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Breeding Advances of *Metasequoia glyptostroboides* for Stress Tolerance and Ecological Restoration

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Abstract This study summarizes the new progress of *Metasequoia glyptostroboides* in stress-resistant breeding and ecological restoration. Research has found that *Metasequoia glyptostroboides* has a high genetic diversity, providing a rich basis for stress resistance improvement. The use of natural or synthetic superabsorbent polymers can enhance the drought resistance and salt tolerance of *Metasequoia glyptostroboides* seedlings, as well as improve their growth and physiological conditions. The root system of *Metasequoia glyptostroboides* is highly malleable and can adapt to both aquatic and terrestrial environments, which makes it more ecologically adaptable. With the assistance of ectomycorrhizal fungi and rhizogenic bacteria, the ability of *Metasequoia glyptostroboides* to resist salt stress can be further enhanced. Efficient tissue culture and rapid propagation techniques have provided technical support for the protection of *Metasequoia glyptostroboides* germplasm resources and large-scale ecological restoration. This study aims to provide theoretical and practical references for the stress resistance improvement and ecological restoration utilization of *Metasequoia glyptostroboides*.

Keywords Metasequoia glyptostroboides; Stress resistance breeding; Ecological restoration; Root plasticity; Biological measures

1 Introduction

Metasequoia glyptostroboides, also known as "living fossils", is a world-renowned relict tree species. It is native to central China and has now been widely introduced to all over the world. Because of its unique evolutionary history and scarcity, it holds high value in botanical and ecological research. Metasequoia glyptostroboides can grow both in water and on land. The morphology and function of its root system vary greatly, which enables it to adapt to different ecological environments (Yang et al., 2019).

Metasequoia glyptostroboides plays many roles in the ecosystem. It can serve as a carbon sink, helping to protect biodiversity, and is often used as a pioneer tree species in ecological restoration projects. Guo et al. (2025) demonstrated that Metasequoia glyptostroboides can improve soil structure, increase organic carbon accumulation, and enhance the stability and resilience of ecosystems. Its genetic diversity and adaptability provide guarantees for its survival under climate change and human interference (Chen et al., 2020; Li et al., 2025a). However, the natural renewal capacity is not strong, and the seed vitality and germination rate have declined. This indicates that strengthening protection and artificial breeding is extremely urgent (Li et al., 2012; Shen et al., 2024).

This study summarizes the latest progress of *Metasequoia glyptostroboides* in stress resistance breeding and ecological restoration in recent years, analyzes its physiological responses and molecular regulatory mechanisms under adverse conditions such as salinization and drought, assesses the effects of different breeding and propagation techniques on enhancing the stress resistance and adaptability of *Metasequoia glyptostroboides*, explores its role in ecological restoration and carbon sink functions, and proposes future development directions. This study aims to provide theoretical basis and practical reference for the protection, sustainable utilization and ecological restoration promotion of *Metasequoia glyptostroboides*.

2 Biological and Ecological Characteristics of M. glyptostroboides

2.1 Taxonomy, morphology, and growth traits

Metasequoia glyptostroboides is a rare deciduous coniferous tree and is often referred to as a "living fossil". Its



trunk is tall and straight, and its bark is reddish-brown. The leaves are opposite and linear, and turn orange-yellow in autumn. *Metasequoia glyptostroboides* grows very fast and can reach over 30 meters within 50 years, with the highest reaching more than 50 meters. Seeds of different sources grow at very different rates in the same environment, and this difference can persist for many years. Its form is also highly malleable, capable of growing in water as well as surviving on land. Fine roots exhibit significant anatomical and physiological changes in different environments, which endows them with excellent environmental adaptability (Williams, 2005; Yang et al., 2019).

2.2 Natural distribution and ecological functions

Metasequoia glyptostroboides is native to central China. Currently, its wild distribution is very narrow, mainly concentrated in a small area at the junction of Lichuan, Hubei Province, Longshan, Hunan Province and Shizhu, Chongqing City, covering an area of approximately 800 to 1 000 square kilometers, with an altitude ranging from 800 to 1 500 meters. It prefers subtropical monsoon climate and humid river valley areas. Although its natural distribution is limited, Metasequoia glyptostroboides has now been widely cultivated in temperate regions around the world through artificial introduction. It plays a very important role in ecology and is commonly found in riverbank areas and urban greening. Metasequoia glyptostroboides can improve the physical and chemical properties of soil, promote the diversity of soil microorganisms, and accelerate the cycling of soil nutrients. In mixed forests, it can significantly increase the available phosphorus content and fungal diversity in the soil. In addition, Metasequoia glyptostroboides releases a relatively large amount of volatile organic compounds, such as α -pinene, which can affect urban air quality and ecosystem functions (Juvik et al., 2015; Zhang et al., 2020; Zhang et al., 2021; Ahn et al., 2022; Li et al., 2025b).

2.3 Genetic diversity and conservation status

Metasequoia glyptostroboides is currently regarded as critically endangered species. The wild population is very small, with less than 6 000 mother trees. Natural renewal is very difficult. The reasons include the self-toxic effect of fallen leaves and the interference of human activities. Genetic research shows that there are certain genetic differences between wild populations and introduced populations, but the overall genetic diversity is still relatively high. Intra-group variation accounts for the majority, but in some groups, inbreeding exists. Climate change and habitat fragmentation have intensified its survival pressure, and the suitable distribution area is constantly shrinking. Now, Metasequoia glyptostroboides has been listed as a critically endangered species by IUCN and a first-class protected plant in China. Protective measures include establishing nature reserves, artificial breeding and global introduction and cultivation (Figure 1). However, there are still significant challenges in native conservation and genetic resource preservation (Zhang et al., 2020; Zhao et al., 2020; Xu et al., 2022; Li et al., 2025a; Li et al., 2025b).

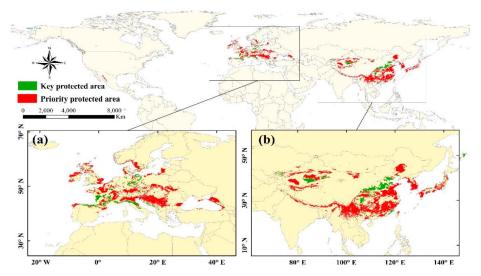


Figure 1 Identification of the priority protected areas and the key protected areas of *M. glyptostroboides*, which are mainly in Europe (a) and in East Asia (b) (Adopted from Zhang et al., 2020)



3 Stress Factors Affecting M. glyptostroboides

3.1 Abiotic stresses: drought, salinity, temperature extremes, flooding

Drought and salinization can slow down plant growth, damage leaves, and also affect photosynthesis and water use efficiency. Research has found that whether it is drought or salinization alone, or both occurring together, they will significantly inhibit the growth and physiological activity of *Metasequoia glyptostroboides* seedlings. However, if some synthetic or natural super absorbent polymers, such as konjac glucomannan, are added to the soil, this pressure can be effectively alleviated, helping plants improve stress resistance and better growth performance (Li et al., 2018; Kong et al., 2022). Extreme temperatures also have a significant impact on the seed germination and seedling survival of *Metasequoia glyptostroboides*. The germination rate will significantly decrease at both 5°C and 35°C. Fan et al. (2020) hold that spring drought will significantly reduce the survival rate of seedlings, which is the main factor restricting the natural distribution and renewal of *Metasequoia glyptostroboides*. *Metasequoia glyptostroboides* has a certain adaptability in waterlogging conditions. Yang et al. (2019) demonstrated in their research that its fine roots can undergo significant structural changes, such as the formation of cortical ventilation tissue or lignification and thickening, which is beneficial for its adaptation to both aquatic and terrestrial environments.

3.2 Biotic stresses: pests and diseases

In its native habitat and artificial forests, *Metasequoia glyptostroboides* is also threatened by various pathogenic fungi. Studies have shown that the combined infection of pathogens such as *Fusarium* spp., *Neocosmospora* spp. and *Phytophthora acerina* is an important cause of metasalopecia glyptostroboides decline and death. This kind of disease is particularly serious in the protective forests of the Yangtze River Basin. If multiple pathogenic bacteria occur simultaneously, the severity of the disease will be more severe, which will have a significant impact on the growth and ecological functions of *Metasequoia glyptostroboides* (Liu et al., 2024). In addition, the litter of *Metasequoia glyptostroboides* forests has a self-toxic effect, which can inhibit seed germination and seedling growth and hinder natural renewal (Xu et al., 2022).

3.3 Climate change implications for survival and adaptation

Climate warming and human activities have also led to the continuous shrinking and migration of the suitable areas for *Metasequoia glyptostroboides*. Over the past 50 years, the average annual temperature and extreme temperature in the distribution area of *Metasequoia glyptostroboides* have increased significantly. The area of the suitable zone has decreased at a rate of approximately 370.8 km² per decade, and the altitude range of the distribution has gradually declined (Zhao et al., 2020). Future climate model predictions show that precipitation in dry months, diurnal temperature differences, and human activity footprints are the main factors determining the expansion or contraction of *Metasequoia glyptostroboides* habitats (Li et al., 2025b). Climate warming has also altered the phenological period of *Metasequoia glyptostroboides*, advancing and prolonging the growing season. However, it has also continued to compress the suitable growth area, intensifying the risk of endangerment (Zhao et al., 2020). The superimposition of climate change and habitat fragmentation has made the degradation and renewal obstacles of *Metasequoia glyptostuca* populations even more serious (Tang et al., 2011; Li et al., 2025b).

4 Traditional Breeding Approaches for Stress Tolerance

4.1 Germplasm collection and selection of superior individuals

The collection of germplasm resources and the assessment of genetic diversity are the basis for *Metasequoia glyptostroboides*' stress-resistant breeding. Li et al. (2025a) demonstrated that after introduction, the population had a relatively high genetic diversity at the species level (He = 0.640), with little difference between the mother trees and the seedlings. This indicates that there are still many excellent genotypes available for utilization in the population, which is helpful for the screening and improvement of stress resistance traits. Chen et al. (2020) found that the parents of *Metasequoia glyptostroboides* exhibit strong trait plasticity in different environments. For instance, leaf area and dry weight vary with environmental and human disturbances. These differences provide a basis for selecting individuals with strong stress resistance.



4.2 Provenance trials and performance evaluation under stress conditions

Through field tests and performance evaluations under different adverse conditions (such as saline-alkali, drought, flooding, etc.), *Metasequoia glyptostroboides* materials that are more adaptable to the environment can be screened out. Studies have found that the fine root structure of *Metasequoia glyptostroboides* has obvious plasticity. It can adapt to aquatic or terrestrial environments through the adjustment of anatomical structure, enhancing the adaptability to environmental pressure (Yang et al., 2019). Some functional traits, such as leaf dry matter content and specific leaf area, vary greatly under different terrains and disturbance conditions, which also reflects the stress adaptability of *Metasequoia glyptostroboides* (Chen et al., 2020).

4.3 Hybridization and clonal propagation for desired traits

In terms of breeding methods, hybrid breeding and asexual reproduction (such as cuttings and tissue culture) are important means to obtain and expand excellent stress-resistant genotypes. At present, the tissue culture and micropropagation system of *Metasequoia glyptostroboides* has been established. By optimizing the ratio of culture medium and hormones, the formation of buds and roots can be efficiently induced, thereby achieving rapid propagation of superior individuals (Xiong et al., 2019; Chornobrov et al., 2020). Xiong et al. 's research in 2024 also found that exogenous hormones and culture conditions can regulate the formation mechanism of adventite roots, which provides theoretical support for asexual reproduction and the improvement of stress-resistant traits.

5 Molecular and Genomic Breeding Advances

5.1 Development of molecular markers (SSR, SNP, AFLP) for trait mapping

Metasequoia glyptostroboides is a critically endangered species. The conservation of its genetic diversity and the selection and breeding of superior traits rely on molecular marker technology. Wang et al. (2020) demonstrated that high-throughput sequencing has developed 28 polymorphic SSR loci, with an average of approximately 8 alleles at each locus, enhancing the ability to distinguish genotypes in wild individuals and providing a fundamental tool for germplasm resource management and trait mapping. Li et al. (2025a) analyzed the introduced population using these polymorphic SSR markers and found that Metasequoia glyptostroboides had a relatively high genetic diversity at the species level (He = 0.640), and moderate differentiation among populations (Fst=0.117), indicating that molecular markers have significant value in genetic resource conservation and targeted breeding. However, at present, there are still few studies on SNP and AFLP in Metasequoia glyptostroboides, and further development is needed in the future.

5.2 Transcriptomic and genomic studies on stress-responsive genes

In recent years, transcriptomics has provided new ideas for revealing the molecular mechanism of *Metasequoia glyptostroboides*' stress resistance traits. Transcriptome and hormone analyses of adventite formation indicated that some differentially expressed genes (DEGs) were associated with hormone signal transduction and phenylpropanoid biosynthesis pathways, and 13 transcription factor families were found to be involved in regulation. This indicates that the interaction between hormones and gene expression is crucial for *Metasequoia glyptostroboides*' adaptation to adverse conditions and root development (Figure 2) (Xiong et al., 2024). Furthermore, the phenotypic study of root structure also found that *Metasequoia glyptostroboides* adapted to different aquatic and terrestrial environments through changes in fine root anatomical structure and chemical composition (such as the deposition of lignin and linolenic acid), suggesting that there is a large diversity and complex regulatory network of its stress-related genes (Yang et al., 2019).

5.3 Prospects of genomic selection and CRISPR/Cas-based editing in M. glyptostroboides

At present, there are no direct application reports of *Metasequoia glyptostroboides* genome selection (GS) and CRISPR/Cas gene editing. However, the existing molecular markers and transcriptome data provide a scientific basis for these cutting-edge technologies. Analysis of highly polymorphic SSR markers and population genetic structure provided parameters and candidate genes for genome selection (Wang et al., 2020; Li et al., 2025a). The stress-related genes and regulatory networks discovered in transcriptome studies also provide potential targets for gene editing (Xiong et al., 2024). In the future, with the advancement of *Metasequoia glyptostroboides* genome sequencing and functional gene annotation, genome selection and CRISPR/Cas technologies are expected to accelerate the breeding of new stress-resistant varieties and promote their application in ecological restoration.



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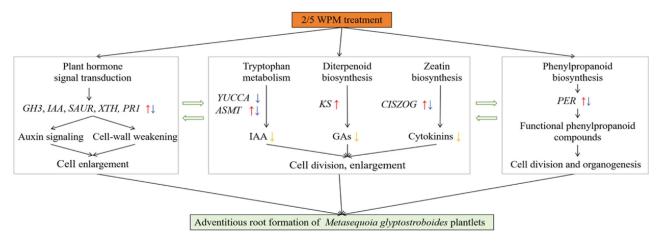


Figure 2 A possible network of AR-promoting potential of 2/5-strength WPM for *Metasequoia glyptostroboides* (Adopted from Xiong et al., 2024)

Image caption: Red arrows indicated up-regulated DEGs, and blue arrows indicated down-regulated DEGs. Green arrows indicated an interaction between the corresponding pathway. Orange arrows indicated the decrease in hormone accumulation. The complex interactions between hormones biosynthesis and the expression of genes related to plant hormone signal transduction and phenylpropanoid biosynthesis pathway contributed to the AR formation of *M. glyptostroboides* induced by 2/5-strength WPM under in vitro culture (Adopted from Xiong et al., 2024)

6 Role of M. glyptostroboides in Ecological Restoration

6.1 Applications in wetland, riparian, and urban ecosystems

Metasequoia glyptostroboides has strong adaptability to water environments and its root system shows phenotypic plasticity. It is often used in the restoration of wetlands, riverbanks and urban ecosystems. Yang et al. (2019) found that Metasequoia glyptostroboides can adapt to different habitats by adjusting the structure of its root system (such as forming cortical air cavities or lignification and thickening). This change gives it an advantage in survival and growth in wetlands and riverbank areas. In urban greening and mixed forest construction, Metasequoia glyptostroboides can also improve the physical and chemical properties of the soil. When mixed with other tree species (such as Bischofia polycarpa), it can significantly increase the diversity of soil fungi and archaea, and enhance the availability of phosphorus in the soil, which is helpful for slowing down soil degradation in urban forests (Zhang et al., 2021).

6.2 Contributions to biodiversity enhancement and carbon sequestration

Studies on the planting patterns in the lakeside zone have shown that the mixed planting of *Metasequoia glyptostroboides* and other plants can significantly increase soil organic carbon and carbon pool stability, thereby enhancing carbon fixation capacity (Guo et al., 2025). In coastal shelter forests, with the increase of forest age, the soil organic carbon storage of *Metasequoia glyptostroboides* plantations continues to rise, and soil nutrients are improved simultaneously, providing support for regional carbon sinks and ecosystem service functions. The introduction and cultivation of *Metasequoia glyptostroboides* can also increase regional plant diversity, improve habitat structure and promote the stability and restoration of the ecosystem (Tang et al., 2011; Zhang et al., 2021).

6.3 Integrating stress-tolerant breeding lines into restoration programs

The natural regeneration capacity of *Metasequoia glyptostroboides* is limited. One reason is the decline in population genetic diversity, and the other reason is the self-toxicity of litter (Li et al., 2012; Xu et al., 2022). Therefore, in ecological restoration projects, it is crucial to select breeding materials with strong stress resistance (such as salt-tolerant, flood-tolerant or infertile strains). The latest molecular breeding and tissue culture techniques can provide support for the large-scale propagation of *Metasequoia glyptostroboides* with strong stress resistance. This is conducive to breaking through the bottleneck of natural renewal and enhancing the population vitality and recovery effect (Xiong et al., 2019; Chornobrov et al., 2020; Li et al., 2025a). In addition, the rational intermixing of these stress-resistant strains with native plants can further enhance the stability and diversity of the ecosystem (Zhang et al., 2021; Guo et al., 2025).



7 Case Study: Breeding and Field Application of Stress-Tolerant *M. glyptostroboides* 7.1 Research background and breeding objectives

Metasequoia glyptostroboides is a rare relict tree species with strong adaptability and high ecological value. It is often used for ecological restoration and landscaping. However, it is prone to stress in drought and saline-alkali environments, so enhancing its stress resistance has become an important goal in breeding. The current research focus is on utilizing the genetic diversity of Metasequoia glyptostroboides to select and breed superior strains with better stress resistance for ecological restoration and sustainable utilization (Li et al., 2018; Kong et al., 2022; Li et al., 2025a).

7.2 Methods: germplasm evaluation, molecular tools, and field trials

The stress-resistant breeding of *Metasequoia glyptostroboides* has adopted a variety of methods. Li et al. (2025a) evaluated the genetic diversity of the introduced population by using multi-site SSR molecular markers. These data reveal the richness and population structure of germplasm resources, providing a reference for breeding. An efficient tissue culture and micropropagation system was established to rapidly propagate superior genotypes, solving the problem of low propagation efficiency of traditional methods (Xiong et al., 2019). In terms of enhancing stress resistance, Li et al. (2018) and Kong et al. (2022) also combined field and greenhouse experiments to test different treatment methods, such as inoculating growing-promoting bacteria and adding superabsorbent polymers, to observe their effects on the growth and physiological indicators of seedlings. Through root anatomy and physiological analysis, it was also found that *Metasequoia glyptostroboides* could show obvious phenotypic plasticity between the aquatic and terrestrial environments, providing an anatomical basis for studying its stress resistance mechanism (Yang et al., 2019).

7.3 Outcomes: improved lines, ecological benefits, and practical adoption

These methods have screened out many excellent drought-resistant and salt-tolerant varieties. In field applications, inoculation of growth promotive bacteria or addition of polymers can significantly increase the growth amount of seedlings, enhance the photosynthetic capacity of leaves and the activity of antioxidant enzymes, and also reduce the ionic toxicity caused by salt stress, thereby improving overall stress resistance (Li et al., 2018; Kong et al., 2022). The establishment of the micropropagation system has also enabled the large-scale promotion of superior strains, providing reliable seedlings for ecological restoration projects (Xiong et al., 2019). In practical restoration applications, these *Metasequoia glyptostroboides* have improved soil structure, increased vegetation coverage and ecosystem stability, and brought about good ecological and social benefits (Li et al., 2018; Kong et al., 2022; Li et al., 2025a).

8 Challenges and Limitations

8.1 Long lifecycle and delayed breeding outcomes

Metasequoia glyptostroboides is a long-lived tree with a long life cycle and a slow alternation of generations. This has led to very slow progress in the selection and breeding of new varieties and the improvement of their traits under traditional breeding methods. It often takes a long time from hybridization to stable traits, and thus it is difficult to respond quickly to environmental changes and adverse stress (Xiong et al., 2019; Li et al., 2025a).

8.2 Technical gaps in transformation and genome editing for woody species

At present, *Metasequoia glyptostroboides* and other woody plants all face many challenges in genetic transformation and gene editing. The efficient genetic transformation system is still not mature, the efficiency of gene editing is low, and the tissue culture and regeneration system is also unstable. These problems have severely restricted the progress of molecular breeding and precision improvement (Xiong et al., 2019). Although some breakthroughs have been made in in vitro rapid propagation technology, the genetic manipulation of woody plants is still more difficult compared with herbaceous crops.

8.3 Need for wider genetic resource exploration and international collaboration

The natural distribution range of *Metasequoia glyptostroboides* is very small, its genetic basis is relatively limited, and the diversity of existing breeding materials is insufficient. Although introduction and artificial cultivation have expanded the population distribution, the genetic differentiation among populations is not significant, and



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inbreeding problems still exist in some populations, which affects the potential of genetic improvement (Li et al., 2025a). Therefore, it is necessary to enhance the collection, evaluation and sharing of genetic resources on a global scale, promote international cooperation, enrich the basic materials for breeding, and improve the stress resistance and adaptability of *Metasequoia glyptostroboides*.

9 Future Perspectives

9.1 Integration of multi-omics for trait dissection and stress adaptation

The combination of multi-omics technologies such as genomics, transcriptomics, proteomics and metabolomics will become a powerful tool for studying the stress resistance of *Metasequoia glyptostroboides*. Yang et al. (2019) found that this tree has obvious phenotypic plasticity in different environments. For instance, its root structure and physiological characteristics will adjust with environmental changes, thereby helping it adapt to aquatic or terrestrial environments. Through multi-omics joint analysis, key genes, regulatory networks and metabolic pathways related to adverse conditions such as drought resistance and salt tolerance can be identified, providing a theoretical basis for precision breeding and molecular design (Li et al., 2018; Yang et al., 2019). Population genetics studies have shown that the genetic diversity within the population of *Metasequoia glyptostroboides* is relatively high, which creates conditions for in-depth multi-omics research and trait association analysis (Li et al., 2025a).

9.2 Combining conventional breeding with synthetic biology for accelerated improvement

In traditional breeding, such as the selection of superior individual plants and hybrid breeding, some achievements have been made in the improvement of the stress-resistant traits of *Metasequoia glyptostroboides*. However, due to its long generation cycle and complex genetic background, its progress has been relatively slow. The introduction of synthetic biology tools can significantly accelerate the improvement of target traits. The superior genotypes can be rapidly propagated and preserved by using tissue culture and micropropagation systems (Xiong et al., 2019). Exogenous stress resistance genes or regulatory elements can also be introduced into the target material to enhance its drought resistance or salt tolerance (Li et al., 2018; Kong et al., 2022). In the future, the combination of traditional breeding and synthetic biology is expected to more efficiently cultivate new stress-resistant varieties suitable for ecological restoration.

9.3 Role of policy and conservation programs in supporting breeding applications

Policies and conservation projects are also crucial for the stress-resistant breeding and ecological restoration of *Metasequoia glyptostroboides*. The research by Li et al. (2025a) indicates that protecting its genetic structure and diversity requires scientific management and policy guidance, as well as the formulation of differentiated protection and utilization plans. The ecological restoration and endangered species protection policies issued by the state and local authorities have provided guarantees for the promotion of stress-resistant species and the restoration of their habitats. Establishing germplasm resource banks, conducting population dynamic monitoring and implementing ecological compensation mechanisms are useful for enhancing the genetic diversity and adaptability of *Metasequoia glyptostroboides* and promoting its application in ecological restoration (Xiong et al., 2019; Li et al., 2025a).

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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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