability and guide biochar design and application in heterogeneous landscapes.

Keywords: Biochar, Microbiome, Saline-alkali soil.

1. INTRODUCTION

Soil salinization has become one of the major problems restricting global food security and land use efficiency, posing a severe challenge to the ecological environment and socioeconomic system. Saline-alkali soils are typically characterized by poor permeability, low nutrient availability, and reduced microbial activity [1]. These stress factors collectively weaken soil ecosystem functioning and significantly reduce crop productivity [2]. It is estimated that saline-alkali soils in China cover approximately 340,000 km2, among which around 124,000 km2 have agricultural potential after appropriate reclamation [3]. Various remediation approaches have been explored, including freshwater leaching, application of chemical amendments (e.g., flue gas desulfurization gypsum, addition of organic fertilizers (e.g., manure, compost), and cultivation of salt-tolerant plants [4]. However, most of these methods primarily target short term physicochemical amelioration and provide limited support for long-term ecological restoration.

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Although freshwater leaching can effectively remove soluble salts, it is constrained by water scarcity in arid and semi-arid regions. Moreover, this nonselective process often results in the loss of key nutrients such as K^+ and dissolved organic carbon [5] and can disturb fragile native microbial communities. In chemical amelioration, desulfurized gypsum rapidly reduces soil pH and exchangeable sodium percentage (ESP) through Ca^{2+}-Na^+ exchange reactions. However, such physicochemical processes neglect biological recovery, offering neither carbon sources nor stable habitats for microbial communities [3]. Application of organic fertilizers can replenish carbon, but they tend to be unstable due to rapid decomposition and may even contribute to secondary salinization because of high salt content. Phytoremediation based on salt-tolerant plants is ecologically sustainable but proceeds extremely slowly. For instance, a study has found that in order to significantly enhance the carbon cycling function of microorganisms in saline-alkali paddy fields, a long-term succession process of over 15 years is required [6]. Therefore, conventional approaches remain limited in terms of efficiency, sustainability, and ecological restoration capacity, highlighting the need for novel strategies that integrate physical, chemical, and biological synergistic effects.

In recent years, biochar, a highly stable carbon based amendment, has gained increasing attention for its broad potential in soil improvement [7]. Biochar exerts multiple physical, chemical, and biological effects on soils, which can significantly enhance soil health and fertility. For instance, it can regulate ionic composition via ion exchange and provide a persistent carbon source. Additionally, due to its high stability, porous structure, and nutrient retention capacity, the biochar can markedly improve the physicochemical conditions and microbial habitats in saline-alkali soils [8, 9]. Most current studies have focused on the analysis of physical and chemical indicators, but there is still a lack of systematic explanation for the biological mechanisms that drive the ecological function recovery. Since soil ecological processes such as nutrient cycling and organic matter decomposition are fundamentally driven by microbial metabolism, understanding the biological drivers is essential. Huang *et al*. [10] compared sterilized and non-sterilized soils and found that biochar induced remediation was largely mediated by microbial activity. This suggested that biochar's physicochemical properties primarily acted as catalytic triggers, while microbial responses were the key drivers of ecosystem recovery. Building upon this understanding, long term field studies by Xu *et al*. in 2025 further demonstrated that effective soil restoration was closely associated with the succession of carbon-metabolism functional genes. These findings highlight the biological essence of biochar's ameliorative effects and underscore the need for multi-omics approaches to decode the microbial regulatory mechanisms involved.

Therefore, this review aims to elucidate the intrinsic mechanisms through which biochar improves saline-alkali soils from physical, chemical, and biological perspectives. By integrating the latest multi-omics data, particularly metagenomic insights, it explores how biochar regulates key functional genes involved in the cycling of carbon (C), nitrogen (N), and phosphorus (P). Moreover, the review also highlights existing knowledge gaps and proposes future research directions to further enhance our understanding of the role of biochar in soil remediation.

2. THE MICROBIAL REGULATORY MECHANISM MEDIATED BY BIOCHAR

Biochar affects microbial communities and functional genes in saline-alkali soils through various interconnected mechanisms, including physical, chemical, electron transfer, and nutrient supply processes, as shown in the Figure **1** [11]. By improving the soil's physicochemical properties, biochar helps reshape microbial community structures and supports the restoration of ecosystem functions. These processes include improving soil structure, enhancing ion exchange, increasing water retention, and creating a more stable environment for microbial growth. All of these contribute to soil recovery and promote better plant growth.

2.1. Physical Regulation by Porous Structure and Microbial Shelter of Biochar

Saline-alkali soils are typically characterized by low porosity, compact structure, and poor aeration and permeability [12], which limit both plant growth and microbial activity. The addition of biochar to these soils helps improve their physicochemical structure, creating a more stable environment for microorganisms. The porous network and large surface area of biochar help enhance water retention and aeration, reduce the upward movement of salts, and support the formation and stabilization of soil aggregates, thereby increasing resistance to erosion [13]. The pores within biochar provide refuge spaces for microorganisms, mitigating physiological stress under high osmotic pressure and reducing the risk of protozoan predation [14]. These physical benefits allow microorganisms to survive and

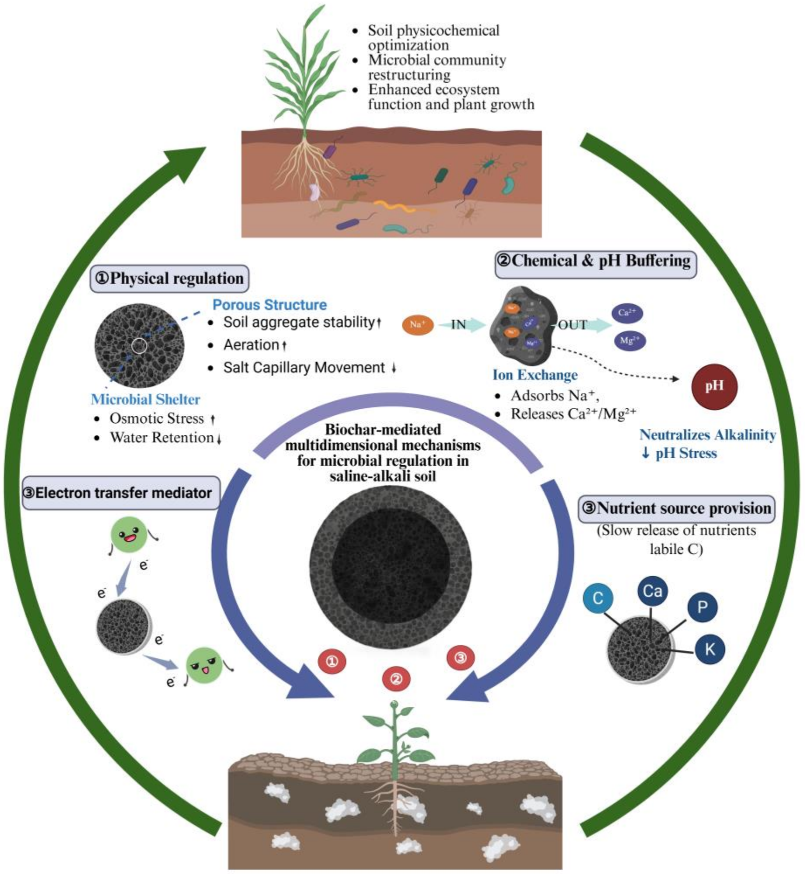

Figure 1: Diagram of the multidimensional mechanism of microbial regulation in saline-alkali land mediated by biochar.

thrive, contributing to important soil processes. Additionally, biochar's rough surfaces and functional groups help specific microbes, such as plant growth promoting rhizobacteria, to attach and establish themselves [15]. These microbes improve soil health by cycling nutrients, fixing nitrogen, and producing substances that support plant growth. Through these actions, biochar encourages the formation of stable microbial zones in the soil, where dominant microbes improve soil properties through acid production, nitrogen fixation, and the release of extracellular polymers. This creates a positive cycle, where biochar's physical protection supports microbial activity, and microbial activity, in turn, improves soil conditions.

2.2. Chemical Regulation by Ion Exchange and Stress Alleviation of Biochar

The surface chemical properties of biochar are crucial for improving the ion exchange capacity and regulating soil pH. In saline-alkali soils, high pH (>9.0) and elevated Na^+ concentrations in saline-alkali soils are toxic to microorganisms, constraining their physiological activity and community stability. Biochar surfaces are rich in negatively charged functional groups such as carboxyl and phenolic hydroxyl moieties [14], which significantly enhance their cation exchange capacity (CEC). These properties enable effective adsorption and replacement of Na^+ from the soil solution, thereby mitigating ion toxicity and osmotic stress [9]. In addition, biochar, particularly that derived from crop residues, contains abundant alkaline ash and surface basic functional groups that impart strong pH buffering capacity, neutralizing localized alkalinity and bringing soil pH toward neutrality [16]. This buffering process substantially improved the chemical environment for microbial metabolism, supported the recovery of key biogeochemical processes such as N cycling and carbon degradation. Overall, through the combined effects of ion exchange and pH buffering, biochar effectively alleviates salinity stress and stabilizes microbial community structure and function.

2.3. The Nutritional and Electronic Regulation Effects of Energy and Nutrient Redistribution

Saline-alkali soils are generally characterized by nutrient deficiencies and energy limitations that impede microbial metabolism. The application of biochar significantly improves the microbial metabolic environment by enhancing nutrient supply and facilitating electron transfer. Its slow release of essential elements, such as potassium, calcium, magnesium, and P, provides a sustained nutrient source for microbial growth [17], while labile organic fractions serve as readily available carbon substrates to stimulate indigenous microbial activity. Moreover, the aromatic and graphitized structure of biochar endows it with electrochemical activity, allowing it to function as an electron transfer mediator [18]. Within localized anaerobic microsites in saline soils, biochar can facilitate extracellular electron transfer, thereby promoting electron flow and metabolic efficiency among denitrifying and iron-reducing bacteria, thereby accelerating N and C cycling processes [10]. In addition to promoting microbial activity, biochar can help balance nutrient and energy fluxes within the soil, creating a more favorable environment for diverse microbial populations [19]. Consequently, through the dual mechanisms of nutrient provision and electron mediation, biochar drives the restoration and enhancement of microbial metabolism by redistributing energy and nutrient fluxes.

Overall, biochar transforms microbial habitats in saline-alkali soils from low activity to high functioning states through the synergistic mechanisms of physical protection, chemical buffering, and nutrient and electron provision. This multidimensional regulation not only enhances soil physicochemical properties and structural stability but also promotes microbial community optimization and functional gene succession, thereby establishing a biological foundation for the restoration and stabilization of saline-alkali ecosystems.

3. MICROBIAL RESPONSES TO BIOCHAR

Biochar achieves this transformation of saline-alkali soil through various mechanisms such as physical protection, chemical buffering, and the provision of nutrients or electrons. It converts the soil from a state of high salinity, high acidity, and nutrient deficiency into an environment suitable for microbial survival. The improved environment features better aeration, appropriate pH levels, and sufficient nutrients. These changes create a more favorable environment for microbial growth and activity, which in turn enhances soil fertility and microbial diversity. As the principal drivers of soil ecosystem functioning, microorganisms exhibit directed responses in community composition, physiology, and functional potential to these environmental improvements. By promoting microbial growth, biochar helps optimize microbial community dynamics and functional gene expression, supporting crucial processes like nutrient cycling and organic matter degradation [20]. Such microbiological shifts tightly couple with biochar induced physicochemical amelioration and together constitute the core biological impetus for ecosystem functional recovery in saline-alkali soils.

3.1. Biochar Promotes the Directional Succession of Microbial Communities

After the application of biochar, the diversity and structural composition of the microbial community have undergone significant changes, which in turn affect the soil nutrient cycling and plant growth process [21]. In the original saline-alkali environment, high salt content and high pH inhibited the growth of most microorganisms, leading to low community diversity and a tendency towards single functions [22]. The porous structure of biochar provides attachment sites and physical shelter for microorganisms. The surface alkaline functional groups and ash components can buffer excessively high pH. Meanwhile, the microporous effect can fix or reduce the bioinert availability of salt ions such as Na^+ and Cl^-. In addition, biochar, as a relatively stable carbon source and an increase in soil cation exchange capacity (CEC), helps improve carbon and nitrogen supply and the C/N ratio [23], thereby reducing salt stress as a whole and optimizing the microenvironment. After the application of biochar, the α diversity of bacteria (such as Shannon and Chao1 indices) has significantly increased, and the β diversity also shows a clear trend of directional succession. For instance, Qiu *et al.* [24] discovered that adding biochar to the saline-alkali soil in northwest China significantly altered soil pH, CEC and salt ions, and led to an increase in microbial diversity and community reorganization. Wang *et al.* [25] found that under salt stress conditions, the changes in the composition of soil bacterial communities are closely related to the application of biochar. Biochar can drive changes in bacterial communities by increasing soil organic carbon, available nutrients, etc. In conclusion, biochar can reshape microbial communities and promote their directional succession.

3.2. Functional Responses via Nutrient Regulation and Functional-Gene Remodeling

Biochar serves as a critical biogeochemical regulator in the rehabilitation of saline-alkali soils, fundamentally orchestrating the cycles of C, N, and P. Its effects are seen not only in the restructuring of microbial communities but also in the regulation of functional genes related to these cycles (Figure **2**). Biochar functions by engineering a hospitable micro-habitat, providing

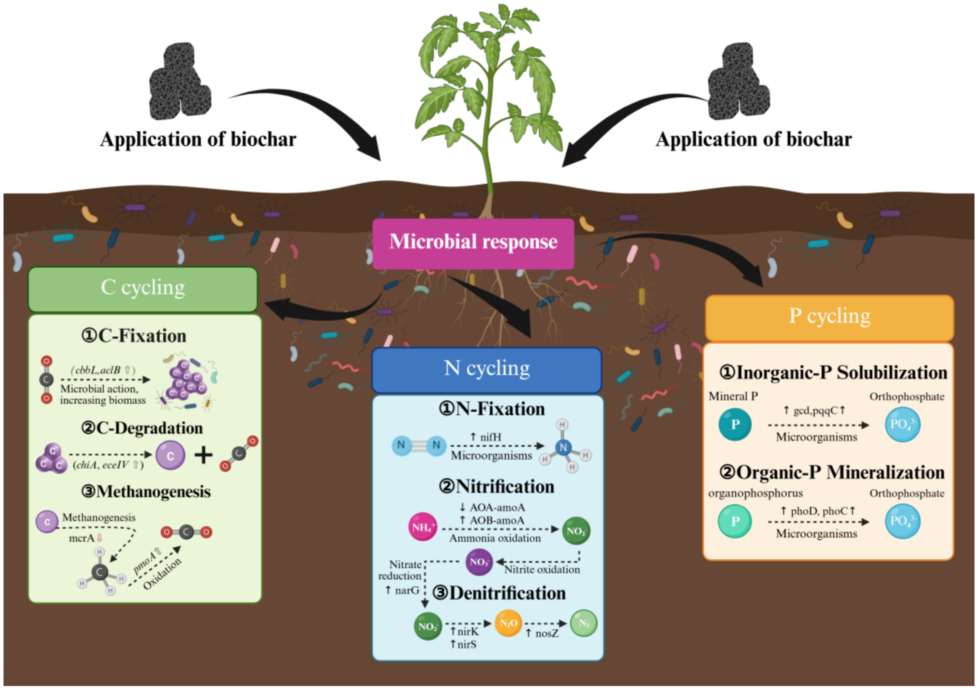

Figure 2: Biochar reshapes functional gene networks for C, N, and P cycling.

essential pore space as physical refugia and neutralizing soil alkalinity. This environmental amelioration relieves the physiological stress on the microbiome. As a result, the microbial community undergoes a bioenergetic shift: resources are reallocated from the synthesis of stress-response molecules to the expression of metabolic genes. This transition facilitates the re-assembly of robust functional gene networks, which removes the previous limitations on nutrient mineralization and fixation [26].

3.2.1. N Cycling

Soil N cycling, comprising fixation, nitrification, and denitrification, constitutes the metabolic backbone of global biogeochemical cycles [27, 28]. These processes are jointly driven by functional microorganisms (such as ammonia-oxidizing bacteria (AOB), ammonia-oxidizing archaea (AOA), denitrifying bacteria, etc.) and their related genes (such as *nifH, amoA, norB, nosZ*, etc.) [29]. In the context of remediation, biochar intervention markedly reshapes the structure of N-cycling communities by ameliorating the hostile physicochemical environment of saline-alkali soils [30]. Long-term application evidence in saline-alkali lands indicates that biochar, particularly when used in conjunction with nitrogen fertilizer, reshapes the ecological niches of AOA, AOB, and complete ammonia-oxidizing bacteria by regulating soil pH and ammonium nitrogen availability. The AOA can tolerate higher pH and lower nutrient requirements, while AOB prefers neutral to slightly alkaline conditions [31, 32]. In saline-alkali lands, the cation exchange properties of biochar enhance nutrient availability, gradually neutralizing the previously high-salt and high-alkali environment, which is more conducive to the proliferation of AOB populations [33]. Ding *et al.* [34] found that the abundance of the AOA amoA gene decreased, while the abundance of the AOB amoA gene increased, resulting in a significant decrease in the AOA/AOB ratio, indicating a functional succession of ammonia oxidation function from AOA-dominated to AOB-dominated. In addition, biochar also has a significant impact on the nitrogen fixation and denitrification processes. The stable carbon source and porous protective structure of biochar are conducive to the enrichment of nitrogen-fixing microorganisms (such as Proteobacteria and Acidobacteria), increasing the soil nitrogen fixation capacity and significantly enhancing the abundance of *nifH* genes, thereby promoting the biological nitrogen fixation function [35]. During denitrification, biochar modulates redox status and optimizes key enzyme expression, significantly lowering the *norB*/nosZ ratio, indicative of more complete denitrification, enhanced N_2O reduction, and reduced greenhouse-gas emissions [36, 37]. Collectively, biochar remodels N-cycling guilds and key gene networks by alleviating salinity-alkalinity stress, improving nutrient supply, and optimizing redox conditions, ultimately achieving coordinated optimization of N-cycle structure and function.

3.2.2. P Cycling

P is among the most limiting nutrients in saline–alkali soils. Under high pH conditions, P readily precipitates with calcium as insoluble phosphates, markedly reducing its bioavailability [38]. Effective P cycling depends on microbially mediated solubilization and mineralization, both of which are strengthened and stabilized when biochar optimizes the physicochemical environment and activates functional microbes. During inorganic-P solubilization, biochar's porous matrix provides stable colonization sites for P-solubilizing microorganisms, while its strong pH-buffering capacity improves the metabolic milieu [39, 40], thereby promoting expression of P solubilization genes. For example, Fan *et al.* [41] research found that the application of biochar in desert saline-alkali soil not only increased the relative abundance of phosphorus-solubilizing bacteria *Sphingomonas*, but also increased the *gcd* gene encoding gluconate dehydrogenase and the *pqqC* gene encoding pyrrolidine quinoline quinone synthesis protein, accelerating the dissolution and transformation of stationary phosphorus. Ye *et al.* [42] discovered that biochar significantly enriched phosphorus-solubilizing bacteria such as Proteobacteria by regulating the abundance of phosphorus cycling functional genes like *gcd, phoA,* and *phaD,*pppthereby altering the phosphorus conversion pathway. For organic P mineralization, microorganisms in alkaline conditions rely mainly on the alkaline phosphatase system. *phoD* and *phoC* govern organic P mineralization and inorganic P transport, respectively. Deinert *et al.* [23] discovered that biochar could increase the copy number of the phosphorus-activating gene *phoC/phoD* by 2-3 times, and up-regulate the expression of the phosphorus transporter gene *pstS* by 7.82%, directly driving organic phosphorus mineralization. Howell *et al.* [36] pointed out that when biochar was co-applied with organic fertilizer, the expression level of alkaline phosphatase-related genes could be further upregulated, revealing the remodeling effect of biochar on the community structure carrying phoD genes. Hou *et al*. [43] observed a pronounced increase in *Rhodopseudomonas* abundance and its contribution within *phoD* communities, with positive correlations to labile/available P and negative correlations to insoluble minerals (hydroxyapatite). Altogether, by coupling physical shelter, chemical buffering, and microbial metabolic activation, biochar shifts P cycling from chemically dominated to biologically driven processes, substantially improving P bioavailability and cycling efficiency in saline-alkali soils [41, 43].

3.2.3. C Cycling

Soil C cycling is one of the most fundamental biogeochemical processes in ecosystems, encompassing key pathways such as carbon fixation, decomposition, and methane metabolism. The dynamic equilibrium of this cycle is driven by soil microbial communities, in which distinct functional guilds, such as autotrophic carbon fixers, methanogens, and methane-oxidizing bacteria, collectively regulate carbon fluxes through their respective functional genes (e.g., *cbbL, mcrA,* and *pmoA*) [44]. By improving the physicochemical environment and microbial niches of saline–alkali soils, biochar systematically restructures the C cycle from fixation to emission. In native saline soils, high ESP and low nutrient availability severely suppress autotrophic carbon fixation [45]. Biochar alleviates such stress, enhances nutrient accessibility, and diversifies microbial habitats, thereby creating favorable ecological niches for autotrophic carbon fixers. Wang *et al.* [12]. found that biochar significantly enriched key carbon-fixing groups such as *Acidobacteria* and promoted the expression of key genes (*cbbL, aclB*) in the Calvin-Benson-Bashan cycle and the anti-TCA cycle, thereby enhancing the carbon fixation potential. Simultaneously, biochar influences methane metabolism through redox regulation. Its porous architecture improves soil aeration and oxygen diffusion, altering the ecological balance between methanogenic archaea and methane-oxidizing bacteria. Experimental results indicated that biochar markedly suppresses the activity of strictly anaerobic methanogens while enriching *pmoA* bearing methanotrophs [46, 47], promoting CH_4 to CO_2 conversion and reducing greenhouse-gas emissions, representing a microbial niche shift from reduced to oxidized carbon states. During the carbon degradation process, the decomposition of organic matter by microorganisms relies on a variety of carbohydrate-active enzymes and their encoding genes, which jointly mediate the stepwise degradation of cellulose, hemicellulose and other complex organic carbons [48]. Saline-alkali stress can reshape the potential for carbon degradation. Metagenomic studies have shown that increased salinization reduces the diversity of functional genes related to the carbon cycle and has a negative feedback effect on the carbon cycle [49]. Based on this, biochar further influences the composition and functional potential of carbon degradation-related functional groups by regulating micro-environmental conditions such as soil salinity conductivity, pH, and substrate supply [50]. Studies have shown that biochar can inhibit the mineralization process of exogenous organic matter and reduce the abundance of functional bacteria related to organic carbon decomposition, thereby weakening the intensity of carbon mineralization and warming potential [51]. However, some studies have observed that biochar can reduce cumulative CO_2 emissions, but at high application rates or under specific conditions [52], it may also promote CO_2 accumulation and release, indicating that the regulatory effect of biochar on the carbon degradation process is jointly constrained by its own physical and chemical properties and soil salinity characteristics. Overall, biochar exerts synergistic effects across key stages of the C cycle, via enhancing carbon fixation, promoting methane oxidation, and regulating carbon degradation. By shifting the balance between carbon inputs and outputs, biochar has been reported to reduce net carbon losses and, under certain conditions, enhance carbon retention in saline–alkali soils, with implications for carbon-sink restoration in degraded saline landscapes.

4. OMICS EVIDENCE FROM GENETIC POTENTIAL TO SOIL FUNCTION

4.1. Microbial Enzyme Coupling and Metabolic Enhancement Mediated by Functional Genes

Evidence indicates that the role of biochar in saline-alkali soil remediation extends beyond physicochemical improvement and is closely associated with enhanced microbial metabolic activity and reconstructed enzymatic functionality. Soil microorganisms govern material cycling and energy conversion, with their population structures and genetic functions determining both the efficiency and direction of nutrient turnover [53]. Biochar can lower salt concentrations, balance ions, and increase carbon availability, thereby shifting microbial communities from stress adapted to metabolically active states, which in turn boosts key enzymatic activities [50, 54]. An increasing body of multi-omics research has revealed that biochar's ecological effects are not confined to physicochemical amelioration. Its application significantly remodels microbial functional-gene expression profiles, which exhibit strong positive correlations with enzymatic activities. Bai *et al*. [30] reported consistent trends between the upregulation of functional genes and enhanced enzyme activities, suggesting a molecular foundation for biochar-induced metabolic reinforcement. Similarly, Ding *et al*. [20] demonstrated that biochar modulates the expression of N cycling genes (*amoA, norB, nosZ*), promoting nitrogen transformation and enzymatic activation. Long term field experiments corroborated these findings, showing that a single biochar application maintained elevated enzyme activity and nutrient availability over several years while substantially increasing rice yields [55]. Collectively, biochar enhances microbial functional gene expression and metabolic capacity by alleviating ionic stress, optimizing microenvironments, and improving substrate supply. This establishes a coordinated coupling between the molecular and functional levels. Gene upregulation provides the driving force for metabolic reactions, while enhanced enzymatic activity reflects strengthened system functionality. The synergy of these processes facilitates sustained restoration of nutrient cycling and energy flow in saline-alkali soils.

4.2. Microbial Regulation of Greenhouse Gases and Environmental Optimization Driven by Functional Genes

The mechanism by which biochar regulates the emissions of greenhouse gases (CO_2, CH_4, N_2O) in saline-alkali soil is not a single cycle effect, but is closely associated with the systemic reorganization of microbial functional genes [56, 57]. Existing studies have found that after the application of biochar, functional genes related to carbon fixation, methane oxidation and N_2O reduction (such as *cbbL, pmoA, nosZ*) are mostly upregulated, and the emissions of CO_2, CH_4, and N_2O decrease (Table **1**). It indicates that biochar from different raw materials affects the net emission flux in saline-alkali land by reshaping the key functional gene combinations of the carbon cycle, methane cycle and nitrogen cycle. From the perspective of biogeochemistry, biochar reshapes the microbial environment through physical means (optimizing pore structure and aeration) and chemical means (regulating pH value, redox potential, and soil enzyme activity), thereby enhancing the synergistic regulation between the carbon and nitrogen cycles and forming a comprehensive emission reduction effect [58]. Specifically, at the nitrogen cycle level, the application of biochar is conducive to the enrichment of *nosZ*-type denitrifying bacteria communities and may enhance the electron transfer efficiency in the N_2O terminal reduction stage, enabling N_2O to be more fully reduced to N_2, thereby reducing emissions [57, 59]. In addition, in calcareous or saline-alkali habitats, the application of biochar can significantly alter the distribution of soil enzyme activities. By reducing metabolic entropy and enhancing the physical protection of carbon mineralization, it effectively reduces CO_2 emissions and increases the soil's carbon sequestration potential [60]. Therefore, the regulation of key genes involved in carbon and nitrogen cycling mediated by biochar may be one of the main ways to achieve synergistic reduction of greenhouse gas emissions.

Table 1: Effects of biochar on soil microbial functional genes and greenhouse gas.

Biochar Raw Material	Involvement Process	Changes in Functional Genes	Greenhouse Gases	References
Rice straw	methane oxidation	*mcrA*↓; *pmoA*↑	CH_4↓;N_2O↓	Han *et al*. [61]
Rice straw	denitrification; nitrification	*nosZ*↑; *nirS,nirK*↓; *AOB-amoA*↓	N_2O↓	Dong *et al*. [62]
Wheat straw	carbon mineralization; denitrification	*cbbL*↑; *nosZ*↑	N_2O↓;CO_2↓	Yang *et al*. [63]
Rice straw	denitrification	*nosZ Clade I*↑; *nosZ/(nirS+nirK)*↑	N_2O↓	Wei *et al*. [64]
Yellow pine	denitrification	*nirK*↓; *nosZ*↑	N_2O↓	Bhattarai *et al*. [65]
Corn stalk	denitrification; nitrification	*nirK,nirS*↓; *nosZ*↑; *AOB-amoA*↑	N_2O↓;NH_3↓	Gao *et al.* [37]
Fruit tree prunings	carbon mineralization	*cbbL*↑	CO_2↓	Sakin *et al*. [60]

4.3. The Influence of Functional Genes on the Recovery of Plant Productivity

Under saline-alkali stress, biochar reconfigures the molecular foundation of plant resistance by modulating rhizosphere microenvironments and reinforcing interactions with functional microbial consortia. By optimizing rhizosphere aeration, water retention, and cation exchange capacity (CEC), biochar mitigates soil compaction and ionic toxicity. These physicochemical improvements provide a stable habitat while acting as a porous carrier and carbon source for plant growth-promoting rhizobacteria [66]. This rhizosphere enrichment induces specific genetic responses. Notably, the upregulation of hormone modulating genes, such as *acdS* and *ipdC*, promotes nitrogen assimilation and regulates endogenous ethylene levels. These molecular adjustments mitigate stress-induced growth inhibition and stimulate robust root development [67]. Field studies of saline-alkali field systems have also confirmed the role of biochar mediation in microbiota-plant regulation [68]. Empirical evidence validates that biochar driven ecological optimization is mechanistically linked to crop performance. Specifically, Zhang *et al*. [69] reported that biochar enriched metabolically versatile taxa, notably Proteobacteria and Bacteroidota. This taxonomic restructuring expands the soil's genomic capacity for nutrient mobilization, a potential that directly correlates with increased grain yield. Similarly, Che *et al.* [70] observed that biochar mitigation of osmotic stress sustained grain filling dynamics, a phenotypic stability underpinned by the transcriptional regulation of sink strength related genes. Furthermore, Wang *et al*. [71] demonstrated that biochar optimized cytosolic ionic homeostasis and root sugar metabolism. These physiological adjustments, driven by the modulated expression of ion transporters and metabolic enzymes, provide the bioenergetic basis for vigorous root hair development and nitrogen capture. Furthermore, the co-application of biochar and functional microorganisms establishes a positive feedback cycle involving functional microbial nodes, nutrient flux, and plant vigor, which significantly boosts productivity [72]. Recent studies on cotton have confirmed that the combined application of biochar and arbush mycorrhizal fungi (AMF) shows a significant synergistic effect, enhancing the adaptability of crops to saline-alkali environments by optimizing soil quality and plant physiological defense mechanisms [73]. This synergistic repair strategy exhibits a stronger molecular response with the participation of trace elements. For instance, the synergistic effect of molybdenum and AMF can significantly up-regulate the expression of key functional genes such as nifH, thereby enhancing the biological nitrogen fixation efficiency and physiological resistance of crops under salt stress [74]. Genomic analysis reveals that this is driven by the upregulation of genes governing root development, salt stress response, and antioxidant defense, which are tightly coupled to rhizosphere metabolic activity [70]. Consequently, biochar activates a synergistic “soil-microbe-plant” system, driving saline-alkali ecosystems from a stress-dominated state toward functional restoration. Overall, biochar is increasingly recognized as more than a physicochemical soil amendment, because it can modify soil microhabitats and resource availability in ways that are associated with changes in microbe–plant interactions and gene expression patterns. By strengthening the linkage between microbial metabolism and plant response gene expression, biochar reshapes rhizosphere ecological networks, enhancing crop yield, stress tolerance, and nutrient use efficiency.

5. FUTURE PERSPECTIVES

The role of biochar in the remediation of saline-alkali soils has evolved significantly over time. Initially, research mainly focused on the physicochemical improvement of soils. However, recent studies have expanded the understanding of biochar's benefits, and recognized its critical role in regulating microbial metabolism. Biochar helps to improve soil structure, alleviate salinity stress, and activate key microbial functional genes, creating a combined process of structural optimization, community reshaping, and functional restoration. This process facilitates the gradual recovery of soil ecosystem functions, enhances soil health, and boosts agricultural productivity.

Despite rapid progress, several uncertainties still limit the predictability and scalability of biochar-based restoration in saline–alkali landscapes. A primary gap is that "salinity" is often treated as a single stressor, whereas the ionic composition can differ markedly among sites and may lead to contrasting responses. The relative dominance of Na^+ versus mixed salts, the presence of bicarbonate and carbonate alkalinity, and the balance between Cl^- and SO_4^{2-} can alter osmotic stress, sodicity-driven dispersion, nutrient antagonism, and microbial selection pressures. Future studies therefore need to move beyond bulk electrical conductivity and explicitly resolve ion-specific effects, linking biochar properties and application rates to shifts in ion activities, exchangeable sodium percentage, and plant–microbe performance across compositionally distinct saline–alkali soils. Comparative experiments that keep total salinity constant while varying ionic regimes would help disentangle whether observed benefits are driven mainly by reduced Na^+ toxicity, improved aggregation, altered alkalinity, or changes in nutrient availability.

A second gap concerns the scope and durability of pH buffering. Biochar is frequently reported to moderate soil pH, yet the buffering direction, magnitude, and persistence are expected to depend on carbonate alkalinity, native buffering capacity, biochar ash content, and the kinetics of surface functional group evolution. It remains unclear when biochar can meaningfully counteract alkaline conditions in carbonate-rich soils, or conversely, when high-ash biochars may exacerbate alkalinity. Future work should quantify pH buffering as a time-dependent process and report it alongside dissolved inorganic carbon dynamics, carbonate equilibria, and cation exchange processes, thereby clarifying the boundary conditions under which pH moderation is realistic and agronomically relevant.

Long-term performance is another underdeveloped area. Biochar undergoes aging, oxidation, pore clogging, and interactions with minerals and salts that can change surface chemistry, sorption capacity, and habitat structure. In saline–alkali soils, repeated wetting–drying cycles and salt crystallization may further accelerate physical fragmentation or the collapse of pore networks, potentially weakening the very mechanisms invoked to explain microbial regulation and nutrient cycling. Long-duration field trials and mesocosm studies that track biochar physicochemical evolution, soil structure, and microbial functions over multiple seasons are essential to determine whether initial gains persist, plateau, or reverse. Particular attention should be paid to thresholds where salinity fluctuations and sodicity-driven dispersion undermine aggregate stability and microbial habitat quality.

Finally, carbon stability remains insufficiently constrained. Reported changes in CO_2 fluxes and organic carbon pools are often interpreted as enhanced sequestration, yet distinguishing true stabilization from redistribution among pools, priming effects, or transient suppression of decomposition requires more rigorous partitioning. Future research should explicitly separate biochar-derived carbon from native soil organic carbon and quantify the persistence of each fraction under saline–alkali conditions. Coupling isotopic tracing with fractionation approaches and high-resolution molecular characterization would help identify whether biochar promotes formation of mineral-associated organic matter, protects carbon within aggregates, or merely shifts microbial metabolism without long-term storage gains.

Within this context, multi-omics should be used not as an endpoint but as a hypothesis-generating and hypothesis-testing toolkit tied to process measurements. Integrative designs that combine time-resolved metagenomics or metatranscriptomics with targeted metabolomics, extracellular enzyme assays, and greenhouse-gas flux monitoring can identify pathways that consistently respond to biochar across ionic regimes and pH domains. However, most current omics-based inferences remain correlative. Stronger causal evidence will require manipulative validation, such as isotope probing to link taxa to carbon and nitrogen transformations, controlled inoculation or depletion experiments to test the functional necessity of candidate groups, and biochar property engineering to verify whether specific surface chemistries or pore architectures directly drive the observed molecular and biogeochemical responses. Establishing standardized omics workflows and metadata reporting, particularly for ionic composition, carbonate alkalinity, and biochar aging state, will further enable cross-study synthesis and improve the transferability of mechanistic conclusions.

6. CONCLUSION

This review synthesizes current evidence that biochar can alleviate saline-alkali stress by coupling physicochemical amelioration with biological regulation. By bringing together soil process measurements and published multi-omics observations, we highlight microbial regulation as a key explanatory layer that links biochar properties to changes in carbon, nitrogen, and phosphorus cycling. Improvements in soil aggregation, water status, and ion exchange are frequently accompanied by shifts in microbial community composition and functional gene or transcript profiles that align with enhanced biogeochemical cycling and improved plant performance.

At the same time, the magnitude and persistence of these responses vary with soil ionic composition and alkalinity, baseline organic matter, climate and management, and the feedstock, production conditions, and aging state of biochar. Much of the mechanistic evidence, including multi-omics signatures, remains association-based, highlighting the need for causal validation and long-term assessment. Future progress will depend on cross-site field studies that report ion-resolved chemistry and track biochar transformation over time, together with process-resolved measurements and integrative multi-omics designs that link taxa and pathways to quantified carbon, nitrogen, and phosphorus fluxes and greenhouse gas outcomes. Such evidence will strengthen the predictability of biochar performance and support evidence-based deployment strategies for restoring heterogeneous saline-alkali landscapes.

CONFLICTS OF INTEREST

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

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