

Genomic Insights into *Robinia pseudoacacia*: Implications for Silviculture and Beyond

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Abstract *Robinia pseudoacacia*, commonly known as black locust, is a versatile tree species valued for its rapid growth, nitrogen-fixing ability, and high-quality timber. This study explores the genomic insights uncovered in recent years, providing a comprehensive understanding of the genetic composition and functional genomics of this species. Advances in next-generation sequencing technologies have facilitated the assembly of the black locust genome, revealing key genes and pathways involved in its growth, development, and stress responses. These insights are crucial for improving silvicultural practices, enabling the development of improved varieties with higher growth rates, better wood quality, and increased resistance to pests and diseases. Understanding the genomic basis of nitrogen fixation in *R. pseudoacacia* can lead to the development of more efficient agroforestry systems, contributing to sustainable agriculture and soil improvement. This study also explores the potential of genetic modification and biotechnological approaches to further enhance the desirable traits of black locust, paving the way for its expanded use in various applications, including bioenergy production and ecological restoration. Overall, integrating genomic data with traditional breeding and silvicultural techniques holds great promise for optimizing the utilization of *R. pseudoacacia*, addressing both economic and environmental challenges.

Keywords Genomic insights; *Robinia pseudoacacia*; Silviculture; Nitrogen fixation next-generation sequencing

1 Introduction

Robinia pseudoacacia L., commonly known as black locust, is a tree species of significant economic and ecological importance. Native to North America, it has been widely planted across the globe for various purposes, including timber production, honey production, and soil improvement. Its adaptability to different environmental conditions and its ability to improve soil fertility through nitrogen fixation make it a valuable species in forestry and agroforestry systems (Malvolti et al., 2015; Dong et al., 2019).

The black locust has been extensively utilized in silviculture due to its rapid growth and resilience. In regions such as Hungary, it plays a crucial role in forest management, where superior clones are selected for plantations on varying quality sites (Malvolti et al., 2015). The species' ability to thrive in diverse environments and its utility in biomass production underscore its significance. Additionally, the genetic diversity within black locust cultivars is essential for maintaining the health and productivity of plantations. Molecular markers, such as SSR (Simple Sequence Repeat) markers, have been employed to assess and conserve this genetic diversity, ensuring the sustainability of black locust populations.

This study aims to synthesize the current genomic insights into *Robinia pseudoacacia*. It will assess the genetic diversity and population structure of *Robinia pseudoacacia* in different provenances and breeding programs; explore the symbiotic relationship between *Robinia pseudoacacia* and its associated rhizobia, focusing on the genetic basis of these interactions; and explore the epigenetic variation of *Robinia pseudoacacia*, especially DNA methylation patterns, and its effects on gene expression and plant development. A comprehensive understanding of the genetic and epigenetic mechanisms behind the adaptability and resilience of this species is of great significance for its conservation, breeding and sustainable management, providing information for forestry practices and enhancing understanding of the potential of *Robinia pseudoacacia* beyond traditional forestry applications.

2 Genomic Characteristics of *Robinia pseudoacacia*

2.1 Genome structure and organization

Robinia pseudoacacia, commonly known as black locust, exhibits a typical chloroplast genome structure that includes two single copy regions (large and small single copy sections) and a pair of inverted repeats (IRs). The genome sizes range from 155 364 bp to 155 655 bp, with variations observed among different varieties (Yu et al., 2019). The chloroplast genomes contain 124~130 protein-coding genes, with some genes containing introns, such as the *rpoC1* gene with the longest introns at 2 828 bp. Additionally, the genome-wide pattern of DNA methylation in *R. pseudoacacia* reveals significant methylation in CG, CHG, and CHH contexts, with intergenic regions showing the highest methylation levels (Zhang et al., 2021).

2.2 Gene content and functional annotation

The gene content of *R. pseudoacacia* includes a variety of functional genes, with a significant number of simple sequence repeats (SSRs) identified. A study identified 170 SSR loci distributed in 162 non-redundant sequences, with dinucleotide repeats being the most predominant (Dong et al., 2019). Furthermore, the development of EST-SSR markers has facilitated the genetic diversity analysis and DNA fingerprinting of *R. pseudoacacia* cultivars, revealing a high level of polymorphism and genetic differentiation among different cultivars. The functional annotation of these genes indicates their involvement in various biological processes, including catalytic activity, metabolic processes, and cellular processes (Zhang et al., 2021).

2.3 Comparative genomics with related species

Comparative genomic analysis of *R. pseudoacacia* with related species such as *Sophora japonica* has highlighted the superior performance of *R. pseudoacacia* in terms of functional traits. *R. pseudoacacia* exhibits greater photosynthetic capacity, higher leaf nitrogen concentration, and lower carbon-to-nitrogen ratio compared to *S. japonica*, which contributes to its superior ecological strategies and invasive potential (Luo et al., 2016). Additionally, phylogenetic analysis using chloroplast genomes has shown that *R. pseudoacacia* is closely related to *Lotus japonicus*, while being more distantly related to *Acacia ligulata*. This comparative analysis provides insights into the evolutionary relationships and adaptive traits of *R. pseudoacacia*, which are crucial for its management and utilization in silviculture.

3 Evolutionary History and Genetic Diversity

3.1 Phylogenetic relationships

Robinia pseudoacacia, commonly known as black locust, has been the subject of various phylogenetic studies to understand its evolutionary relationships. Research has shown that the symbiotic genes of *R. pseudoacacia* rhizobia, derived from different geographical regions such as Poland and Japan, exhibit significant sequence conservation. This suggests that the symbiotic apparatus of *R. pseudoacacia* rhizobia might have evolved under strong host plant constraints, indicating a vertical transmission of these genes (Mierzwa et al., 2010). Additionally, studies on the phylogenetic structure of *R. pseudoacacia* forests in the Loess Plateau, China, have highlighted the influence of habitat on phylogeny, showing that species richness is closely correlated with phylogenetic diversity (Zhao et al., 2020).

3.2 Population genetics and genetic variation

The genetic diversity and population structure of *R. pseudoacacia* have been extensively studied using various molecular markers. For instance, simple sequence repeat (SSR) markers have revealed vast genetic differentiation among different populations in China (Figure 1), with an average of 8.352 alleles per locus and a mean Shannon's index of 1.302. This study also found that 93% of the genetic variation was within collection sites, while 7% was among sites, indicating a high level of genetic diversity within populations (Guo et al., 2021). Similarly, inter-simple sequence repeat (ISSR) markers have shown that genetic differentiation among populations is relatively small, whereas within populations it is greater, suggesting a high level of genetic diversity at the species level.

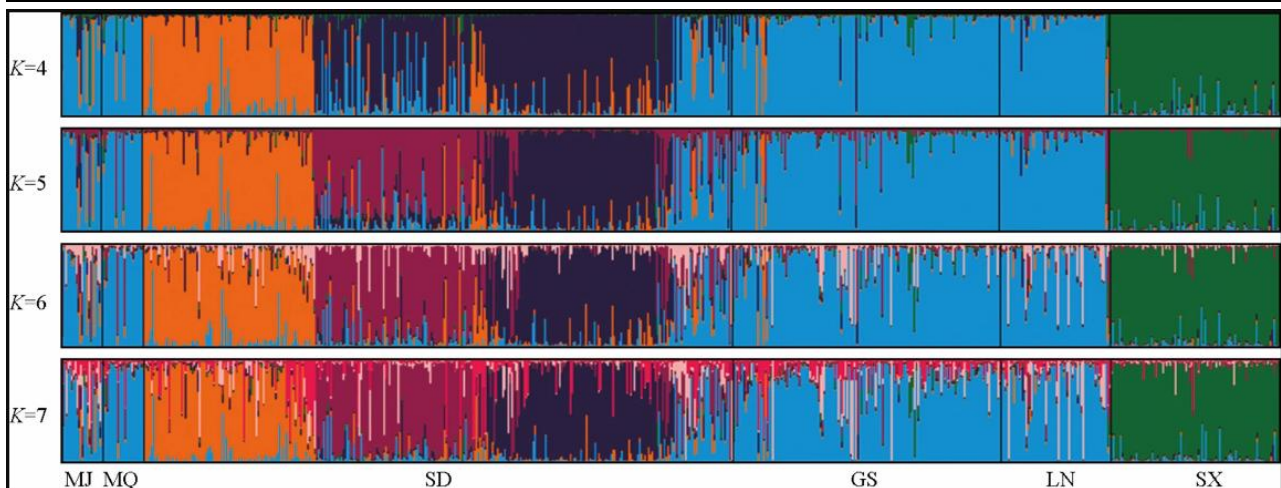


Figure 1 Genetic diversity and population structure of *Robinia pseudoacacia* from six improved variety bases in China as revealed by simple sequence repeat markers (Adopted from Guo et al., 2021)

Image caption: Genetic structure of black locust populations in China ($K=4-7$). Each individual is shown as a vertical line partitioned into K colored segments whose length is proportional to the individual coefficients of membership in $K=4-K=7$ genetic clusters that represent the populations assessed. The populations from left to right in the above figure are MJ (Mengjin), MQ (Minquan), SD (Shandong), GS (Gansu), LN (Liaoning) and SX (Shanxi), respectively. And among them, MJ and MQ belong to HN (Henan Province) (Adopted from Guo et al., 2021)

Guo et al. (2021) used simple sequence repeat markers to analyze population genetics and genetic variation, showing the genetic diversity and population structure of *Robinia pseudoacacia* populations in six different elite variety bases in China, ranging from $K=4$ to $K=7$. Under different genetic clusters, each individual is divided into segments of different colors by vertical lines, indicating the proportion of individual membership coefficients in different genetic clusters. As the K value increases, the genetic structure of the population shows higher complexity, especially the Shandong and Gansu populations, which show significant genetic mixing and differentiation. This demonstrates significant genetic variation and differentiation across geographic locations in the black locust population, highlighting the potential impact of gene flow on population structure.

Studies on the genetic diversity of *R. pseudoacacia* from different provenances have shown significant variation in phenotypic and physiological traits. For example, the Kentucky provenance exhibited the largest coefficient of variation, indicating high genetic variation among and within provenances, which is useful for breeding programs (Guo et al., 2022). Another study using allozymes found that the genetic distance among provenances in Europe and America was not significantly different, suggesting that *R. pseudoacacia* has maintained high genetic diversity across its range (Yang et al., 2004).

3.3 Historical biogeography and migration patterns

The historical biogeography and migration patterns of *R. pseudoacacia* have been influenced by both natural and anthropogenic factors. In Japan, the invasive nature of *R. pseudoacacia* has been studied to understand its migration patterns. It was found that both sympatric and allopatric dispersals were active, with younger individuals being more prevalent in low-water channel areas, indicating recent migration events (Yaegashi et al., 2020). This suggests that effective management strategies should focus on regular removal of migrants to control the spread of this invasive species.

In China, the introduction of *R. pseudoacacia* has enhanced the heterogeneity of understory environments, providing migration opportunities for various species and playing a crucial role in maintaining and increasing biodiversity (Zhao et al., 2020). Additionally, the genetic diversity of *R. pseudoacacia* in China has been shaped by the introduction of different varieties and provenances, which has contributed to its widespread distribution and adaptation to various environmental conditions. Overall, the evolutionary history and genetic diversity of *R. pseudoacacia* highlight its adaptability and resilience, making it a valuable species for silviculture and

conservation efforts. Understanding its phylogenetic relationships, population genetics, and historical biogeography can provide insights into its management and sustainable development.

4 Genomic Insights into Key Biological Traits

4.1 Growth and development

The growth and development of legumes, particularly in the context of symbiotic nitrogen fixation (SNF), have been significantly advanced through genomic studies. The complete genome sequences of rhizobial microsymbionts such as *Mesorhizobium loti* and *Sinorhizobium meliloti* have provided a comprehensive gene inventory that is crucial for understanding the genetic basis of root nodule formation and nitrogen fixation (Weidner et al., 2003). Additionally, the identification of nearly 200 genes required for SNF in legumes like *Medicago truncatula* and *Lotus japonicus* has shed light on the complex genetic networks involved in nodule development and function (Roy et al., 2019). These discoveries have not only enhanced our understanding of plant-microbe interactions but also paved the way for the development of high-yielding legume cultivars with improved growth traits (Dwivedi et al., 2015).

4.2 Stress responses and adaptation

Stress responses and adaptation mechanisms in legumes are critical for optimizing SNF under various environmental conditions. Genetic differences in stress tolerance have been identified in both host plants and rhizobia, which are essential for enhancing SNF efficiency. Advances in genomics have facilitated the identification of quantitative trait loci (QTL) and candidate genes associated with stress adaptation, enabling the breeding of legume cultivars that can withstand multiple stresses (Dwivedi et al., 2015). Moreover, the use of computational models based on metabolic reconstruction pathways has provided deeper insights into genotype-phenotype relationships, helping researchers to quantify SNF and identify bottlenecks in specific legume-rhizobia systems.

4.3 Nitrogen fixation and symbiotic interactions

Symbiotic nitrogen fixation is a complex trait governed by multiple genes with varying effects. The complete genome sequences of several rhizobium species and the identification of SNP markers from nodulation genes have been instrumental in understanding the genetic basis of SNF. The discovery of nearly 200 genes required for SNF has advanced our knowledge of the evolution of this trait and its relationship to other beneficial endosymbioses (Roy et al., 2020). Furthermore, the identification of genes involved in the very early steps of root nodule organogenesis has provided crucial insights into the molecular mechanisms underlying symbiotic interactions. These genomic insights are essential for developing legume cultivars with high symbiotic efficiency, thereby enhancing agricultural productivity and sustainability.

5 Applications in Silviculture

5.1 Breeding strategies and genetic improvement

Robinia pseudoacacia exhibits significant genetic variation among and within provenances, which is beneficial for breeding programs aimed at improving various traits such as ornamental value, food value, and stress resistance (Guo et al., 2022). The high genetic diversity and population structure revealed by simple sequence repeat markers further support the potential for genetic improvement and conservation efforts (Guo et al., 2021). Additionally, the influence of seed geographic provenance and germination treatments on seedling characteristics highlights the importance of selecting high-quality reproductive material for afforestation and breeding programs (Roman et al., 2022).

5.2 Pest and disease resistance

The ability of *Robinia pseudoacacia* to form symbiotic relationships with nitrogen-fixing bacteria, such as *Mesorhizobium* and *Sinorhizobium* species, enhances its resilience and adaptability in various environments (Wei et al., 2009). This symbiotic relationship not only improves soil fertility but also contributes to the plant's overall health and resistance to pests and diseases. Moreover, the genetic diversity within *R. pseudoacacia* populations can be leveraged to select and breed individuals with enhanced resistance to specific pests and diseases, thereby improving the overall health and productivity of plantations.

5.3 Enhancing wood quality and biomass production

Robinia pseudoacacia is recognized for its potential in biomass production, particularly in marginal lands and post-mining landscapes where other species may struggle to thrive (Grünwald et al., 2009). The species' drought tolerance and nitrogen-fixing ability make it a suitable candidate for short-rotation coppice cultivation, which can yield substantial biomass for energy production. Additionally, mixed cropping with *R. pseudoacacia* has been shown to influence wood chemistry, anatomy, and gene expression in co-cultivated species, potentially enhancing wood quality and biomass production (Euring et al., 2020). The superior performance of *R. pseudoacacia* in terms of total biomass and functional traits compared to native species further underscores its value in biomass production (Luo et al., 2016).

6 Beyond Silviculture: Environmental and Economic Implications

6.1 Role in ecosystem services

Robinia pseudoacacia, commonly known as black locust, plays a significant role in ecosystem services, particularly through its symbiotic relationships with nitrogen-fixing bacteria. The species is nodulated by *Mesorhizobium* and *Sinorhizobium* species, which share similar nodulation genes with native American symbionts. This symbiotic relationship enhances soil fertility by fixing atmospheric nitrogen, thereby improving soil quality and promoting the growth of other plant species in the ecosystem (Wei et al., 2009). Additionally, the genetic diversity and adaptability of *R. pseudoacacia*, as revealed by simple sequence repeat markers, suggest that it can thrive in various environmental conditions, further contributing to ecosystem resilience and biodiversity.

6.2 Potential for bioenergy and bioproducts

R. pseudoacacia has significant potential for bioenergy and bioproducts due to its fast growth rate and high biomass production. The species' ability to fix nitrogen not only improves soil fertility but also reduces the need for synthetic fertilizers, making it an environmentally sustainable option for bioenergy production. The genetic diversity within *R. pseudoacacia* populations, as indicated by the presence of multiple alleles per locus and high Shannon's index values, suggests that selective breeding programs could enhance traits desirable for bioenergy production, such as increased biomass yield and stress tolerance. This genetic variability provides a robust foundation for developing high-yielding varieties tailored for bioenergy applications.

6.3 Economic value and market potential

The economic value of *R. pseudoacacia* extends beyond its ecological benefits. Its wood is highly valued for its durability and resistance to decay, making it suitable for various applications, including furniture, flooring, and construction. The genetic diversity and population structure studies of *R. pseudoacacia* in China highlight the potential for breeding programs to develop improved varieties with enhanced wood quality and growth characteristics (Guo et al., 2021). Furthermore, the species' role in improving soil fertility and supporting sustainable agriculture can lead to increased agricultural productivity and economic benefits for farmers. The market potential for *R. pseudoacacia*-derived products, including bioenergy, timber, and other bioproducts, is substantial, offering opportunities for economic development and job creation in rural areas.

7 Future Directions in *Robinia pseudoacacia* Genomics

7.1 Emerging genomic technologies

The advancement of genomic technologies presents new opportunities for the study of *Robinia pseudoacacia*. High-resolution mapping of DNA methylation, as demonstrated in recent studies, reveals significant epigenetic variation between sexual and asexual progenies, which can influence gene expression and plant development (Zhang et al., 2021). Whole-genome bisulfite sequencing and other next-generation sequencing technologies can be further utilized to explore the epigenetic mechanisms underlying the adaptability and resilience of *R. pseudoacacia* in various environments. Additionally, the use of simple sequence repeat (SSR) markers has already provided insights into the genetic diversity and population structure of *R. pseudoacacia*. Future research should focus on integrating these genomic tools to develop a comprehensive understanding of the genetic and epigenetic factors that contribute to the species' invasive potential and ecological impact.

7.2 Integrative approaches in genomic research

Integrative approaches that combine genomic, transcriptomic, and phenotypic data are essential for a holistic understanding of *Robinia pseudoacacia*. For instance, the study of functional traits and their plasticity under different environmental conditions has highlighted the superior performance of *R. pseudoacacia* compared to native species (Luo et al., 2016). By integrating genomic data with functional trait analysis, researchers can identify key genes and regulatory networks that drive these adaptive traits. Moreover, the symbiotic relationships between *R. pseudoacacia* and nitrogen-fixing bacteria, such as *Mesorhizobium* and *Sinorhizobium* species, can be further explored through metagenomic and metatranscriptomic approaches to understand the genetic basis of these interactions and their ecological implications. Such integrative studies will provide valuable insights for breeding programs aimed at enhancing the beneficial traits of *R. pseudoacacia* while mitigating its invasive characteristics.

7.3 Long-term conservation and sustainable utilization

The long-term conservation and sustainable utilization of *Robinia pseudoacacia* require a multifaceted approach that incorporates genomic insights. Understanding the genetic diversity and population structure of *R. pseudoacacia* is crucial for developing effective conservation strategies. Additionally, the role of DNA methylation in regulating gene expression and plant development can inform breeding programs aimed at producing resilient and high-performing varieties. Sustainable management practices should also consider the ecological impacts of *R. pseudoacacia* afforestation, such as its effects on soil erosion control and plant community structure (Hu et al., 2021). By integrating genomic data with ecological and functional trait studies, researchers can develop management frameworks that balance the ecological benefits and potential risks associated with *R. pseudoacacia* plantations. Furthermore, the use of endophytes and biochar to enhance the phytoremediation capabilities of *R. pseudoacacia* highlights the potential for innovative biotechnological applications in environmental management (Kalmykova et al., 2022).

8 Concluding Remarks

This study has explored the genomic landscape of *Robinia pseudoacacia*, offering detailed insights into its genetic makeup and functional traits that contribute to its ecological and economic value. Our analysis revealed several key findings: Firstly, the genetic basis of *R. pseudoacacia*'s rapid growth and nitrogen-fixing ability provides potential avenues for enhancing these traits through selective breeding programs. Secondly, the resilience of *R. pseudoacacia* to environmental stresses such as drought and poor soil conditions is underpinned by specific genes, which could be targeted to improve the survivability of other forest species in harsh environments. Thirdly, the invasive potential of *R. pseudoacacia*, driven by its robust genomic attributes, highlights the need for careful management strategies in non-native regions to prevent ecological imbalances.

The genomic insights gained from this review have profound implications for both research and practical applications in silviculture and ecological management. For researchers, the identified genes associated with growth and stress resistance can serve as focal points for further genetic studies and cross-species comparisons. This could lead to breakthroughs in forest tree breeding that prioritize ecological resilience and productivity. For practitioners, understanding the genomic drivers of *R. pseudoacacia*'s characteristics informs better management practices, particularly in controlling its spread in non-native areas while harnessing its benefits for soil improvement and reforestation projects.

The genomic examination of *Robinia pseudoacacia* provides valuable insights that bridge fundamental biological research with tangible applications in forestry and environmental management. As we continue to face global challenges such as climate change and habitat degradation, the findings from this review underscore the importance of leveraging genomic science to foster sustainable forestry practices. It is crucial that future research continues to expand on the genetic knowledge base of *R. pseudoacacia*, ensuring that its cultivation and management are guided by scientific evidence aimed at maximizing its ecological benefits while minimizing potential harms. Through such integrated approaches, the potential of *R. pseudoacacia* as a beneficial yet manageable forest resource can be fully realized, contributing to more resilient forest ecosystems worldwide.

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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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