Research Advances on the Effects of Rhizosphere Aeration on Rice Root Morphology and Physiology: Postprint

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Abstract

Rhizosphere oxygen is an important environmental factor influencing the rhizosphere environment of paddy fields and the physiological metabolism of rice root systems. Existing reviews on rice rhizosphere oxygen have predominantly approached the topic from the perspective of hypoxic or anoxic stress. With technological advancements and improvements in productivity, an increasing number of researchers have implemented active rhizosphere oxygenation measures in rice cultivation, yielding certain research findings. Rhizosphere oxygenation significantly influences the morphology and structure of hydroponic rice roots, resulting in thin and elongated root characteristics; under oxygenated conditions, an intrinsic consistency exists among rice root morphology, structure, and functional requirements. Rhizosphere oxygenation exhibits a significant promoting effect on root activity across different rice growth stages, with enhancement ranging from 10% to 150% and showing substantial inter-cultivar variation. From the perspectives of rice root morphology, physiological activity, and root nitrogen transformation, oxygenation treatment facilitates nitrogen uptake by rice roots; however, its impact on nitrogen accumulation depends on the method and extent of oxygenation, as excessive oxygenation inhibits nitrogen utilization in rice plants, thereby limiting biomass increase, which subsequently suppresses nitrogen uptake and accumulation. The response pattern of rice to rhizosphere oxygenation does not simply represent the reverse of its response to hypoxic or anoxic stress; the dramatic reduction in rice biomass and yield under saturated oxygen treatment underscores the complexity of rice responses to oxygen-rich conditions. Investigating the effects of rhizosphere oxygenation on rice seedlings before the three-leaf stage, refining research on the influence of rhizosphere oxygenation on rice nitrogen metabolism, quantifying field oxygen requirements for rice, and exploring simple and practical seedling-stage oxygenation measures may prove significant for further advancing the theory and improving the technology of rice seedling cultivation.

Full Text

Preamble

Advances in the Effects of Rhizosphere Oxygen Enhancement on Rice Root Morphology and Physiology

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Abstract: Rhizosphere oxygen is a critical environmental factor influencing the paddy field environment and physiological metabolism of rice roots. Existing reviews on rice rhizosphere oxygen have predominantly focused on hypoxia or anoxia stress. However, with technological advances and increased productivity, an increasing number of researchers have implemented active rhizosphere oxygen enhancement measures in rice cultivation, yielding substantial research findings. Rhizosphere oxygen enhancement significantly affects root morphology and structure in hydroponic rice, resulting in slender and elongated root characteristics. There exists an intrinsic consistency among root morphology, structure, and functional requirements under oxygen-enhanced conditions. Rhizosphere oxygen enhancement markedly promotes root vigor across all growth stages, with increases ranging from 10% to 150% and substantial inter-varietal differences. From the perspectives of root morphology, physiological activity, and nitrogen transformation in the root zone, oxygen enhancement treatments facilitate nitrogen uptake by rice roots. However, the effects on nitrogen accumulation depend on the method and degree of oxygen enhancement; excessive oxygen inhibits nitrogen utilization, thereby limiting biomass increase and consequently suppressing nitrogen absorption and accumulation. The response patterns of rice to oxygen enhancement are not simply the reverse of those to hypoxia or anoxia stress, as demonstrated by the dramatic reduction in biomass and yield under oxygen-saturation treatments, highlighting the complexity of rice responses to oxygen-enriched environments. Exploring the effects of rhizosphere oxygen enhancement on rice seedlings before the three-leaf stage, improving research on nitrogen metabolism impacts, quantifying field oxygen requirements, and developing simple, practical seedling-stage oxygenation measures may significantly contribute to advancing rice seedling cultivation theory and technology.

Keywords: Rice; Oxygen enhancement; Root morphology; Root activity; Nitrogen metabolism

Adequate oxygen supply is essential for maintaining a healthy rhizosphere environment and ensuring normal physiological metabolism in rice. Rhizosphere oxygen deficiency triggers a series of physicochemical changes that severely affect rice growth and development [1-5]. As a wetland plant, rice possesses well-developed aerenchyma that transports oxygen to the roots, satisfying root oxygen demand and improving the rhizosphere environment to adapt to waterlogged conditions. Nevertheless, oxygen deficiency remains a key limiting factor for rice growth [6-8]. Since rice roots directly interact with soil oxygen, clarifying the response characteristics of root morphology and physiology to rhizosphere oxygen enhancement, elucidating the regulatory mechanisms, and exploring effective oxygenation measures are crucial for improving rice cultivation theory and practice.

Rice Root Oxygen Demand

Oxygen participates in oxidative phosphorylation in rice root cells, which serves as the primary energy source for root growth and development. In the 1980s, Japanese scholar Shigenori Morita pioneered quantitative research on rice oxygen requirements, establishing oxygen demand rates under hydroponic conditions: 0.27~0.79 mg · g^{1} · h^{1} at tillering stage, 0.95~0.88 mg · g^{1} · h^{1} at jointing stage, 0.98~1.07 mg · g^{1} · h^{1} at booting stage, 0.93 mg · g^{1} · h^{1} at heading stage, 0.85 mg · g^{1} · h^{1} at full heading stage, and 0.68 mg · g^{1} · h^{1} at maturity stage [9]. Under hypoxic or anoxic conditions, rice root respiration relies primarily on anaerobic respiration, generating only 3%~5% of the energy produced under adequate oxygen supply [10-12], while producing intermediate metabolites detrimental to root growth and metabolism, which significantly constrains both root and shoot development.

Oxygen maintains a healthy rhizosphere environment by preventing damage from reductive substances. Soil oxygen deficiency reduces redox potential, leading to accumulation of toxic water-soluble reductive substances such as NO , Mn^{2} , Fe^{2} , and H S in the rice rhizosphere [1,13-16]. Oxygen present around roots, whether originally in soil or released through root radial oxygen loss (ROL), can oxidize these reductive substances, preventing their phytotoxic effects.

Oxygen in rice roots originates from two sources: oxygen absorbed by shoots (leaves and sheaths from air and photosynthesis) and oxygen absorbed directly from soil. A substantial portion of shoot-absorbed oxygen is transported to roots through aerenchyma in leaf sheaths and stems, with oxygen transport across the stem-root junction reaching approximately 0.8 mg · cm^{2} · h^{1} during mid-growth stages [2]. Bai Kezhi et al. [17] measured that downward oxygen transport in rice seedlings accounts for about 50% (range: 30%~70%) of total shoot oxygen uptake. Japanese scholar Takashi Sasaki also reported that 40%~48% of oxygen absorbed by rice "mat roots" is transported to submerged roots [18]. However, oxygen supplied solely through shoot aerenchyma is insufficient for root growth requirements. Yin Weiyi et al. [19] demonstrated that under wet cultivation, internal oxygen transport in rice seedlings meets only 30%~60% of root respiratory demand, with oxygen deficiency being particularly severe during the booting to heading stage when both oxygen and water demands peak [20].

Root oxygen uptake from soil occurs via short-distance intercellular diffusion, which requires direct contact between root epidermal cells and oxygen. Appropriate soil oxygen concentration is essential for normal root physiological processes. Root elongation ceases when surface oxygen concentration falls below 0.001 mol · m^{3} [21]. Paddy soil oxygen concentration must be maintained at 3%~5% of atmospheric levels to ensure normal root oxygen absorption [2,22]. However, paddy soils are complex systems coexisting with solid, liquid, and gas phases, containing both gaseous and dissolved oxygen. Existing oxygen concentration metrics cannot directly reflect soil oxygen status, so soil redox potential (Eh) is commonly used. Soil Eh typically ranges from -450 to 720 mV [23]. Ding Changpu [6] systematically summarized that Eh values for major Chinese paddy soils range from -70 to 670 mV based on in situ measurements. Xu Xiangyu et al. [24] reported that cold waterlogged paddy soils have Eh values between -48.5 and -198.0 mV. According to DeLaune et al. [25], soil Eh below +350 mV indicates oxygen depletion, confirming that cold waterlogged soils suffer severe oxygen deficiency. Paddy soil Eh values of 300~400 mV (oxidative conditions) are favorable for healthy root growth [2].

Effects of Rhizosphere Oxygen Enhancement on Rice Root Morphology and Structure

Rhizosphere oxygen content influences root number, length, diameter, surface area, volume, and weight. Oxygen enhancement significantly increases paddy soil redox potential and nitrate nitrogen content, which affect maximum root length and induce lateral root formation [26]. Multiple aerated hydroponic experiments have yielded consistent results regarding oxygen enhancement effects on rice root morphology. Wang Danying et al. [27] found that oxygen enhancement significantly increased root length and maximum root length across seven varieties while reducing root number, diameter, and unit-length root weight, though root dry weight per plant increased. Deng Dan et al. [28] reported that oxygen enhancement significantly increased maximum root length while reducing root diameter and adventitious root number, with total root length and root dry weight also decreasing significantly. Zhao Feng et al. [29] demonstrated that regardless of ammonium-nitrate or ammonium-only nutrient solutions, oxygen enhancement (8.5~9.0 mg · L^{1}) produced significantly greater root number, maximum root length, root volume, and root dry mass compared to controls (0.5~2.0 mg · L^{1}), while root diameter was smaller than controls (in ammonium-nitrate solution) or showed no significant difference (in ammonium-only solution). Similar results appear in studies by Colmer [30], Kotula et al. [31], Zhao Feng et al. [32], Xu Chunmei et al. [33-34], and Zhao Xia et al. [35]. Collectively, oxygen enhancement increases hydroponic rice root length while decreasing root diameter, producing slender and elongated root morphology. This response aligns with adaptations of many plants (e.g., sawgrass, cattail [36], and *Salvinia natans* [26]) that shorten root length to cope with hypoxia or anoxia. In soil cultivation studies, water-controlled (oxygen-enhanced) treatments increased root number [37-38], whereas aerated hydroponic studies decreased root number [28,32-33,39], likely due to differences in oxygenation methods and degrees, as excessively high rhizosphere oxygen concentrations are unfavorable for increasing root number [35].

Total root length, surface area, volume, and weight are mathematically derived from individual root length, diameter, and number. The effects of oxygen enhancement on these comprehensive indices represent the integrated mathematical outcome of its effects on individual parameters, controlled by the degree of oxygenation. Morphological changes in rice roots under oxygen enhancement share similarities with those under drought stress. Hao Shurong et al. [40] found that water stress during tillering reduced root diameter, producing slender roots, with consistent morphological changes reported in other drought stress studies [41-45].

Anatomically, rice roots consist of three parts: stele, cortex, and epidermis. Functionally, rice transports oxygen obtained through photosynthesis and gas exchange in shoots to roots via aerenchyma, maintaining appropriate root oxygen concentration and metabolic rates. Simultaneously, roots release oxygen through radial oxygen loss (ROL), creating a small "oxidized zone" that protects against reductive substance damage.

Root porosity reflects aerenchyma development; greater porosity indicates more developed aerenchyma and stronger oxygen transport capacity. Hypoxia or anoxia induces increased root porosity to enhance oxygen transport [30,39], while simultaneously forming a dense barrier at the root base between the epidermis and cortex to reduce ROL and increase oxygen diffusion to root tips, prioritizing normal rhizosphere conditions in the apical region [25,30,39,46-51]. This highly lignified structure also prevents invasion by reductive substances produced under flooded conditions. Numerous studies confirm that aerenchyma and ROL barriers are key to flood tolerance in aquatic plant roots [47,52-56]. Conversely, under oxygen-enhanced conditions, rice root porosity significantly decreases [30,39,57-58], and ROL barriers either do not form or are weakly induced [30,39,55], representing adaptive anatomical regulation. ROL barriers are generally formed through suberization and lignification of the exodermis and/or sclerenchyma [51,56,58]. Feng Ke et al. [59] compared root anatomical structures under different water conditions, finding that under flooded conditions, exodermal sclerenchyma cells were tightly arranged with heavily thickened walls, whereas under upland conditions, this barrier function weakened with less cell wall thickening. Oxygen enhancement can be analogized to upland conditions, where roots in oxygen-rich environments have reduced requirements for preventing oxygen leakage and reductive substance invasion, eliminating the need for ROL barriers. Consequently, exodermal cell wall thickening is less pronounced than under hypoxic or anoxic (flooded) conditions, manifesting morphologically as reduced root diameter and slender roots. This explains the similarity between root morphological changes under oxygen enhancement and drought stress. In summary, an intrinsic consistency exists among root morphology, structure, and functional requirements under oxygen-enhanced conditions.

3. Effects of Rhizosphere Oxygen Enhancement on Rice Root Vigor

Root vigor reflects the intensity of root metabolic activity and serves as an important indicator for assessing root physiological functions. In most rice rhizosphere oxygen studies, root vigor represents a key parameter. Current indicators include -naphthylamine oxidation capacity, triphenyltetrazolium chloride (TTC) reduction capacity, and root bleeding intensity. -naphthylamine oxidation or TTC reduction intensity represents root vigor per unit root weight, with accuracy depending on sampling representativeness. In contrast, root bleeding intensity provides higher reproducibility and reliability, with further analysis of bleeding sap enabling more in-depth investigations.

Studies employing various oxygenation methods—including controlled irrigation, oxygen-enhanced irrigation, oxygen fertilizers, and aerated hydroponics—demonstrate that rhizosphere oxygen enhancement significantly increases root vigor by 10% to 150% (Table 1). Substantial inter-varietal differences exist in rice responses to oxygen enhancement. Wang Danying et al. [27] attributed these differences to inherent root vigor levels, with high-vigor conventional indica varieties (Xiangzaoxian 11 and Yongjing 18) showing significant improvements under oxygen enhancement, while low-vigor varieties (Xiangzaoxian 24 and Chunjiang 06) exhibited minimal changes. Rhizosphere oxygen enhancement promotes root vigor across all growth stages, particularly during late growth phases, increasing SOD activity, reducing MDA content, and extending leaf functional duration, which is crucial for yield improvement [60-62].

4. Effects of Rhizosphere Oxygen Enhancement on Rice Nitrogen Absorption and Utilization

a) Effects on Nitrogen Absorption

From perspectives of root morphology, physiological activity, and nitrogen transformation in the root zone, oxygen enhancement treatments facilitate nitrogen uptake by rice roots. Morphologically, oxygen enhancement produces slender, elongated roots with increased fine root proportion. Since water and nutrient absorption primarily occurs through root hairs and fine roots—termed "active roots" as the main tissues for soil resource acquisition [66]—increased fine roots under oxygen enhancement promote nitrogen absorption. Additionally, oxygen enhancement increases total root absorption area, particularly active absorption area, benefiting nitrogen uptake. Wang Danying et al. [27] reported that oxygen enhancement significantly increased active absorption area without affecting root volume or total absorption area, while Zhao Xia et al. [35] found that moderate oxygen enhancement increased both active and total absorption areas, consistent with water-controlled irrigation results [37].

Anatomically, oxygen-enhanced conditions induce adaptive adjustments: reduced requirements for preventing oxygen leakage and reductive substance invasion result in less exodermal cell wall thickening compared to hypoxic conditions [27], creating looser exodermal sclerenchyma and increased root surface permeability that facilitates nitrogen absorption. Physiologically, active transport is the primary nitrogen acquisition pathway, directly influenced by root vigor and respiration intensity, which are oxygen-dependent. As previously discussed, oxygen enhancement significantly increases root vigor, enhancing active nitrogen absorption capacity. Increased soluble sugar content in oxygen-enhanced roots promotes respiratory metabolism [33]. Xu Chunmei et al. [66] demonstrated that hypoxic stress reduced root vigor and respiration, decreasing nutrient absorption and resulting in reduced root nitrogen content, soluble protein content, and nitrogen accumulation, thereby confirming oxygen's importance for nitrogen uptake from the opposite perspective.

Beyond direct root effects, oxygen enhancement improves the rhizosphere environment to promote nitrogen absorption. He Shengde et al. [67] found that external oxygenation significantly increased rhizosphere redox potential, altering nutrient forms to facilitate nitrogen uptake. Under oxygen-enhanced conditions, enhanced nitrification increases NO content, creating mixed ammonium-nitrate nutritional environments favorable for nitrogen absorption [68-70]. Additionally, flooded paddy soils strongly adsorb phosphorus, creating low phosphorus availability and frequent deficiency. Alternating wet-dry conditions or increasing rhizosphere dissolved oxygen through root ROL can enhance phosphorus availability [71-72], promoting nutrient balance that facilitates nitrogen absorption and dry matter accumulation.

b) Effects on Nitrogen Accumulation

Despite promoting nitrogen uptake, oxygen enhancement' s effects on nitrogen accumulation are complex. Moderate oxygen enhancement can increase key nitrogen metabolism enzyme activities and photosynthetic nitrogen use efficiency [35], enhancing nitrogen absorption and accumulation. In aerated hydroponic experiments, Zhao Feng et al. [29] found that oxygen enhancement significantly increased root nitrogen accumulation regardless of nitrogen form. Zhao Xia et al. [35] reported that oxygen enhancement significantly increased nitrogen accumulation in roots, stems, and leaves across two varieties, particularly under medium oxygen treatment (2.3~5.5 mg·L ^{1}). Hu Zhihua et al. [73] demonstrated that three oxygenation modes (CaO , micro-nano bubble oxygenated irrigation, and wet-dry alternation) significantly improved nitrogen absorption and accumulation compared to flooded controls.

Conversely, excessive oxygen enhancement significantly reduces nitrogen accumulation [32,34,74]. Further analysis reveals that while plant nitrogen content shows no significant differences across treatments, plant biomass differs significantly. Excessive oxygenation (saturation treatment) severely inhibited rice growth, reducing biomass by 12.5%~71.5% across varieties and growth stages [32,34,74], accompanied by significant reductions in nitrogen accumulation. Excessive oxygenation increased shoot nitrate reductase activity while inhibiting glutamine synthetase activity, potentially causing nitrogen to accumulate as nitrate, nitrite, or ammonium without timely conversion to amino acids, thereby inhibiting nitrogen metabolism completion [32]. When nitrogen assimilation is suppressed, carbohydrate accumulation and photosynthetic activity decrease, ultimately affecting dry matter accumulation and yield formation [75].

In summary, oxygen enhancement facilitates nitrogen uptake, but its effects on nitrogen absorption and accumulation depend on method and degree. Excessive oxygenation inhibits nitrogen utilization, limiting biomass increase and consequently suppressing nitrogen absorption and accumulation.

5. Perspectives on Rice Rhizosphere Oxygen Enhancement Research

a) Investigating Effects on Rice Seedlings

Rhizosphere oxygen may critically affect rice seedlings. During seedling cultivation, particularly in early stages, nursery soil remains saturated, allowing oxygen entry only as dissolved oxygen. With oxygen diffusion in water being only one ten-thousandth of that in air [1,47,76-77], external oxygen enters nursery soil extremely slowly. Under competition from soil microorganisms, nursery soil rapidly becomes hypoxic or anoxic. Although rice seedlings begin forming aerenchyma as part of normal root development [78], complete aerenchyma only forms after the three-leaf stage [79]. Before this stage, seedlings lack unobstructed oxygen transport channels, making rhizosphere oxygen crucial for root respiratory metabolism. Yin Weiyi et al. [19] confirmed that under wet cultivation, internal oxygen transport in three-leaf stage seedlings meets only 30%~60% of root respiratory demand.

Current rhizosphere oxygen research primarily focuses on post-tillering stages, with limited studies on seedlings and scarce reports specifically targeting pre-three-leaf stage seedlings. Therefore, exploring oxygen enhancement effects on pre-three-leaf stage seedlings and developing simple, practical seedling-stage oxygenation measures could significantly advance rice seedling cultivation theory and technology.

b) Improving Research on Nitrogen Metabolism Effects

Over the past century, most oxygen-plant growth relationship research has focused on hypoxia stress, yielding extensive results [4,14,80-81]. Recently, increasing studies have investigated rice responses to oxygen enhancement, reflecting a shift from passive stress response to active environmental modification in high-yield cultivation research. However, research on nitrogen metabolism effects remains limited, with unclear understanding of how oxygen enhancement influences nitrogen absorption and metabolism.

For instance, Zhao Feng et al. [32] found that saturated oxygen hydroponics significantly increased leaf nitrate reductase activity (NRA) while decreasing leaf glutamine synthetase activity (GSA). In similar research, Xu Chunmei et al. [33] reported that saturated oxygen hydroponics significantly increased root GSA, while Zhao Xia et al. [35] found that oxygenated hydroponics decreased leaf NRA and increased leaf GSA, while simultaneously increasing root NRA and decreasing root GSA. These discrepancies may stem from differences in oxygenation methods, degrees, or rice varieties. Additionally, few studies have examined effects on nitrite reductase (NiR), another key nitrogen metabolism enzyme. Previous research extensively investigated nitrogen metabolism under hypoxia/anoxia, showing that low oxygen induces increased root NRA [3,82-83] while inhibiting NiR activity, leading to nitrite accumulation [83-85]. This occurs because hypoxia inhibits aerobic respiration, prompting roots to use nitrate reduction to nitrite as an alternative electron acceptor to oxidize NADH and NADPH and generate ATP [11,26]. Thus, nitrogen metabolism changes under hypoxia represent qualitative metabolic pathway adaptations rather than quantitative rate changes. Consequently, oxygen enrichment effects are not simple reversals of hypoxia effects but require comprehensive investigation considering oxygenation method, degree, and rhizosphere interactions. Key research priorities include determining optimal oxygen requirements and inter-varietal differences.

c) Quantifying Field Oxygen Requirements

Initial understanding of oxygen-enhanced rice cultivation derived from irrigation research. Intermittent, wet, thin-film, and furrow irrigation methods regulate soil water-air ratios, improving soil aeration and promoting growth and yield. Some studies have applied chemical oxygen fertilizers [57,86]. However, irrigation regulation and oxygen fertilizer application only provide coarse control over field aeration, with water and fertilizer effects complicating isolation of oxygen' s specific impacts, limiting understanding to qualitative levels. Recent studies using controlled oxygenation methods (micro-nano bubble oxygenated irrigation, aerated hydroponics) have advanced research from qualitative to quantitative stages. Rhizosphere oxygen concentration is not "the higher the better" but has an optimal threshold. Hu Zhihua et al. [74] investigated hydroponic effects of different rhizosphere oxygen concentrations (1.0, 3.0, 5.5, and 7.5 $\text{mg} \cdot \text{L}^{-1}$) on yield and nitrogen utilization, finding that all three rice materials achieved maximum nitrogen use efficiency and grain yield at 3.0 $\text{mg} \cdot \text{L}^{-1}$, consistent with Zhao Xia et al. [35]. Notably, high oxygen treatment (7.5 $\text{mg} \cdot \text{L}^{-1}$) reduced yields far below medium (3.0 and 5.5 $\text{mg} \cdot \text{L}^{-1}$) and low (1.0 $\text{mg} \cdot \text{L}^{-1}$) oxygen treatments, with maximum reductions reaching 88%, suggesting oxygen saturation stress may be more detrimental than oxygen deficiency, as corroborated by Zhao Feng et al. [32] and Xu Chunmei et al. [34]. However, due to substantial differences between field and hydroponic conditions, these conclusions require further field validation. Particularly since paddy soils are complex solid-liquid-gas systems containing both gaseous and dissolved oxygen, existing oxygen concentration metrics cannot directly reflect soil oxygen status. Therefore, developing suitable field soil oxygen indicators and measurement methods represents the first step toward quantifying field oxygen requirements, with further research needed on precise rhizosphere oxygen control in field production.

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