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Effect of Rhizosphere Oxygen Content on Plant Growth and Research Progress on Plant Resistance to Hypoxic Stress

Peixuan Yang

College of Forestry, Southwest Forestry University, Kunming, 650224, China

Abstract

Oxygen is a nutritional factor for plant life activities, and root hypoxia causes a large number of reactive oxygen species to be produced in the plant, which causes oxidative stress on the plant and affects normal growth. To understand the response and adaptation mechanism of plants and how to change rhizosphere oxygen content, it is essential to study the crop production and the breeding of resistant varieties. This paper investigates the effect of the rhizosphere oxygen environment on plants and the harm of a low oxygen environment to plants, including normal plant oxygen demand, the effect of low oxygen content on the rhizosphere environment, and oxygen content on plants. Finally, the measures are summarized to reduce the damage caused by hypoxia stress to plants. Further research problems and research directions of rhizosphere oxygen content are proposed, which provides new ideas for follow-up research.

Keywords

Rhizosphere oxygen content; Plant growth; Response mechanism.

1. INTRODUCTION

Oxygen provides energy for the growth of plant cells, and it is necessary to maintain the normal physiological metabolism and growth and development of plants. Plant cell growth and metabolism require adequate oxygen. However, crop production conditions, such as flooding, improper irrigation, and matrix cultivation often cause insufficient oxygen supply at the plant rhizosphere, resulting in hypoxia or stress. Therefore, the rhizosphere oxygen content in the soil is too low. This oxygen stress can adversely affect crop growth, yield, and quality and, in severe cases, leads to plant death. Insufficient oxygen supply to the root system affects or inhibits the aerobic respiration of plant roots. It can disturb energy metabolism and reduce plant roots' water absorption and nutrients. Then, it slows down the speed of photosynthesis, causes the root system to stop growing or even necrosis, and ultimately affects the normal growth and development of plants. Therefore, oxygen is an essential nutritional factor in crop production. In recent years, the average annual area of flood disasters in China has exceeded 97,000 square kilometers, and the area affected by crops in the country has been expanded. The Huang-Huai Plain and the middle and lower reaches of the Yangtze River are the most serious [1]. The essential harm of waterlogging to plants is that too much soil moisture leads to a lack of oxygen in the root system.

The oxygen diffusion rate in water is only one-ten-thousandth of that of air. The soil moisture content is high, and the speed of oxygen entering the soil depths through the water layer is considerably slowed down. The consumption and supply of oxygen in the soil are unbalanced, resulting in a significant reduction in the amount of oxygen in the soil. Rhizosphere hypoxia seriously restricts crop growth. Therefore, the adaptation mechanism of the rhizosphere oxygen environment, the change of intracellular oxygen concentration, and oxygenation

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measures in plants have become the focus of studying the physiological and biochemical reactions and molecular mechanisms of plants in the hypoxic environment [2]. This paper summarizes the influence of the rhizosphere oxygen environment on plants and the harm of a low oxygen environment to plants, which is measured to avoid hypoxia damage. Further research problems and research directions of rhizosphere oxygen content are proposed to provide a reference for the relevant research on plant resistance to hypoxic stress.

2. THE NORMAL OXYGEN CONTENT OF PLANTS

In general, the O_2 content in soil air reaches 15%, which can meet the respiratory needs of plants. The minimum soil oxygen demand for crop roots varies from crop to crop (cotton 3%, maize 6%, wheat 5%) [3]. At least 3% to 5% of paddy soil can meet the oxygen demand of rice. Under normal respiratory conditions, when oxygen levels are below 5%, the roots of most crops stop growing. Some studies have conducted quantitative studies on rice oxygen demand and determined the oxygen demand of hydroponic rice at different stages. In hydroponics, it is called extreme hypoxia when the oxygen concentration in the solution is 0 mg L^{-1}. When the oxygen concentration is less than 3 mg L^{-1}, it is named hypoxia. The dissolved oxygen concentration reaches more than 4 mg L^{-1} to meet the needs of most plant growth. Another study found that hypoxia symptoms of hydroponic tomatoes worsened when dissolved oxygen in the nutrient solution was less than 3 mg L^{-1} [4].

3. PLANT RHIZOSPHERE RESPIRATION AND LOW OXYGEN ADAPTATION SIGNALING

Plant root tissues utilize proteins and amino acids for respiratory metabolism, providing energy (such as ATP) and carbon frameworks for root biomass synthesis, maintenance, and ion uptake. Cells can directly or indirectly sense oxygen levels in the body, resulting in a series of responses adapted to hypoxia. Although some genes in animal fungi can be directly involved in oxygen sensing under hypoxic and anaerobic conditions, similar gene homologs have not been found in plants. They may have their direct sensing mechanisms or use only indirect sensing mechanisms [5]. The production of reactive oxygen species (ROS) and nitric oxide (NO), as well as changes in adenosine (ATP, ADP, and AMP), carbohydrate consumption, and pyruvate levels, can cause changes in energy status. SnRK1 is a branch of the SNF1 family, and it is a plant energy sensor closely related to the hypoxic response. When plant seeds germinate under waterlogging and hypoxic conditions, sucrose depletion activates the energy sensor SnRK1A and calcineurin-like neurophosphatase B interaction kinase. Arabidopsis kinases KIN10 and KIN11 limit energy expenditure under hypoxic conditions [6]. Theoretically, reducing energy expenditure benefits plants when ATP levels are reduced. Selective expression and silencing of mRNAs under hypoxic stress is a way to avoid energy waste. In other eukaryotes, SnRK1 and rapamycin kinase target proteins have modulated several subsets of silencing intracellular mRNA, including genes encoding various riboproteins and transcription factors [7].Ca^{2+} and NO are involved in oxygen signaling as the second messenger in cells, and the Ca^{2+} signaling pathway is studied in-depth. Studies have shown that within a few minutes after the onset of maize hypoxia, the concentration of Ca^{2+} in the cytosol increases, and the mRNA levels of intracellular ethanol dehydrogenase (ADH) and sucrose synthase (SS) increase. Inhibition of hypoxia-induced expression of ADH and SS genes greatly enhanced the sensitivity of maize plants to hypoxia. In maize suspension culture, decreasing O_2 concentration led to a rapid increase in intracellular Ca^{2+} concentration, restoration of oxygen supply, and restoration of Ca^{2+} to normal levels. It is a change in Ca^{2+} concentration preceded by changes in gene expression and physiological biochemistry [8]. Another study has shown that the decrease in solute pH and ATP depletion triggered a Ca^{2+} response under hypoxic stress, which opened the Ca^{2+} channel in intracellular

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calcium storage. It results in a rapid increase in intracellular Ca^{2+} concentration, binding to calmodulin (CaM), and inducing changes in downstream physiological and biochemical metabolic pathways to maintain the stability of cell walls, cell membranes, and membrane proteins [9].

4. THE DAMAGE OF LOW RHIZOSPHERE OXYGEN TO PLANTS

4.1. Seed germination

Seeds can germinate in a strictly oxygen-starved environment. However, this germination and early growth come at the expense of post-germination root and initial leaf growth. Seeds germinate in an oxygen-deficient environment, and aerobic respiration is severely inhibited. Energy reserves are depleted to meet the ATP needed for growth, starch decomposition accelerates, and the hydrocele elongates from the surface of the water and grows rapidly [10].

4.2. Plant growth

The root system is a direct organ that suffers from hypoxic stress. In hypoxia, plant energy metabolism is disturbed. Aerobic respiration slows down or stops, and anaerobic respiration increases, which results in insufficient energy in plant tissue cells. In the case of extreme hypoxia, H+ in the vacuole gradually penetrates the cytoplasm, reducing the pH of the cytoplasm [11]. Under acidic conditions, lactate dehydrogenase activity is inhibited, and pyruvate decarboxylation is activated. Then, production capacity decreases, and when ATP is deficient, the ATPases on vacuoles slow down the rate at which H+ is pumped into vacuoles, which causes cytoplasmic acidification. Cytoplasmic acidification is a leading cause of cell damage or death. Meanwhile, the accumulation of anaerobic respiratory products, such as lactic acid, ethanol, and acetaldehyde, also can produce cell toxicity, which inevitably affects the normal physiological function of plant tissues. Therefore, under hypoxia conditions, the absorption and transport of water and nutrients by root tissues is significantly slowed down, hindering plant growth and development [12]. Long-term hypoxic stress forces chloroplast cystic membrane degradation, and some mitochondrial membrane systems are also disrupted.

4.3. Plant diseases

Soil flooding can exacerbate plant disease levels, which makes plants more susceptible to disease. Under flooded hypoxia conditions, root damage is more susceptible to Phytophthora infection, and increased root secretions favor the survival of pathogen spores. A hypoxic environment inhibits the active and effective defense response of plants after infection. The biosynthesis of plant antitoxins in peas and soybeans is significantly inhibited at 1% O_2 concentration, and tomatoes no longer continue to synthesize plant antitoxins under hypoxic conditions. Phenol oxidase requires molecular oxygen to inactivate specific pathogens, which forms a physical barrier to prevent other pathogens from entering, and hypoxia inhibits this process to some extent [13].

4.4. Measures to reduce the damage caused by hypoxic stress to plants

In field production, in order to improve the soil structure and increase the oxygen content of the soil, the soil texture is generally improved by deep ploughing, loose soil, rational drainage and irrigation, and organic fertilizer application. Nowadays, aerobic irrigation has become an emerging form of aeration. Aerobic irrigation is an efficient and water-saving irrigation system that delivers oxygen directly to the root system of the crop by adding air to the irrigation water. It optimizes the rhizosphere gas environment, promotes crop growth, and increases yields. There are three methods of oxygenation in irrigation water: mechanical aeration, chemically dissolved oxygen, and micro-nano bubble aeration [14]. Mechanical aeration is a commonly used aerobic irrigation method. However, its efficiency is low, and it is difficult to quickly

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increase the dissolved oxygen value of irrigation water. Chemical dissolved oxygen is the addition of peroxide to irrigation water, decomposition, and release of O_2 into the water, increasing the amount of dissolved oxygen in the water. However, peroxides have specific corrosive properties, and adverse reactions are the subject of further research. In hydroponics, air and nutrient solutions are in contact to increase the amount of dissolved oxygen. In pneumatics, the air is mixed into a dedicated liquid supply port to create bubbles and water droplets or mist droplets while stirring the reservoir to increase the dissolved oxygen content. The nutrient solution membrane method (NET) is where the nutrient solution flows and comes into contact with the air to increase the oxygen concentration. Micro and nanobubble aeration is a new type of human water quality aeration technology, which refers to the mixed bubbles close to the middle of microbubbles and nanobubbles. The oxygen components are melted from the micro and nanobubbles to enhance the water quality [15].

In addition, applying exogenous plant growth regulators that can reduce plant hypoxia damage has recently become a research hotspot. The timely and scientific application of exogenous plant growth regulators can effectively reduce the damage of hypoxia and improve the ability of plants to tolerate hypoxia. After spraying γ-aminobutyric acid (GABA) to melon leaves under hypoxia stress, the antioxidant enzyme activity increased. The content of reactive oxygen species in vivo decreased, and the tolerance of plants to hypoxia was enhanced. Adding polyamines to the nutrient solution or spraying the leaves with polyamines can improve the hypoxia tolerance of cucumber plants [16]. Another study is shown that exogenous rapeseed lactone, spermidine, putrescine, etc., could improve the hypoxia tolerance of plants to a certain extent and reduce hypoxia damage [17]. Therefore, the rational selection of exogenous substances, through the immersion of seeds, foliar spraying, and application of the rhizosphere of cultivated crops, regulates the physiological metabolism of plants. Thereby, it can improve the ability of crops to tolerate hypoxia stress, which is a portable and efficient measure.

Finally, it is possible to mine from the aspect of hypoxia genes. The anaerobic gene binding capacity and transcriptional activity of the first anaerobic transcription factor HIF-1 isolated from higher organisms were induced by hypoxia, while the activity of HIF-1 was regulated by ROS concentration. ROS acts as a second messenger, which participates in antioxidant processes and is subject to coercion-induced regulation [18]. The formic acid dehydrogenase gene was cloned from barley root, and it was found that the expression of this gene was induced by hypoxia and iron deficiency stress. Formate metabolism may be an unknown metabolic pathway present in non-photosynthetic tissues. The discovery of this phenomenon links hypoxia to the metabolism of iron, a key cogenerator and element in chlorophyll and hemoglobin synthesis [19]. It provides a new way to explore the physiological adaptability of plants under hypoxic stress.

5. CONCLUSION

In recent years, although researchers at home and abroad have conducted extensive and meticulous research on the adaptation and response of plants to hypoxia, there are still many problems. Further study is needed and measured to improve rhizosphere oxygen concentration, especially mining hypoxia tolerance genes.

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