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Short Title: *Robinia pseudoacacia* ecophysiological responses



REVIEW ARTICLE

Ecophysiological responses of *Robinia pseudoacacia* to several ecological factors

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Abstract

Robinia pseudoacacia is a widely distributed tree species with strong adaptability to diverse ecological conditions. This review synthesizes recent research on its ecophysiological responses to key ecological stressors, including changes in water availability, nitrogen deposition, and atmospheric dust pollution. Seedlings show greater sensitivity to rainfall frequency than to rainfall intensity; reduced precipitation frequency significantly impairs photosynthetic traits, biomass accumulation, and growth. The interactive effects of precipitation patterns and nitrogen deposition are complex: High precipitation frequency promotes biomass, while nitrogen addition can stimulate growth but may inhibit nitrogen fixation under water stress. Under moderate dust deposition, *R. pseudoacacia* displays remarkable physiological plasticity: Dust particles act as a protective shield against excess solar radiation and enhance photosystem II photochemical efficiency. Across varying nitrogen supply levels, the species maintains relatively consistent growth and photosynthetic rates through rapid regulation of nitrogen fixation, an advantage in nitrogen-limited environments. These findings highlight the multifaceted adaptive strategies of *R. pseudoacacia*, providing insights for predicting its performance under future climate change and for developing forest management and restoration practices.

Keywords: Atmospheric dust deposition, Black locust, Ecophysiological adaptation, Nitrogen fixation, Photosynthetic efficiency, Water availability

Introduction

Robinia pseudoacacia L. (black locust) is a deciduous tree species native to North America that has become naturalized across temperate regions worldwide. This species belongs to the Fabaceae family and is characterized by its exceptional adaptability to various ecological conditions, rapid growth rate, and ability to fix atmospheric nitrogen through symbiotic relationships with rhizobia bacteria. The ecological significance of *R. pseudoacacia* extends beyond its role as a pioneer species; it serves important functions in soil stabilization, erosion control, and ecosystem restoration projects across degraded landscapes. Its capacity to thrive in nutrient-poor soils and withstand harsh ecological conditions has made it a subject of considerable scientific interest, particularly in the context of climate change and increasing ecological stressors (Liu, et al. 2026, Xie, et al. 2026). The global distribution of *R. pseudoacacia* has expanded significantly since its introduction to Europe in the early 17th century, and it now occupies substantial areas in Asia, Australia, and other temperate regions. This widespread distribution has prompted extensive research into its ecological impacts, invasive potential, and

physiological responses to ecological variables. The species demonstrates remarkable phenotypic plasticity, enabling it to adjust its morphological and physiological traits in response to varying ecological conditions. Understanding the mechanisms underlying this plasticity is crucial for predicting the species' future distribution patterns and ecological performance under projected climate change scenarios (Liu, 2021, Wang, 2021).

Ecological stressors such as water availability fluctuations, nitrogen deposition, and atmospheric pollution represent significant challenges to plant growth and survival. Climate change projections indicate that many regions will experience altered precipitation patterns, including more frequent drought events and changes in rainfall distribution. Additionally, anthropogenic nitrogen deposition has substantially increased over the past century, with profound implications for plant nutrition, community composition, and ecosystem functioning. Atmospheric dust pollution, resulting from industrial activities, urbanization, and land degradation, poses additional challenges to plant physiological processes, particularly in regions adjacent to deserts, volcanic areas, or industrial zones. Recent research has provided valuable insights into how *R. pseudoacacia* responds to these ecological challenges at multiple organizational levels, from molecular and cellular processes to whole-plant performance and ecosystem-level effects. This study aims to synthesize these recent findings, focusing on the ecophysiological responses of *R. pseudoacacia* to water availability, nitrogen deposition, and dust pollution. By integrating findings from multiple studies, this review seeks to provide a comprehensive understanding of the adaptive strategies employed by this species and to identify knowledge gaps that warrant further investigation. The insights gained from this synthesis will contribute to improved predictions of *R. pseudoacacia* performance under future ecological conditions and inform management strategies for both native and introduced populations.

Literature Review

Responses to water availability and precipitation patterns

Water availability is a fundamental determinant of plant growth, survival, and distribution, and understanding how species respond to variations in water supply is essential for predicting their performance under changing climatic conditions. A comprehensive investigation into the responses of *R. pseudoacacia* seedlings to different rainfall regimes was conducted to examine both rainfall intensity and frequency as independent variables. The study revealed that seedlings exhibited significantly greater sensitivity to rainfall frequency than to rainfall intensity, a finding with important implications for understanding plant responses to projected changes in precipitation patterns under climate change scenarios. More specifically, the experiment manipulated rainfall intensity into three levels, low, medium, and high, while simultaneously varying rainfall frequency across all combinations of intensity and frequency. The results demonstrated that lower rainfall frequency, regardless of intensity, significantly reduced photosynthetic traits including net photosynthetic rate, stomatal conductance, and transpiration rate. These reductions in gas exchange parameters were accompanied by decreased biomass accumulation across all plant components, including leaves, stems, and roots. The root-to-shoot ratio also decreased under low-frequency treatments, suggesting that water stress induced by infrequent rainfall events preferentially affects root growth and resource allocation patterns. The greater sensitivity to rainfall frequency is likely due to the intermittent nature of soil water deficit experienced by plants under infrequent rainfall regimes. When rainfall events are spaced further apart, plants experience more prolonged periods of soil water deficit between events, even when the total water received remains constant. This prolonged exposure to water stress triggers physiological responses including stomatal closure, reduced carbon assimilation, and altered resource allocation. In contrast, more frequent rainfall events, even at lower intensities, maintain higher soil water content and reduce the duration and severity of water stress experienced by plants (Li, et al. 2022, Guo, et al. 2024).

Wang, et al. 2023 further explored the interactive effects of precipitation patterns and nitrogen deposition on *R. pseudoacacia* growth, providing additional insights into the complex relationships between water availability and nutrient dynamics. The study demonstrated that high precipitation frequency significantly increased biomass accumulation compared to low-frequency treatments, consistent with the findings of Li, et al. 2022. However, the interactive effects with nitrogen deposition revealed more nuanced response patterns that highlight the complexity of plant responses to multiple simultaneous stressors. This study employed a factorial design combining three precipitation frequencies with multiple nitrogen addition levels, allowing for detailed analysis of main effects and interactions. The positive effects of high precipitation frequency on biomass were most pronounced at moderate nitrogen availability. Under low nitrogen conditions, the benefits of frequent precipitation were somewhat diminished, suggesting that water and nitrogen availability interact to constrain plant growth. Conversely, under high nitrogen conditions, the positive effects of frequent precipitation were enhanced, indicating synergistic interactions between these two resources.

Nitrogen fixation and nitrogen deposition responses

As a Fabaceae tree species, *R. pseudoacacia* possesses the ability to form symbiotic associations with nitrogen-fixing rhizobia bacteria, enabling it to access atmospheric nitrogen as an alternative nitrogen source. This capability provides a significant competitive advantage in nitrogen-limited environments and contributes to the species' success as a pioneer species on degraded or disturbed sites. Wang, et al. 2021 investigated the nitrogen fixation capacity of *R. pseudoacacia* and the mechanisms that allow the species to maintain consistent growth across a broad range of nitrogen availability. Wang, et al. 2021 grew *R. pseudoacacia* seedlings under controlled conditions with nitrogen supply ranging from zero to levels exceeding typical soil nitrogen concentrations. Contrary to expectations that growth would increase monotonically with nitrogen supply, the study found that plants achieved similar growth rates and photosynthetic performance across all nitrogen treatments. This unexpected result was explained by the rapid upregulation of nitrogen

fixation activity under low nitrogen conditions, which compensated for the limited external nitrogen supply. The nitrogen fixation process in *R. pseudoacacia* involves the formation of nodules on roots, where rhizobia bacteria convert atmospheric nitrogen into ammonia through the enzyme nitrogenase. Nodule biomass and nitrogenase activity were significantly higher in plants grown under low nitrogen conditions compared to those receiving adequate or high nitrogen. This regulatory response demonstrates the species' ability to sense internal nitrogen status and adjust its investment in nitrogen fixation accordingly. When external nitrogen is abundant, the energetic costs of maintaining active nodules outweigh the benefits, leading to reduced nodule formation and activity (Wang, et al. 2021).

The implications of these findings extend beyond understanding the physiology of *R. pseudoacacia*. In the context of increasing anthropogenic nitrogen deposition, the ability to regulate nitrogen fixation in response to nitrogen availability may influence the species' competitive interactions with non-fixing plants and its contributions to ecosystem nitrogen cycling. Wang, et al. 2023 further explored these interactions by examining how nitrogen deposition affects *R. pseudoacacia* under different precipitation regimes. Their findings indicated that nitrogen deposition can inhibit nitrogen fixation activity, particularly under water stress conditions, while simultaneously promoting growth through enhanced nitrogen availability. The interactive effects of nitrogen deposition and water availability on *R. pseudoacacia* present a complex picture of resource allocation trade-offs. Under conditions of adequate water supply, added nitrogen stimulates growth and reduces the plant's reliance on energetically expensive nitrogen fixation. However, under water stress conditions, the relationship becomes more complicated. Nitrogen deposition under drought conditions could partially alleviate water stress effects by promoting osmotic adjustment and maintaining turgor pressure, but simultaneously reduce nitrogen fixation activity due to the combined stresses on nodule function (Wang, et al. 2023, Xiang, et al. 2024).

Responses to atmospheric dust deposition

Atmospheric dust deposition is an often-overlooked stressor that substantially affects plant physiology. De Micco, et al. 2023 conducted an innovative study examining the effects of anthropogenic dust on leaf anatomical and ecophysiological traits of *R. pseudoacacia* growing on Vesuvius Volcano in Italy. This unique study site provided an opportunity to investigate plant responses to naturally occurring dust deposition under field conditions, complementing controlled-environment studies that may not fully capture the complexity of natural systems. The volcanic environment around Vesuvius is characterized by frequent dust deposition events resulting from both natural processes and anthropogenic activities. De Micco, et al. 2023 compared *R. pseudoacacia* trees growing in high-dust and low-dust areas, examining a comprehensive suite of anatomical and physiological parameters. Their findings revealed that dust deposition, rather than being purely detrimental, can enhance certain aspects of plant physiological performance under specific conditions. One of the most striking findings from the study by De Micco, et al. 2023 was that dust deposition enhanced photosystem II efficiency in *R. pseudoacacia* leaves. This counterintuitive result was attributed to the protective effect of dust particles, which act as a physical shield against excess solar radiation. In Mediterranean environments, where solar irradiance can reach levels that cause photoinhibition and damage to the photosynthetic apparatus, the presence of a dust layer on leaf surfaces can reduce the amount of light reaching the photosynthetic tissues to more optimal levels. This protective effect outweighs any negative effects of dust on gas exchange through stomatal blockage. The anatomical responses of *R. pseudoacacia* to dust deposition included modifications to leaf thickness, cuticle development, and mesophyll structure. Trees growing in high-dust environments exhibited thicker leaves with more developed palisade mesophyll, traits typically associated with adaptation to high-light environments. The cuticle was also thicker in dust-exposed leaves, potentially providing additional protection against water loss and physical damage from dust particles. These anatomical modifications represent phenotypic plasticity responses that allow the species to adjust its morphology to local ecological conditions. The ecophysiological implications of dust deposition responses extend to considerations of plant performance in urban and industrial environments. As urbanization continues to expand globally. Understanding how plants respond to atmospheric pollutants including dust becomes increasingly important for urban forestry and landscaping applications, *R. pseudoacacia* may be particularly well-suited for planting in dusty or polluted environments, given its ability to not only tolerate but potentially benefit from moderate dust deposition through enhanced photoprotection (Isinkalar, et al. 2025).

Interactive effects of multiple stressors

Ecological stressors rarely occur in isolation, and understanding the interactive effects of multiple simultaneous stresses is crucial for predicting plant performance under realistic field conditions. The studies reviewed here collectively demonstrate that *R. pseudoacacia* responses to individual stressors can be significantly modified by the presence of additional stressors, highlighting the importance of multi-factor experimental approaches in ecological research. The interaction between water availability and nitrogen dynamics represents a particularly important area of investigation, given projected changes in both precipitation patterns and nitrogen deposition under future climate scenarios. Wang, et al. 2023 demonstrated that the effects of nitrogen deposition on *R. pseudoacacia* growth and nitrogen fixation are contingent upon water availability. Under well-watered conditions, added nitrogen promotes growth and reduces nitrogen fixation activity, representing a straightforward resource optimization response. However, under water stress conditions, the relationship becomes more complex, with nitrogen deposition potentially alleviating some aspects of water stress while simultaneously imposing additional constraints on nitrogen fixation. These interactive effects involve multiple physiological processes across scales. At the cellular level, water stress affects membrane stability, enzyme activity, and metabolic processes, while nitrogen availability influences protein synthesis, photosynthetic capacity, and osmotic adjustment. The integration of these processes at the

whole-plant level determines growth responses and resource allocation patterns. The ability of *R. pseudoacacia* to adjust its nitrogen fixation activity in response to both water and nitrogen availability represents a key adaptive trait that allows the species to optimize resource acquisition under varying ecological conditions. Furthermore, the interaction between dust deposition and water availability adds complexity. Dust particles on leaf surfaces can affect both light interception and gas exchange, with implications for water use efficiency and carbon assimilation. Under water stress conditions, the reduction in light intensity caused by dust deposition might reduce transpiration rates and improve water use efficiency, while under well-watered conditions, the same dust layer might limit photosynthetic rates by reducing light availability below optimal levels. These context-dependent effects underscore the importance of considering multiple ecological factors simultaneously when predicting plant responses to ecological change (Wang, et al. 2023, Zhang, et al. 2024).

Discussion

Adaptive significance of physiological plasticity

The collective findings from recent research on *R. pseudoacacia* highlight the remarkable physiological plasticity of this species and its significance for ecological success across diverse environments. In response to nitrogen availability, dust deposition, and water availability, *R. pseudoacacia* adjusts its nitrogen fixation rates, leaf anatomy, and resource allocation patterns, representing a suite of adaptive traits that enable *R. pseudoacacia* to persist and thrive under challenging ecological conditions. This plasticity has important implications for understanding the species' invasive potential and its likely responses to future ecological change. The regulatory mechanisms underlying nitrogen fixation plasticity in *R. pseudoacacia* deserve particular attention. The ability to rapidly upregulate nitrogen fixation under nitrogen-limiting conditions provides a significant competitive advantage in nutrient-poor environments where many other species cannot establish or persist (Wang, et al. 2021). This capability explains, in part, the success of *R. pseudoacacia* as a pioneer species on degraded sites, abandoned agricultural lands, and other disturbed habitats where soil nitrogen content is typically low. The energetic costs of maintaining nitrogen fixation capacity are offset by the benefits of nitrogen independence, allowing *R. pseudoacacia* to colonize and dominate sites where competition from other species is reduced. The finding that rainfall frequency has stronger effects on *R. pseudoacacia* seedlings than rainfall intensity has important implications for predicting species responses to climate change. Climate models project that many regions will experience changes in precipitation patterns, including longer intervals between rainfall events and more intense individual storms. The sensitivity of *R. pseudoacacia* to rainfall frequency suggests that such changes could significantly impact seedling establishment and early growth, potentially affecting recruitment success and population dynamics. However, the species' ability to adjust root-to-shoot ratios and other morphological traits in response to water availability may provide some buffering against these effects. The positive effects of dust deposition on photosystem II photochemical efficiency represent an unexpected finding that challenges conventional assumptions about the impacts of atmospheric pollution on plant physiology (De Micco, et al. 2023, Isinkaralar, et al. 2025). While dust deposition is generally considered detrimental to plant growth due to reduced light interception and stomatal blockage, the protective effect against excess solar radiation in Mediterranean environments demonstrates that the net effect of ecological stressors can be context-dependent. This finding has implications for urban forestry and the selection of species for planting in polluted environments, suggesting that *R. pseudoacacia* may be particularly well-suited for such applications.

Implications for forest management and restoration

The ecophysiological insights gained from recent research on *R. pseudoacacia* have practical applications for forest management, restoration ecology, and urban forestry. Understanding the conditions under which the species performs optimally, and the stressors to which it is most sensitive, can inform decisions about where and how to use *R. pseudoacacia* in planting programs. The species' ability to fix nitrogen makes it valuable for soil improvement and site restoration, but its invasive potential in some regions requires careful consideration of management approaches. For restoration applications on degraded sites, the nitrogen fixation capability of *R. pseudoacacia* can accelerate soil development and facilitate the establishment of other species. However, the benefits of nitrogen fixation may be reduced under drought conditions, when nitrogen fixation activity is inhibited (Wang, et al. 2023, Xiang, et al. 2024). This has implications for the timing of restoration plantings and the selection of sites where *R. pseudoacacia* is likely to provide the greatest benefits. In regions experiencing increasing drought frequency, the use of *R. pseudoacacia* in restoration may require supplemental irrigation during establishment or selection of drought-tolerant provenances. The sensitivity of *R. pseudoacacia* seedlings to rainfall frequency has implications for regeneration management in both natural and planted forests. Silvicultural practices that maintain soil moisture between rainfall events, such as mulching or understory vegetation management, may improve seedling establishment success in regions with infrequent rainfall. Additionally, the timing of planting operations to coincide with periods of reliable precipitation may enhance survival and early growth. These considerations are particularly important in the context of climate change, when historical patterns of precipitation timing and frequency may no longer be reliable predictors of future conditions. In urban and industrial settings, the tolerance of *R. pseudoacacia* to dust deposition and its ability to benefit from moderate dust exposure make it a candidate species for pollution mitigation and urban greening programs. The species' rapid growth and nitrogen fixation capability can contribute to carbon sequestration and soil improvement, while its tolerance of atmospheric pollutants makes it suitable for planting along roadsides, in industrial areas, and in other locations where air quality is compromised. However, management considerations must also address the potential for *R. pseudoacacia* to become invasive and displace native vegetation in some contexts.

Future research directions

While recent research has significantly advanced our understanding of *R. pseudoacacia* responses to ecological stressors, several knowledge gaps remain that warrant further investigation. The studies reviewed here have primarily focused on seedling and young plant responses under controlled or semi-controlled conditions. Long-term studies examining mature tree responses under field conditions are needed to validate and extend these findings to operational scales. Additionally, the genetic basis of physiological plasticity in *R. pseudoacacia* remains poorly understood, and research in this area could inform breeding programs and provenance selection for specific applications. The interactive effects of multiple stressors represent a key priority for future research. Given that plants in natural environments typically experience multiple simultaneous stressors, multi-factor experiments that examine realistic combinations of ecological variables would provide valuable insights into the integrated responses of *R. pseudoacacia* to complex ecological conditions. Climate change projections indicate that many regions will experience simultaneous changes in precipitation patterns, temperature regimes, and nitrogen deposition rates. Research examining *R. pseudoacacia* responses to these combined changes, particularly under field conditions, would improve predictions of future species performance and distribution. Additionally, studies comparing responses among different provenances or genotypes could reveal adaptive variation that might be leveraged for climate-adapted planting programs. The identification of drought-tolerant or heat-tolerant genotypes would be particularly valuable for ensuring the success of restoration and afforestation projects under future climate conditions. Finally, the ecosystem-level consequences of *R. pseudoacacia* responses to ecological stressors deserve greater research attention. The species' ability to fix nitrogen has implications for soil nitrogen cycling, with potential effects on neighboring plants and soil microbial communities. Changes in nitrogen fixation rates under drought or high nitrogen deposition conditions could alter these ecosystem effects, with consequences for community composition and ecosystem functioning. Research examining these broader ecological implications would contribute to a more complete understanding of *R. pseudoacacia* in the context of global change.

Conclusion

This study has synthesized recent research findings on the ecophysiological responses of *R. pseudoacacia* to ecological stressors including water availability, nitrogen deposition, and atmospheric dust pollution. The collective evidence demonstrates that *R. pseudoacacia* possesses remarkable physiological plasticity that enables it to adjust its morphology, physiology, and resource allocation in response to varying ecological conditions. Key findings include the greater sensitivity of seedlings to rainfall frequency than to rainfall intensity, the ability to maintain consistent growth across varying nitrogen supply levels through rapid nitrogen fixation regulation, and the unexpected enhancement of photosystem II efficiency under moderate dust deposition conditions. The adaptive significance of these response patterns extends beyond individual plant performance to influence population dynamics, community interactions, and ecosystem processes. The nitrogen fixation capability of *R. pseudoacacia* provides competitive advantages in nutrient-poor environments and contributes to soil development on degraded sites, while the species' tolerance of atmospheric pollutants makes it suitable for urban and industrial applications. However, the sensitivity to rainfall frequency and the inhibition of nitrogen fixation under combined water and nitrogen stress highlight potential vulnerabilities that may become increasingly relevant under future climate scenarios. The practical implications of these findings for forest management, restoration ecology, and urban forestry are substantial. Understanding the conditions under which *R. pseudoacacia* performs optimally, and the stressors to which it is most sensitive, can inform decisions about species selection, planting timing, and site preparation for afforestation and restoration projects. The species' ability to thrive under challenging ecological conditions makes it valuable for specific applications, while its potential for invasiveness requires careful management consideration in regions where it is not native. Future research should address key knowledge gaps, particularly regarding long-term responses of mature trees under field conditions, the genetic basis of physiological plasticity, and the interactive effects of multiple simultaneous stressors. Multi-factor experiments examining realistic combinations of ecological variables would provide valuable insights for predicting *R. pseudoacacia* performance under future climate conditions. Additionally, research on ecosystem-level consequences of species responses to ecological change would contribute to a more complete understanding of the ecological implications of *R. pseudoacacia* in changing environments.

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