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Quality and Yield Responses of Bayberry to Soil pH Regulation

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Abstract The acidity or alkalinity (pH) of the soil has a significant impact on the growth, fruit quality and yield of *Morella rubra*. Many studies have shown that the appropriate pH range is generally between 5.0 and 6.5. Within this range, the root system of the bayberry is more vigorous, capable of better absorbing nutrients, and the fruit development is also more normal. This not only increases the sugar-acid ratio in the fruit, but also boosts the content of anthocyanins and vitamin C, making the taste better and enhancing the antioxidant capacity. If the soil is too acidic or too alkaline, it will affect flower bud differentiation, reduce fruit setting rate, cause poor fruit enlargement, and ultimately lead to unstable yield and poor quality. Methods such as applying lime, increasing organic matter or adding biochar can alleviate soil acidification to a certain extent, improve the rhizosphere environment, and thereby increase the yield and fruit quality of bayberries. Future research still needs to explore the pH critical points at different growth stages of bayberries in greater detail, clarify the molecular mechanisms involved, and examine whether long-term regulatory measures have any impact on the ecological environment. Overall, scientifically adjusting soil pH is an important method to ensure high yield and quality of bayberries while maintaining sustainable development.

Keywords Bayberry (Morella rubra); Soil pH; Fruit quality; Output regulation; Sustainable agriculture

1 Introduction

Bayberry (*Morella rubra*) is a common and important fruit tree in southern China. It has a unique taste, is rich in nutrition and contains many active substances, so it has attracted much attention. The fruit of the bayberry contains vitamin C, anthocyanins and phenols, etc. These components not only make the fruit have high edible value, but also play an antioxidant and anti-inflammatory role. In recent years, people's interest in healthy food has been increasing. Therefore, the industrialized cultivation and quality improvement of bayberries have also become the research focus (Ren et al., 2021).

The pH of the soil has a significant impact on the growth, yield and fruit quality of fruit trees. Generally speaking, bayberries prefer to grow in acidic soil with a pH of 4.5~6.5. Soil pH not only affects plant nutrient absorption, but also alters the microbial community in the rhizosphere and their metabolic activities, all of which indirectly affect fruit tree health and fruit quality (Li et al., 2023). Studies have found that if the soil is too acidic, it is prone to bayberry decline disease, which is mainly related to the decrease in aluminum toxicity and microbial diversity, and the result will affect yield and quality (Chen et al., 2022; Hong et al., 2023). If the pH is too low or too high, the sugar, protein and vitamin C in the fruit will decrease, while the acid content will increase and the taste will deteriorate (Bao et al., 2005).

This study collates and summarizes the research on the influence of soil pH regulation on the quality and yield of bayberries in recent years. The focus is on the mechanism by which soil pH changes affect the growth, nutritional components, flavor and related microbial communities of bayberries. By integrating the physiological responses, yield changes and quality indicators under different soil pH conditions, it is hoped to provide some theoretical and practical references for the cultivation and management of bayberries, thereby improving the quality and yield of fruits.

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2 Soil pH and Nutrient Dynamics

2.1 Macronutrient availability: N, P, K responses to acidic vs. neutral soils

The pH of the soil can affect the utilization rate of major elements such as nitrogen (N), phosphorus (P), and potassium (K) in the rhizosphere of the bayberry. Studies have found that the more acidic the soil is, the more difficult these elements are to be absorbed, and the growth and fruit quality of bayberries will deteriorate (Li et al., 2022). In soils with strong acidity, the relationship between N, P, K and some metal elements (such As Cu, Cr, Ni, As, Cd) will change, thereby affecting the nutrient absorption of bayberries (Hong et al., 2023). In addition, the influence of soil pH on microbial communities can also indirectly change the availability of nutrients (Ren et al., 2021; 2022).

2.2 Micronutrient balance: Iron, manganese, aluminum toxicity at low pH

In acidic soil, the solubility of iron (Fe) and manganese (Mn) increases, making it easy for plants to absorb excessive amounts, resulting in toxicity (Che et al., 2022). Especially when the pH is lower than 5.0, a large amount of aluminum (Al³⁺) is released, which will directly hinder the growth of the root system of the bayberry and also reduce the microbial diversity in the rhizosphere, thereby causing atrophy disease. Aluminum toxicity not only harms root tissues, but also interferes with the absorption of nutrients such as Ca, Mg, and P, ultimately affecting the health and yield of plants (Li et al., 2022).

2.3 Soil amendments and buffering capacity

To alleviate acidification and nutrient imbalance, people often use some soil conditioners, such as biochar, organic fertilizer and lime. Studies have shown that biochar and humic acid can increase soil pH, enhance organic matter and available nutrients such as N, P, K, Ca, and Mg, and also improve microbial diversity and metabolic activity (Ren et al., 2021; 2022; 2023). Alkaline conditioners such as lime and calcium magnesium phosphate fertilizer can enhance the buffering capacity of the soil, reduce aluminium toxicity, and help maintain nutrient balance (Li et al., 2022). However, different conditioners have different effects and should be selected based on soil conditions and the growth requirements of bayberries (Ng et al., 2022; Arwenyo et al., 2023).

2.4 Interaction with soil microbial community and rhizosphere processes

Soil pH can also alter the nutrient cycling in the rhizosphere of the bayberry by influencing the microbial community. In acidified soil, the diversity of bacteria and fungi will decline, and the community structure becomes complex but unstable, which will affect the decomposition of organic matter and nutrient transformation (Hong et al., 2023). Conditioning agents such as biochar and organic fertilizers can promote the growth of beneficial microorganisms (such as Mycobacterium, Fusarium, etc.), enhance the metabolic activity of the rhizoum, and make bayberries more adaptable to adverse conditions (Ren et al., 2021; 2022; 2023). In addition, associated plants, such as ryegrass, can also enhance the quality of bayberry fruits by improving the soil environment and microbial structure (Li et al., 2023).

3 Physiological and Morphological Responses

3.1 Root growth and architecture under varying pH

The pH of the soil will directly affect the root system of the bayberry. When the soil is too acidic (with a low pH), the growth of the root system will be suppressed, the types of microorganisms in the rhizosphere will decrease, and the ability of the root system to absorb water and nutrients will also decline. This can easily cause bayberry decay disease (Chen et al., 2022; Hong et al., 2023). In alkaline or saline-alkali soil, if salt-tolerant waxberry is used as the rootstock, the condition of the root system can be significantly improved, making the grafted waxberry grow more normally and the root structure more stable (Saeed et al., 2023). In addition, changes in water pressure and pH often act together, affecting the thickening of the cell walls in the root cortex and the formation of the cork layer. Under drought conditions, the cell walls of the root cortex will be thicker, which helps the root system adapt to adverse conditions (Song et al., 2011).

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3.2 Photosynthesis and chlorophyll stability

Soil pH also indirectly affects the photosynthesis of leaves and the content of chlorophyll by influencing the absorption of nutrients by the root system. In saline-alkali soil, the leaves of bayberries grafted onto salt-tolerant rootstocks are darker in color, have higher chlorophyll levels, stronger photosynthesis, and the plants perform healthier. However, if salt-intolerant rootstocks are used, the leaves tend to turn yellow and lose their green color (Saeed et al., 2023). This indicates that maintaining an appropriate soil pH and a healthy root system is of great significance for sustaining chlorophyll and photosynthesis.

3.3 Water-use efficiency and stomatal regulation

Soil pH can alter the structure and function of the root system, which will affect the absorption and utilization of water by the bayberry. Under the influence of pH changes, the root system may experience thickening of cell walls or the formation of a cork layer, which can reduce water loss and enhance water use efficiency in drought and adverse conditions. Meanwhile, a healthy root system also helps regulate stomatal opening and closing, maintain the balance of transpiration and photosynthesis, and thereby enhance the stress resistance of the plant (Song et al., 2011; Saeed et al., 2023).

3.4 Stress tolerance mechanisms (oxidative stress, ion homeostasis)

Soil acidification can aggravate the toxicity of aluminium, leading to oxidative stress in the root system, a decline in the activity of antioxidant enzymes, damage to root tissue, and disruption of ionic balance. Some molecular-level studies have shown that bayberries can enhance their tolerance to adverse conditions such as drought and low temperatures by regulating transcription factors like bHLH and increasing the activity of antioxidant enzymes (such as APX). When the root system is healthy and the soil pH is appropriate, the homeostasis of rhizosphere ions is easier to maintain, which can reduce the toxicity of harmful ions such as aluminum and enhance the overall stress resistance of the plant (Chen et al., 2022; Xu et al., 2023) (Figure 1).

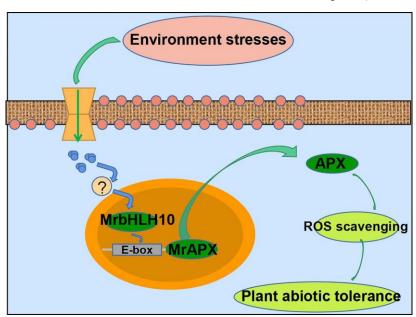


Figure 1 A potential working model for bHLH10 response to abiotic stresses in M. rubra. Under drought and cold stress, activating the environmental stresses signaling pathway and stimulating downstream stress signal transduction in plant cells, the upregulated bHLH10 acts upstream of APX and directly regulates its expression by binding to the E-box motif of its promoter. The activated APX then promotes cytosolic ascorbate peroxidase accumulation to scavenge ROS content under environmental stresses (Adopted from Xu et al., 2023)

4 Impacts on Fruit Yield

4.1 Flowering and fruit set rates

Soil pH has a significant impact on the flowering and fruit setting rates of bayberries. Studies have found that overly acidic soil can reduce the vitality of trees, decrease the microorganisms in the rhitrosphere, make flower

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bud differentiation and fruit setting rates worse, and increase the risk of recession disease (Hong et al., 2023). If the pH is appropriately adjusted, such as by adding humic acid or organic conditioners, the soil environment can be improved, making the trees healthier and enhancing their flowering and fruit setting abilities (Ren et al., 2022).

4.2 Fruit development and size

Soil pH can affect nutrient absorption and root conditions, thereby influencing the development and size of fruits. Studies have shown that in alkaline soil, the single fruit weight and seed weight of bayberries are both lower than those in acidic soil, but the total sugar and total acid contents of the fruits are higher, and the quality is improved. In addition, growing associated plants such as ryegrass can also promote fruit development by regulating pH and improving the microbial environment, increase the contents of vitamin C and flavonoids, and make the fruit flavor better (Li et al., 2023).

4.3 Overall productivity trends under different pH management practices

If the soil is acidified for a long time, the yield of bayberries will decline. This is mainly due to root damage, nutrient imbalance and microbial reduction (Hong et al., 2023). Regulating soil pH, such as applying humic acid, growing associated plants or applying fertilizers reasonably, can significantly increase yield and fruit quality (Ren et al., 2022; Li et al., 2023). In alkaline soil, trees will become shorter and the fruits will be smaller, but the early fruiting rate will be higher, the sugar-acid ratio will increase, and some quality indicators will even improve. Overall, appropriate pH management can ensure stable output and better quality.

4.4 Yield stability in long-term orchard systems

In long-term management, soil pH regulation is crucial to the stability of orchard yields. If the soil keeps acidifying, it will aggravate the decline of bayberries, cause large fluctuations in yield, and increase the pressure of orchard renewal (Hong et al., 2023). Adopting methods such as organic conditioners, associated plants or enhancing microbial diversity can maintain soil health, help stabilize yields, and make orchards more sustainable (Ren et al., 2022; Li et al., 2023; Arous et al., 2024).

5 Impacts on Fruit Quality

5.1 Sugar-acid balance and taste profile

Soil pH can affect the sugar and acid in the fruit, thereby determining the taste and texture of the bayberry. Studies have found that associated ryegrass can improve the soil environment, increasing the sugar content of fruits by 2.26%, reducing the acid content by 9.04%, making the sugar-acid ratio more reasonable and the taste better (Li et al., 2023). In alkaline soil, the total sugar and total acid contents of bayberry fruits will increase, the sugar-acid ratio will rise, and the flavor will be more intense.

5.2 Anthocyanin accumulation and color development

Anthocyanins are important substances that determine the color and antioxidant capacity of bayberries. Studies have shown that when the pH is between 4 and 5, the anthocyanin content in bayberry fruits is the highest, the fruit color is redder and more vivid, and it is more likely to be favored by consumers (Ju et al., 2022). Moreover, at low pH (approximately 1.5), anthocyanins are more stable and the color is less likely to fade (Bao et al., 2005). Studies at the molecular level have also found that during fruit ripening, genes related to anthocyanin synthesis are activated, thereby promoting color formation (Feng et al., 2012).

5.3 Vitamin C and antioxidant compounds

Adjusting soil pH or using associated plants can significantly increase the content of vitamin C and antioxidant substances in bayberry fruits. For example, associated ryegrass can increase vitamin C by 28.45% and total flavonoids by 25%, thereby enhancing antioxidant capacity (Li et al., 2023). Within the pH range of 3 to 5, the antioxidant activity of bayberry juice is relatively high. For instance, the clearance rate of ABTS free radicals is significantly better. This indicates that an appropriate pH is conducive to the accumulation of antioxidant components (Bao et al., 2005; Ju et al., 2022).

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5.4 Storage quality and shelf life

The stability of the pigments and antioxidant substances in fruits is also related to the pH of the soil. Studies have found that in a low pH environment, anthocyanins and pigments in bayberry fruits are more stable, which can extend the storage period and maintain the color (Bao et al., 2005). It has stronger antioxidant capacity and can also slow down the oxidation and deterioration of fruits, thereby extending the shelf life (Ju et al., 2022; Li et al., 2023).

6 Soil pH Regulation Strategies

6.1 Traditional approaches: Lime application, organic matter incorporation

In southern orchards, lime is often used to regulate the pH of acidic soil. It can neutralize acidity, increase pH and also improve the root environment. Returning organic matter to the field, such as applying organic fertilizers or humic acid, can not only buffer the changes in soil pH, but also increase organic carbon, improve soil structure and provide more nutrients. These measures can diversify the microorganisms, help alleviate the disease of bayberry decay, and also improve the fruit quality (Ren et al., 2022; Chen et al., 2022).

6.2 Modern interventions: Biochar, microbial inoculants, nanomaterials

Biochar is a new type of conditioner that can increase soil pH, improve soil properties, promote the reproduction of beneficial microorganisms, and regulate rhizosphere metabolites, thereby making bayberries more resilient and having better fruit quality (Ren et al., 2023; Hu et al., 2024). If microbial inocalants (such as *Bacillus subtilis*) are used together with biochar, the effect will be stronger, which can enhance soil enzyme activity and nutrient utilization and promote plant growth (Deng et al., 2024). Nanomaterials, such as functionalized nano-silica, can also improve rhizosphere microbial communities, enhance antioxidant enzyme activity and stress resistance, reduce the stress of heavy metals, and make bayberries healthier (Ahmed et al., 2024).

6.3 Integrated soil management approaches

Integrated management advocates the combination of multiple methods, such as the use of lime, organic fertilizer, biochar and associated plants together. Companion plants (such as ryegrass) can not only improve soil pH and microbial environment, but also increase sugar, vitamin C and flavonoids in fruits, making the taste and nutrition better. If organic conditioners are used in combination with lime and biochar, it can significantly improve soil health and microbial diversity, and also increase yield, achieving a win-win situation for ecology and economy (Ren et al., 2022; Li et al., 2023; Hu et al., 2024).

6.4 Cost-effectiveness and sustainability considerations

Lime and organic fertilizers are low in cost and easy to use, making them very suitable for large-scale promotion. However, their effects can be influenced by soil type and the frequency of application. Biochar, microbial inoculants and nanomaterials require a larger initial investment, but they can significantly improve soil health and crop stress resistance, which is beneficial to the sustainable development of orchards in the long run (Ren et al., 2023; Ahmed et al., 2024; Deng et al., 2024). The comprehensive management model combining multiple measures can strike a balance among cost, ecology and yield, and it is a sustainable direction for regulating the soil pH of bayberries in the future (Li et al., 2023; Hu et al., 2024).

7 Case Study: Bayberry Production in the Acidic Red Soil Area of South China

7.1 Context: region-specific soil conditions (e.g., acidic red soils of southern China)

The southern part of China is the main production area of bayberries, such as Zhejiang, Fujian and Jiangxi. The soil here is mostly acidic red soil with a pH ranging from 4.5 to 6.5. Long-term cultivation will make the soil more acidic, increase the content of exchangeable aluminum (Al), and reduce the types of microorganisms, which is prone to cause bayberry recession disease and seriously affects the yield and quality (Chen et al., 2022; Hong et al., 2023).

7.2 Intervention: application of lime or biochar to regulate pH

To improve acidified soil, people often use lime and biochar to regulate pH. In a case in Lanxi, Zhejiang Province, researchers applied 20 kilograms of biochar organic fertilizer (containing biochar, pig manure, potassium fertilizer,

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urea, etc.) to each 15-year-old declining bayberry tree and regulated pH through circular furrow application (Ren et al., 2023). Lime application reduces aluminium toxicity by neutralizing acidity and is widely used in orchards (Chen et al., 2022).

7.3 Observed outcomes

In terms of tree body and fruit: After biochar treatment, the vitality of the bayberry tree was significantly enhanced, the leaves and spring shoots grew better, and the sugar and vitamin C contents in the fruit also increased (Ren et al., 2023).

In terms of soil properties: Biochar can increase soil pH, organic matter and available nitrogen, phosphorus and potassium. It can also increase exchangeable calcium and magnesium and reduce harmful aluminum ions (Chen et al., 2022).

Microbial aspect: Biochar promotes the reproduction of beneficial microorganisms such as Mycobacterium and Fusarium, increases diversity, and improves the rhizosphere metabolic environment (Hong et al., 2023).

In terms of metabolites: Under the action of biochar, beneficial metabolites such as antioxidants and amino acids in the rhizosphere soil increase, helping plants to be healthier (Ren et al., 2023.

7.4 Lessons learned: Scalability, farmer adoption, challenges in long-term maintenance

In terms of promotion and application: Lime and biochar for pH adjustment are simple to operate and have obvious effects, making them suitable for promotion in large-scale acidic red soil orchards. Some regions have adopted this as a routine measure (Chen et al., 2022).

In terms of long-term challenges: Soil acidification is a long-term accumulated problem that requires continuous monitoring and regular supplementation of conditioners. Biochar is relatively expensive, so policy and technical support are needed to alleviate the burden on farmers.

In terms of comprehensive management: If measures such as organic fertilizers and associated plants are combined for use, soil health can be better improved and orchards can be made more sustainable (Ren et al., 2023; Hong et al., 2023).

8 Knowledge Gaps and Future Directions

8.1 Thresholds of pH tolerance at different growth stages

At present, there are not many studies on the tolerance of bayberries to soil pH at different growth stages (seedling, flowering, fruiting, senescence). Existing results have shown that when the pH is lower than 4.5, the growth of bayberries will be affected, with a decline in yield and quality, and they are also prone to decay diseases. However, at different stages, the most suitable and critical pH values still lack detailed staged experimental data (Ren et al., 2021; Li et al., 2022). In the future, phased field and greenhouse experiments need to be conducted to draw the pH response curves for each period and determine the thresholds. Only in this way can a basis be provided for precise regulation.

8.2 Molecular basis of pH-regulated nutrient uptake and fruit metabolism

Some studies have now shown that soil pH can affect rhizosphere microorganisms, nutrient utilization rate and fruit metabolite composition (Ren et al., 2021; 2023) (Figure 2). However, the molecular regulatory mechanism of pH changes in bayberries remains unclear. Compared with acid-tolerant crops such as blueberries, studies have found that pH stress can cause changes in the expression of hundreds to thousands of genes, involving nutrient transport, cell wall metabolism and signal transduction (Paya-Milans et al., 2017). Transcriptome and metabolome analyses of bayberry during fruit development and ripening have provided some clues for pH regulation of quality formation (Sun et al., 2024), but the key genes, pathways and their relationship with the rhizosphere environment still require more in-depth research.



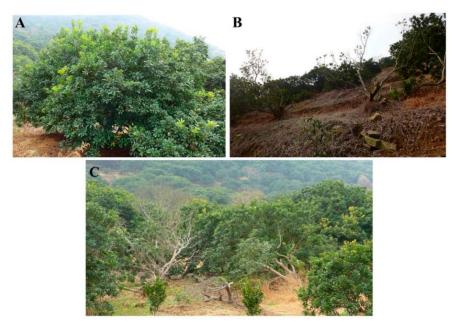


Figure 2 Bayberry trees orchard investigated in this study. Healthy (A) and diseased (B) bayberry trees and the distribution (C) of healthy and diseased bayberry trees (Adopted from Ren et al., 2021)

8.3 Long-term field studies on orchard sustainability

At present, most studies on pH regulation only focus on short-term intervention or changes in yield and quality in a single season, lacking continuous field observations over many years. In long-term orchard management, the relationship between soil acidification, nutrient loss, changes in microbial diversity and the health and yield stability of bayberries has not been systematically explained (Sofo et al., 2020; Ren et al., 2021; Li et al., 2022). Long-term field observations need to be carried out in the future, combining multiple aspects such as soil physicochemical properties, microbial communities, fruit quality and yield, to evaluate the sustainability and ecological effects of different pH control measures (Kalcsits et al., 2020; Sofo et al., 2020) (Figure 3).

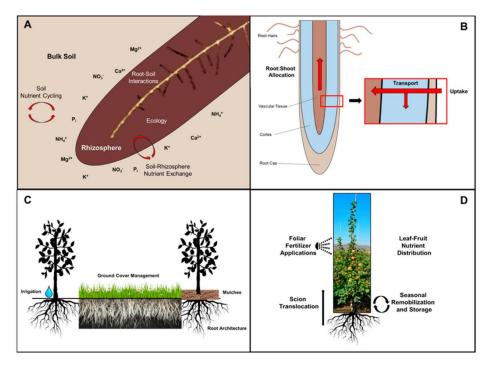


Figure 3 Soil and rhizosphere (A), root (B), orchard (C), and above-ground (D) factors affecting nutrient composition of perennial fruit crops (Adopted from Kalcsits et al., 2020)

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8.4 Climate change interactions with soil pH dynamics

Climate change can affect soil pH and nutrient cycling, such as changes in precipitation patterns and extreme weather. Global research has found that when the annual precipitation is greater than evapotranspiration, the soil pH may suddenly change from alkaline to acidic (Slessarev et al., 2016). However, in the main production areas of bayberries, there is still a lack of targeted research on how climate change affects the dynamics of soil pH and how it acts on the growth of bayberries and the orchard ecosystem. In the future, it is necessary to combine climate models with field monitoring to reveal the relationship among climate, soil and crops, and provide a scientific basis for adaptive management.

9 Conclusion

In recent years, the bayberry industry has encountered two major problems: soil acidification and the disease of decline. Research has found that soil pH is a key factor in determining whether bayberries can grow well, whether the yield is high, and whether the fruit quality is good. Long-term use of chemical fertilizers, coupled with the extension of the orchard's age, will cause the soil pH to gradually decrease, the content of exchangeable aluminum to increase, and the loss of basic nutrients such as calcium, magnesium and potassium. Eventually, it is easy to cause decline disease, making the trees grow poorly and the fruit yield reduced. Generally speaking, the most suitable soil pH for bayberries is between 5.5 and 6.5. If it drops below 4.5, the growth of the tree will be hindered and the quality of the fruit will also decline.

There are many ways to regulate soil pH, such as adding humic acid, biochar, organic fertilizer, lime, etc. These measures not only can increase soil pH, but also can increase organic matter, supplement basic nutrients and improve microbial diversity. This can increase the number of beneficial microorganisms, make the composition of rhizosphere metabolites more reasonable, and ultimately make the tree more vigorous and the fruit more nutritious. Companion plants like ryegrass, along with ecological methods such as bio-organic fertilizers, can also improve the soil environment, increase the content of sugar, vitamin C and antioxidants, make the fruit taste better and be more suitable for storage. For growers, it is best to regularly monitor the soil pH and keep it between 5.5 and 6.5 to avoid relying solely on chemical fertilizers for a long time. Organic fertilizers, biochar, lime and other conditioners can be applied alternately, combined with companion plants and bio-organic fertilizers to maintain soil health and improve fruit quality. If the orchard is severely affected by decay disease, it is advisable to prioritize the use of humic acid and biochar to restore the soil and rejuvenate the trees.

From the perspective of sustainable development, scientific management of soil pH can not only increase yield and quality, but also enhance the stability and stress resistance of orchard ecosystems. By comprehensively applying various measures such as organic fertilizers, biochar and associated plants, the physical and chemical properties of the soil and the biological environment can be simultaneously improved, helping orchards achieve long-term sustainable development and high-quality production. In the future, more long-term field observations and multi-omics studies will be needed to promote the construction of a more precise, ecologically efficient production system for bayberries.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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