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Major Diseases and Sustainable Management Strategies in Chinese Hickory (*Carya cathayensis)* Plantations

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Abstract Chinese hickory (*Carya cathayensis*) is an important perennial woody nut tree species in China. Under long-term intensive management, diseases affecting trunks and branches, leaves, roots, and the root collar have become important constraints on plantation health and stable production. This review summarizes current knowledge of the major diseases of Chinese hickory and advances in sustainable disease management. The principal disease problems include Botryosphaeriaceae-associated trunk canker and dry rot, anthracnose and leaf blight affecting aboveground tissues, as well as *Phytophthora*- and *Fusarium*-associated root rot, collar necrosis, and crown decline. Increasing evidence indicates greater pathogen diversity and a shift toward more complex disease syndromes. Long-term intensive management, soil acidification and nutrient imbalance, understory vegetation loss, rhizosphere microbial disturbance, and climatic stress may increase disease risk by weakening root function and tree vigor. Sustainable management should therefore integrate plantation sanitation, soil restoration and balanced fertilization, biological control and rhizosphere regulation, resistant rootstocks, early disease monitoring, and targeted fungicide application. Future research should strengthen disease-complex identification, long-term epidemiological monitoring, studies of disease-suppressive soils and beneficial microbiomes, and the transition from single-pathogen control toward integrated plantation health management.

Keywords Chinese hickory; Trunk canker; Root rot; Disease complex; Soil health; Rhizosphere microbiome; Sustainable disease management; Plantation health management

1 Introduction

Chinese hickory (*Carya cathayensis*) is a perennial woody nut and oil tree species endemic to China. It is mainly distributed and cultivated in the mountainous areas of eastern China, particularly in Zhejiang and Anhui provinces, with the Tianmu Mountain region along the Zhejiang-Anhui border representing a traditional production center. Its kernels are rich in lipids and contain high proportions of unsaturated fatty acids, including oleic, linoleic, and linolenic acids, which contribute to their nutritional, processing, and commercial value (Huang et al., 2022). With the continued development of processing, branding, and marketing systems, Chinese hickory has become an important specialty forest industry in some mountainous regions and contributes substantially to farm income and local mountain economies. Unlike annual crops, Chinese hickory plantations are expected to remain productive for many years or even decades. Once the trunk, scaffold branches, or root system is chronically damaged by disease, the effects may persist across multiple growing seasons.

As Chinese hickory production has gradually shifted toward more intensive management, practices such as long-term fertilization, repeated understory vegetation removal, and frequent soil-surface disturbance may improve short-term production efficiency while progressively altering soil physicochemical properties and the rhizosphere environment. With increasing years of management, soil pH in Chinese hickory plantations declines, nutrient and extracellular enzyme stoichiometry becomes increasingly imbalanced, and microbial carbon and phosphorus limitations are intensified (Huang et al., 2026). In addition to traditional aboveground diseases such as trunk canker, dry rot, anthracnose, and leaf blight, increasing attention is being paid to root rot, collar necrosis, shoot dieback, and crown decline. Disease development in perennial trees is generally determined by interactions

among pathogens, host condition, and environmental factors, while long-term management and climatic stress may further promote the transition of latent pathogens from low-level colonization to active pathogenicity.

Conventional disease management is generally based on visible symptoms and relies on the removal of diseased tissues, pruning, and fungicide treatments to reduce local pathogen pressure. However, this approach has important limitations for chronic trunk diseases and belowground diseases of perennial trees. Roots and internal woody tissues may already be damaged before obvious leaf yellowing, shoot dieback, or crown decline becomes visible, while similar symptoms of canker, root rot, and decline may involve different pathogens and multiple environmental triggers. For tree disease syndromes with multiple causal factors, the isolation of a single pathogen followed by a single inoculation test may be insufficient to fully explain disease development (Bonello, 2024). Although fungicides can suppress some pathogens, they cannot directly restore acidified soils, damaged root systems, or long-term declines in tree vigor. The persistence of soilborne pathogens also makes it difficult for a single chemical measure to provide stable, long-term control (López-García and Witzell, 2024).

Disease management in Chinese hickory therefore needs to shift gradually from reactive control after symptom appearance toward integrated management aimed at reducing disease risk and maintaining plantation health. The central principle is to combine plantation sanitation, soil and nutrient management, understory vegetation management, biological control, resistant germplasm and rootstocks, early monitoring, and targeted chemical intervention within a coordinated and hierarchical framework. Modern Integrated Disease Management emphasizes the combined use of cultural, biological, genetic, and chemical measures according to pathogen biology, host resistance, and environmental conditions, thereby reducing long-term dependence on any single control measure (Wilson et al., 2025). The concept of agroecological crop protection similarly emphasizes improving soil health, biodiversity, and ecological regulatory functions to reduce the ecological conditions that favor disease development at the production-system level (Deguine et al., 2023).

Against this background, this review focuses on the major diseases and sustainable management of Chinese hickory plantations. It summarizes the principal disease types, pathogen diversity, and epidemiological characteristics; examines the effects of long-term intensive management, soil degradation, rhizosphere microbial changes, and environmental stress on disease development; and systematically evaluates management strategies including plantation sanitation, soil restoration, biological control, resistant rootstocks, disease monitoring and early warning, and rational fungicide use. Future directions are further discussed, particularly the transition from single-pathogen diagnosis to disease-complex identification and from disease suppression to integrated plantation health management, with the aim of providing a basis for stable long-term production and sustainable management of Chinese hickory plantations.

2 Disease Spectrum and Epidemiological Characteristics of Chinese Hickory

2.1 Major disease types and affected plant organs

The major diseases currently reported in Chinese hickory plantations can be broadly classified into three groups: trunk and branch diseases, foliar diseases, and root-collar diseases. Among these, trunk canker and dry rot have the longest research history and have traditionally received the greatest attention in production. These diseases mainly affect the trunk and perennial branches, causing localized bark necrosis, expanding cankers, shoot weakening, and, in severe cases, death of entire branches. Early production-oriented studies long regarded dry rot as one of the most important diseases in the major Chinese hickory-producing regions. Subsequent pathological studies, however, gradually revealed that similar trunk canker symptoms may be associated with different members of the Botryosphaeriaceae. Accordingly, the disease concept has shifted from “one pathogen causing one canker disease” toward a more complex trunk disease system dominated by major pathogens but involving multiple associated species (Liu and Yu, 2017). Foliar diseases mainly include anthracnose, leaf spot, and leaf blight, which primarily damage leaves and young tissues and, under severe conditions, may lead to lesion coalescence, chlorosis, and premature defoliation. The third disease group affects belowground tissues and the root collar, including rot of fine roots, lateral roots, and major roots, as well as basal stem necrosis, and may subsequently result in leaf yellowing, wilting, shoot dieback, and crown decline.

These three disease groups differ in their significance for perennial Chinese hickory trees. Foliar diseases primarily reduce effective leaf area and photosynthetic function during the current growing season. Trunk and branch diseases damage perennial woody tissues and vascular structures, and their effects may persist over multiple growing seasons. Root and root-collar diseases are more cryptic because belowground damage often precedes obvious canopy symptoms and may therefore be mistaken in production for nutrient deficiency, drought stress, or general tree weakness.

2.2 Geographic distribution and disease occurrence in major production areas

Chinese hickory production is strongly concentrated geographically, with the traditional core production belt located in the Tianmu Mountain region along the Zhejiang-Anhui border. Lin'an in Zhejiang Province and Ningguo in Anhui Province are among the most representative areas of intensive cultivation. Following long-term commercial development, these core production areas have also become the regions in which disease studies and case reports are most concentrated. Chinese hickory plantations in the major production areas commonly face soil acidification, nutrient imbalance, soil erosion, and declining tree vigor under prolonged high-input management, together with increasing concerns over dry rot and root rot (Hu et al., 2021). Therefore, regional disease risk should not be assessed simply by comparing Zhejiang and Anhui on the basis of administrative boundaries. Plantation history, slope position, elevation, parent material, stand age, and drainage conditions should also be considered. Even within the same production region, baseline disease risk may differ substantially among plantations.

The suitable cultivation zones of Chinese hickory in Zhejiang are themselves characterized by pronounced environmental heterogeneity in mountainous landscapes. Temperature, precipitation, topography, and soil conditions jointly determine site suitability, and growing environments are far from uniform across regions. Such spatial heterogeneity may also influence disease expression. For example, humid valleys, poorly drained root zones, and exposed plantation slopes may experience different disease risks. However, the current literature on Chinese hickory diseases still shows clear sampling bias. A large proportion of pathogen studies have been conducted in Lin'an and a limited number of key townships, whereas Anhui and other production areas still lack multi-year disease incidence datasets generated using standardized survey methods.

2.3 Seasonal dynamics and environmental conditions favoring disease development

Trunk and branch diseases of Chinese hickory show relatively clear seasonal patterns. Early continuous observations indicated that symptoms of dry rot and canker generally begin to appear in late March and may persist until late November, while the pathogens can overwinter in diseased tissues (Yang et al., 2009). From a production perspective, this indicates a typical pattern of "pathogen overwintering-reactivation in spring-continued expansion during the growing season." Spring budbreak, resumption of tree growth, and increasing rainfall create an important observation window for disease development, while the risk of lesion expansion and pathogen spread increases under warm and humid conditions. In contrast, foliar anthracnose, leaf spot, and leaf blight are more closely associated with prolonged leaf wetness, and concentrated symptom development is more likely during periods of frequent rainfall and sustained high humidity within the canopy. Field monitoring should therefore distinguish among three stages: the onset of pathogen activity, the first appearance of visible symptoms, and periods of high transmission risk.

These seasonal patterns are broadly consistent with the climatic background of the major Chinese hickory-producing regions. Most Chinese hickory plantations in Lin'an are located in hilly and mountainous terrain, where mean annual precipitation is approximately 1,600 mm and is concentrated mainly from April to September; plantations also differ considerably in elevation, slope aspect, and soil type (Zhang et al., 2018a). Even within the same township, leaf-wetness duration, soil drainage rate, and root-zone moisture conditions may differ markedly among slope positions and canopy structures. For trunk and foliar diseases, particular attention should therefore be given to infection windows created by prolonged rainfall and high humidity. For root rot and collar necrosis, risk assessment should also consider soil moisture conditions, poor drainage, and root injury under high-temperature conditions.

2.4 Changes in disease patterns under long-term plantation management

Chinese hickory is a perennial economic tree crop, and plantations are continuously subjected to fertilization, weed control, harvesting, and other forms of human disturbance over long production cycles. Consequently, the soil environment does not remain stable over time. A long-term study in the same production region showed that after 26 years of intensive management, soil organic carbon in the surface and deeper soil layers declined by approximately 19% and 14%, respectively, while surface-soil pH decreased by an average of 0.7 units and total N, P, and K generally declined (Wu et al., 2014a). These changes indicate that long-term management can progressively alter the soil environment on which root function depends, thereby creating an ecological context for pathogen infection that differs substantially from that during the early stages of plantation development.

Larger-scale spatiotemporal surveys further indicate that these changes do not occur uniformly across all production areas. Monitoring of Chinese hickory plantations in Lin'an from 2008 to 2013 showed that soil pH declined from 5.5 to 5.3, while hydrolyzable nitrogen and available potassium decreased by 19.4 and 55.6 mg/kg, respectively. The magnitude of these changes differed among townships such as Daoshi and Qingliangfeng, and was influenced by elevation, parent rock, and management practices (Shen et al., 2016). Accordingly, the conceptual understanding of Chinese hickory health problems is gradually shifting from that of isolated diseases toward a plantation decline syndrome, in which pathogens, the root-zone environment, soil degradation, and long-term changes in tree vigor need to be interpreted within the same plantation-scale framework.

3 Major Aboveground Diseases of Chinese Hickory

3.1 Trunk canker and dry rot: botryosphaeriaceae-centered trunk and branch diseases

Trunk canker and dry rot are currently the best-documented aboveground diseases of Chinese hickory and pose some of the most direct threats to perennial tree health. Early surveys in Zhejiang and Anhui showed that Botryosphaeria canker had already been observed sporadically by the late 1990s, and nearly 90% of the surveyed orchards in the two provinces experienced relatively severe disease between 2005 and 2009. Typical symptoms initially appear as small elliptical lesions on the bark, which subsequently enlarge, become sunken, and extend longitudinally; adjacent lesions may eventually coalesce into large areas of dark-brown to black necrotic tissue. Artificial inoculation of branches and trunks reproduced similar symptoms, confirming the pathogenicity of *Botryosphaeria dothidea* (Zhang and Xu, 2011). Comparative studies of *Botryosphaeria* species associated with Chinese hickory canker have identified several taxa, including *B. dothidea*, *B. qingyuanensis*, *B. fabicerciana*, and *B. corticis*. Among them, *B. dothidea* exhibits broader nitrogen-source utilization and stronger tolerance to osmotic and alkaline stresses, providing a biological explanation for its predominance in diseased tissues (Ma et al., 2023b). Thus, *B. dothidea* is currently regarded as the dominant pathogen associated with trunk canker and dry rot of Chinese hickory, although the disease occurs within a background of substantial Botryosphaeriaceae diversity.

Recent genomic studies have provided further insight into how this ecological predominance may translate into strong tissue-colonizing capacity. Comparative genomic analyses revealed that several unique or expanded genes in *B. dothidea* are associated with secreted glucanases, major facilitator superfamily (MFS) transporters, and orsellinic acid biosynthesis, functions that may contribute to host tissue degradation, nutrient acquisition, and competition with other microorganisms (Liang et al., 2024). The GH28 pectin-degrading enzyme family is also markedly expanded in *B. dothidea*, and BdGH28_3 shows high transcriptional activity during infection and contributes to full pathogen virulence (Liang et al., 2026). The severity of Chinese hickory trunk canker therefore cannot be explained solely by the frequent occurrence of the pathogen; it is also associated with the ability of the pathogen to breach woody tissue barriers and continue colonizing host tissues. This is particularly important in a perennial species such as Chinese hickory because the disease damages bark, cambium, and woody tissues that must remain functional for many years. Recurrent necrosis and canker development on perennial branches and trunks therefore have consequences that differ fundamentally from those of transient foliar lesions.

3.2 Anthracnose and *Colletotrichum* species

Anthracnose is one of the most representative foliar diseases of Chinese hickory. Sporadic symptoms were recorded in Lin'an, Zhejiang, as early as 2009, and by 2011 nearly 50% of surveyed Chinese hickory orchards in

Zhejiang were affected to varying degrees. The disease occurs mainly on leaves and young stems, initially producing localized necrotic lesions, while conspicuous orange conidial masses may develop in the lesion centers under humid conditions. Early studies identified the pathogen as *Colletotrichum gloeosporioides* on the basis of morphology, ITS sequences, inoculation, and reisolation. Of 13 isolates tested, 11 produced typical lesions on inoculated leaves, establishing a clear association between Chinese hickory anthracnose and this fungal group (Zhang and Xu, 2012). From a production perspective, anthracnose differs from trunk and branch diseases in that it primarily damages effective leaf area and young tissues. Under persistently humid conditions, repeated disease development can result in lesion expansion, localized foliar necrosis, and premature leaf drop, thereby affecting canopy function and the maintenance of tree vigor during the current growing season.

However, the identity of the causal agents of Chinese hickory anthracnose needs to be reconsidered in light of major changes in *Colletotrichum* taxonomy over the past decade. The traditionally broad concept of *C. gloeosporioides* actually encompasses multiple closely related species, including *C. fructicola*, and ITS sequences alone are generally insufficient for reliable discrimination among these taxa. *C. fructicola* has subsequently been reported to cause leaf spot and anthracnose on Chinese hickory, and a recent review also listed Chinese hickory among the reported nut-tree hosts of *C. fructicola* (Zakaria, 2025). Early records of *C. gloeosporioides* based primarily on ITS data remain historically and pathologically informative, but future regional surveys should increasingly rely on multilocus phylogenetic analyses for species-level identification.

3.3 Leaf blight and other foliar diseases

In addition to anthracnose, leaf blight has also been clearly documented in Chinese hickory. A survey conducted in Zhejiang in 2012 showed that nearly 40% of Chinese hickory orchards exhibited leaf-blight symptoms, with approximately 6.8% of the surveyed trees affected. The disease initially appears as small brown, water-soaked spots, which gradually enlarge to form black necrotic and sporulating areas, often surrounded by a conspicuous chlorotic halo. Isolation from diseased leaves, morphological identification, and inoculation tests linked the disease to *Alternaria petroselini*, with 8 of 10 isolates reproducing symptoms on Chinese hickory leaves (Liu et al., 2013). A single episode of this type of leaf blight generally does not threaten perennial structural tissues as directly as trunk canker. However, when disease continues to develop throughout the growing season and produces extensive lesions, its major impact is the reduction of healthy leaf area and shortening of the normal functional lifespan of leaves. It therefore remains important in humid years and in plantations with weakened tree vigor.

Current studies of foliar diseases in Chinese hickory are still dominated by first reports and localized case studies, many of which involve limited sample sizes, while some earlier pathogen identifications relied largely on morphology and a small number of loci such as ITS. This issue is particularly relevant to *Pestalotiopsis* and related pestalotioid fungi. Recent multilocus taxonomic studies have shown that a single leaf-spot phenotype may involve several morphologically similar but phylogenetically distinct species, and their pathogenicity can also differ markedly among woody and economically important host plants (Cui et al., 2024). The known spectrum of Chinese hickory foliar diseases is therefore still expanding, but only taxa supported by consistent isolation, species-level identification, and pathogenicity validation should be included among the principal pathogens. This is essential to avoid misclassifying associated fungi, endophytes, or secondary colonizers as primary disease-causing organisms.

3.4 Pathogen diversity and multi-pathogen associations

One of the most important developments in the study of aboveground diseases of Chinese hickory is the increasing recognition that a symptom name cannot be equated directly with a pathogen name. In Ningguo, Anhui Province, another trunk disease of Chinese hickory caused by *Pestalotiopsis vismiae* has been reported. Affected trees developed dark-brown bark lesions and longitudinal cracking, which could extend into the phloem and be accompanied by discoloration of the xylem; severely affected trees could die within several years. Artificial inoculation and reisolation confirmed the pathogenicity of the fungus (Liu et al., 2014). These symptoms partially overlap with those of Botryosphaeriaceae-associated canker, despite involving a phylogenetically distinct fungal

group. This finding demonstrates that field observations of bark cracking, necrosis, and branch dieback cannot be used alone to diagnose *B. dothidea*. In perennial woody plants, similar trunk and branch symptoms may be caused independently by different pathogens, while other fungi may colonize affected tissues secondarily during later stages of disease development.

Such complexity is not unique to Chinese hickory but is a common feature of woody trunk diseases. The Botryosphaeriales include numerous fungi capable of occurring as endophytes or latent colonizers in apparently healthy woody tissues, and morphology combined with a single sequence locus is often insufficient to reliably distinguish closely related taxa. Surveys of branch and trunk cankers in nut trees such as almond, pistachio, and walnut have recovered multiple fungal groups, including Botryosphaeriaceae, *Phaeoacremonium*, and Diatrypaceae, from tissues showing similar symptoms, while pathogenicity varies considerably among isolates (Sohrabi et al., 2020). Studies of pathogen diversity in Chinese hickory therefore need to distinguish three concepts clearly: frequent isolation does not indicate that an organism is the sole pathogen; co-occurrence in diseased tissues does not demonstrate joint pathogenicity; and the ability to reproduce symptoms after inoculation does not imply that all pathogens have equal importance under natural field conditions. Distinguishing a primary pathogen, associated pathogen, and secondary colonizer requires integrated consideration of isolation frequency, tissue localization, pathogenicity, and consistency across different locations and years.

3.5 Effects of aboveground diseases on tree vigor and nut production

As trunk cankers continue to expand, they directly damage the bark, phloem, cambium, and adjacent woody tissues, all of which perform long-term functions in assimilate transport, radial growth, and water conduction. Following infection by *B. dothidea*, host defense in Chinese hickory involves multiple processes, including pathogenesis-related (PR) proteins, cell-wall-associated defenses, and hormonal regulation. Several members of the TLP gene family show marked responses following infection, indicating that the tree allocates substantial defense resources to cope with trunk pathogens (Li et al., 2022). During the early and middle stages of infection, Chinese hickory enhances lignin biosynthesis, peroxidase activity, and cell-wall defense, whereas during later stages many disease-resistance-related pathways and defense genes, including PR1 and WRKY2, show reduced expression (Chen et al., 2025). Severe trunk disease should therefore not be viewed as merely localized bark damage; rather, it continuously consumes host defense resources and disrupts perennial conductive and structural tissues, ultimately contributing to shoot weakening, loss of effective canopy area, and reduced recovery capacity.

The effects of foliar diseases on production occur primarily through reductions in effective photosynthetic area. Leaf spot, anthracnose, and leaf blight initially cause localized necrosis of green tissues and, when severe, may lead to chlorosis and premature defoliation. Their effects on nut production are therefore more likely to be expressed through reduced carbon supply during the current and subsequent growing seasons. Broad studies of plant diseases have shown that pathogen infection not only reduces healthy leaf area but also commonly decreases photosynthetic capacity and chlorophyll content in the remaining foliage, thereby affecting assimilate production and yield formation (Cheaib and Killiny, 2025). However, long-term quantitative evidence directly linking a specific foliar or trunk disease of Chinese hickory with a defined reduction in nut yield per tree remains limited. A more appropriate interpretation is therefore that trunk necrosis and shoot decline reduce the long-term effective canopy, while foliar diseases further decrease photosynthetic area; together, these processes reduce carbon acquisition and recovery capacity, thereby increasing the risk of unstable nut production and premature plantation decline.

4 Root Rot, Collar Rot, and Tree Decline in Chinese Hickory

4.1 Root rot and collar rot caused by *Phytophthora cinnamomi*

Phytophthora cinnamomi is currently one of the best-supported pathogens associated with collar rot and shoot dieback in Chinese hickory. In May 2016, conspicuous shoot dieback and decline were observed in several Chinese hickory plantations in Lin'an, Zhejiang Province. Affected trees initially showed progressive leaf yellowing, wilting, and defoliation, followed by dieback of young shoots. As the disease progressed, necrotic tissues extended upward from the base of the stem, and in severely affected trees stem necrosis reached

approximately 1 m above ground level. Notably, basal necrosis showed a clear spatial correspondence with canopy symptoms, suggesting that belowground and collar infection may contribute to whole-tree decline by disrupting water transport between roots and the canopy. Surveys conducted in five Chinese hickory plantations in Lin'an, including Tuankou and Daoshi, during 2018-2019 consistently detected this symptom type. In Tuankou, disease incidence increased from 4.43% in 2018 to 11.39% in 2019. *P. cinnamomi* was isolated from diseased tissues and plantation soils. After inoculation of Chinese hickory seedlings with the representative isolate ST402, necrotic lesions averaged 3.8 ± 0.4 cm after 7 d and expanded to 5.3 ± 0.6 cm after 14 d, and the same pathogen was subsequently reisolated, thereby establishing a relatively complete link among the pathogen, symptoms, and pathogenicity. A LAMP assay developed for this isolate showed high agreement with field baiting and isolation results, further indicating that *P. cinnamomi* is not merely an incidental isolate from diseased trees but a soilborne pathogen that warrants continued monitoring (Tong et al., 2021).

From the perspective of infection biology, the pathogenicity of *P. cinnamomi* toward Chinese hickory also has a clear molecular basis. Genome and early-infection transcriptome analyses of isolate ST402 predicted 146 candidate RxLR effectors, of which 66 were differentially expressed during 0-36 h after infection. Four strongly induced candidates, PciRxLR1, PciRxLR21, PciRxLR57, and PciRxLR69, were able to suppress PAMP-induced cell death in heterologous plant systems and promote *Phytophthora* pathogenicity (Wang et al., 2025). These findings indicate that the collar necrosis and crown decline observed in the field are not simply consequences of mechanical root injury, but are also associated with the ability of the pathogen to penetrate host tissues and suppress host defense. Nevertheless, the main significance of these molecular findings is to confirm the strong infection potential of the pathogen. From a management perspective, greater emphasis should still be placed on whether the pathogen has entered the plantation, whether root-zone conditions remain favorable for its spread, and whether trees are already showing collar necrosis or early canopy symptoms that can be directly assessed in the field.

4.2 The emerging *Phytophthora* pathogen *Phytophthora cathayensis*

In addition to *P. cinnamomi*, a host-associated new *Phytophthora* species, *Phytophthora cathayensis*, has been identified in declining Chinese hickory plantations. In August 2016, severe crown decline and tree mortality occurred in several Chinese hickory plantations in Zhejiang Province. Affected trees developed conspicuous cankers on the roots and stem base, and removal of the bark revealed tongue-shaped orange-brown necrotic lesions extending along the collar and roots. During surveys in 2017, the same type of *Phytophthora* was repeatedly isolated from active collar lesions. Based on multilocus phylogenetic analyses using ITS, β-tubulin, COI, and HSP90, together with morphological and physiological characteristics, these isolates were identified as a new species in phylogenetic Clade 4 and named *P. cathayensis*. Greenhouse inoculation further showed that the pathogen could infect both Chinese hickory and pecan (*Carya illinoinensis*), although Chinese hickory developed significantly greater lesion length and necrotic area, thereby satisfying the relevant pathogenicity criteria (Morales-Rodríguez et al., 2020; 2021).

The ITS sequence of *P. cathayensis* was identical to that of an unidentified *Phytophthora* isolate recorded from pecan material in the United States in 2009. Together with the marked difference in susceptibility between the two *Carya* species after inoculation, this observation led to the hypothesis that the pathogen may have been disseminated through plant material. However, this transmission pathway remains speculative and should not yet be regarded as a confirmed invasion route. For the major Chinese hickory-producing regions, the more immediate implication is that the occurrence of collar cankers, orange-brown internal necrosis, and crown retraction should not be attributed to *P. cinnamomi* on the basis of symptoms alone. Species-level diagnosis is required. In other words, "*Phytophthora* root rot" in Chinese hickory already involves pathogen diversity, and accurate diagnosis should precede targeted disease management.

4.3 *Fusarium*-Associated root rot

In addition to *Phytophthora*, *Fusarium* represents another important fungal group that requires specific attention in Chinese hickory root rot. In 2026, surveys conducted in Tuankou, Lin'an, Zhejiang Province, covered more

than 27 ha of Chinese hickory plantations, where root rot incidence reached 40%-60%. Disease development generally began in lateral roots, subsequently spread into major roots, and then progressively affected the stem and branches, ultimately resulting in shoot dieback and defoliation. *Fusarium* isolates were obtained from diseased roots collected in June 2024, and representative isolates were identified as *Fusarium solani* using loci including TEF1-α and RPB2. Within 14 d after root-zone inoculation, all inoculated plants developed root necrosis consistent with field symptoms, whereas control plants remained symptomless. The same pathogen was then reisolated from diseased roots. These results provide direct pathogenicity evidence that *F. solani* causes root rot of Chinese hickory and represent the first formal report of this pathogen infecting Chinese hickory in China (Peng et al., 2026).

These findings further demonstrate that root rot symptoms in Chinese hickory should not be broadly attributed to *Phytophthora*, nor should a specific pathogen be diagnosed solely on the basis of blackened roots, root decay, and canopy wilting. In soils surrounding root-rot-affected trees, the gene copy number of *Fusarium graminearum* was significantly higher, while soil pH, soil organic carbon, available N, P, and K, and several enzyme activities were lower than those in the rhizosphere of healthy trees (Fang et al., 2024). However, an increase in the abundance or gene copy number of a particular *Fusarium* taxon in diseased soil indicates only an association with disease status and cannot replace pathogenicity evidence established through isolation, inoculation, and reisolation.

4.4 The continuum from root injury and collar necrosis to crown decline

A key concern in Chinese hickory root rot is how belowground injury is progressively translated into aboveground decline. Continuous observations of healthy, diseased, and dead Chinese hickory trees in Shexian, Anhui Province, showed that healthy trees had well-developed root systems with abundant white fine roots and lateral roots. In contrast, diseased trees exhibited marked reductions in lateral and fibrous roots, and some fine roots detached easily during washing. Separation between the phloem and xylem was also observed in affected roots, while xylem tissues gradually turned brown or black. Correspondingly, healthy trees had dark-green, naturally expanded leaves, whereas diseased trees displayed chlorosis and drooping. One particularly useful field diagnostic feature was that leaves of some diseased trees temporarily regained turgidity during rainfall but wilted again approximately 2 d after rain ceased and sunny conditions returned. This pattern of “temporary recovery after rainfall-renewed wilting under subsequent sunny conditions” is consistent with reduced effective water uptake by damaged roots and suggests that canopy symptoms may represent the external manifestation of substantial structural injury that has already occurred belowground (Bai et al., 2023).

At the whole-tree physiological level, the death of fine and lateral roots first reduces the effective absorptive surface area. As disease progresses into major roots and the collar, the continuity of water and mineral transport from roots to the canopy is further impaired, ultimately resulting in persistent chlorosis, wilting, premature defoliation, and shoot dieback. In perennial Chinese hickory, this process also implies reductions in effective canopy area and assimilate production during the current growing season and may weaken the ability of the tree to regenerate damaged roots and form fruiting shoots for the following year. A more appropriate interpretation is therefore that current field symptoms and root anatomical evidence clearly support a continuum of “root injury-restricted collar transport-crown decline,” while the specific mechanisms involving water transport, mineral nutrition, and carbon allocation still require dedicated whole-tree physiological studies for further validation.

4.5 A multi-pathogen disease-complex framework for root rot-dieback

Taken together, current evidence from pathogen isolation, artificial inoculation, and field surveys suggests that root rot-dieback in Chinese hickory is better understood as a disease complex with a multi-pathogen background rather than as a disorder driven by one fixed pathogen across all production areas. Direct pathogenicity evidence currently involves at least *P. cinnamomi*, *P. cathayensis*, and *F. solani*, while the symptoms reported in different studies overlap substantially, including necrosis of fine and lateral roots, browning or cankering of the root collar, leaf yellowing, summer wilting, premature defoliation, and ultimately shoot dieback and crown decline. Therefore, the same field combination of “root rot + yellow leaves + shoot dieback” does not necessarily indicate the same underlying pathogen. It should be emphasized that the term “multi-pathogen disease complex” is used here as an

integrative framework based on current evidence; it does not imply that co-infection by *Phytophthora* and *Fusarium* has been demonstrated in every diseased tree. At the whole-tree scale, the major diseases of Chinese hickory can be conceptualized as two interconnected disease domains: aboveground trunk canker and belowground root rot-dieback. Damage originating belowground may subsequently manifest as collar necrosis, leaf yellowing, shoot dieback, and crown decline (Figure 1).

Rhizosphere microbiome studies further extend this disease-complex framework from "multiple pathogens" to interactions among pathogens, the rhizosphere, and host health. Clear differences in fungal communities have been detected between the roots and rhizospheres of healthy and diseased Chinese hickory trees. Ascomycota and Basidiomycota together accounted for approximately 93.63% of the detected fungal community, but Basidiomycota was relatively more abundant in healthy root tissues, whereas Ascomycota increased in diseased and dead trees. Genera such as *Xylaria* and *Ilyonectria* occurred mainly in diseased or dead roots, whereas *Condinaea* and *Gliocladiopsis* were more frequently associated with dead plants (Su et al., 2025). Although these genera include known root pathogens of other plant species, they should currently be regarded only as potentially associated fungi in Chinese hickory and should not be equated directly with pathogens that have satisfied Koch's postulates in this host. Increased pathogen pressure and root infection may first damage fine roots and the root collar, while deterioration of the soil environment and disruption of the rhizosphere microbiome may further reduce ecological stability of the root system. Continued loss of root function may then manifest aboveground as canopy chlorosis, shoot dieback, and whole-tree decline.

5 Environmental and Management Drivers of Disease Development in Chinese Hickory

5.1 Intensive Management and Declining Tree Vigor

The major Chinese hickory-producing regions have gradually shifted from relatively semi-natural management systems toward intensive management characterized by monoculture, high fertilizer inputs, repeated understory vegetation removal, and intensive harvesting. Such practices can improve nut yield and harvesting efficiency over the short term, but prolonged implementation progressively reduces organic matter return to the soil, degrades root-zone soil structure, and disrupts nutrient cycling. Comparisons among Chinese hickory plantations under 5, 10, 15, and 20 years of intensive management showed a continuous decline in surface-soil organic carbon. After 20 years of management, total organic carbon, light-fraction organic carbon, and heavy-fraction organic carbon had declined by 38.6%, 68.2%, and 26.0%, respectively, relative to pre-management conditions, with the largest reduction occurring in the more biologically active light-fraction organic carbon pool (Sheng et al., 2015). These findings indicate that long-term intensive management weakens the active soil organic matter base that supports root carbon supply, microbial activity, and nutrient buffering. In perennial Chinese hickory, such gradually accumulating soil degradation may not immediately cause tree mortality, but it can progressively reduce root renewal and stress-recovery capacity, thereby creating a predisposed background for trunk canker, root rot, and crown decline.

The effects of management intensity on plantation health may also be transmitted through soil enzyme activities and rhizosphere microbial networks. Comparisons among unmanaged, reduced-management, and intensively managed Chinese hickory plantations showed that increasing management intensity was associated with declines in soil organic carbon, available nitrogen, available phosphorus, and several soil enzyme activities, together with reduced rhizosphere bacterial diversity and lower stability of co-occurrence networks. In contrast, reduced management intensity favored the recovery of network complexity and key microbial taxa (Fang et al., 2026). "Intensive management" should therefore not be interpreted simply as "high fertilizer input," but rather as a long-term compound pressure generated by frequent fertilization, repeated understory removal, surface disturbance, and persistent pursuit of high production. Its pathological significance lies not in directly "creating" pathogens through any single management practice, but in progressively reducing plantation ecological resilience and tree recovery capacity, thereby allowing pathogens that may persist latently or at low abundance to become more likely to cause overt disease.

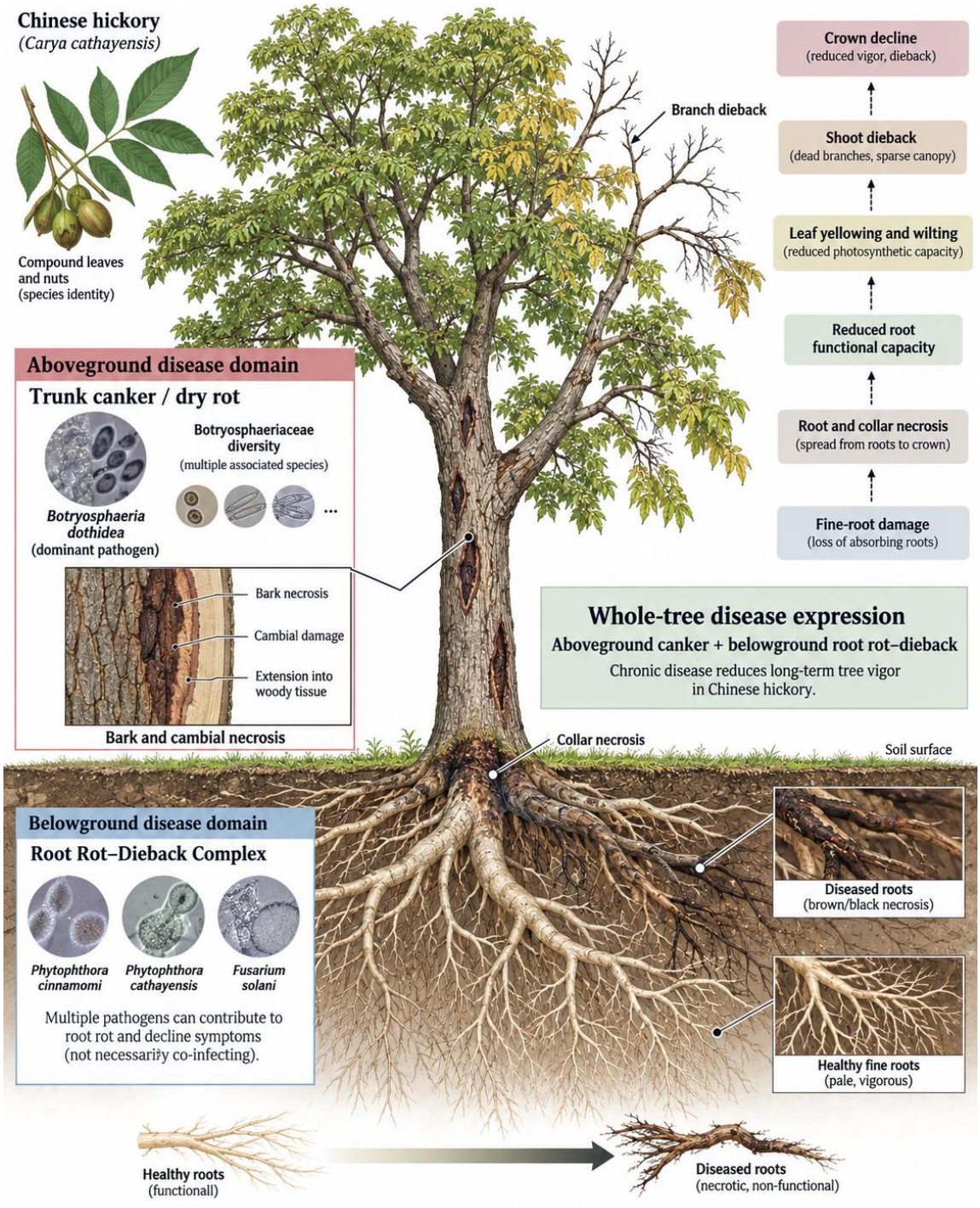


Figure 1 Whole-tree disease architecture of chinese hickory: from trunk canker to root rot-dieback

5.2 Soil acidification and nutrient imbalance

Continuous monitoring of 21 Chinese hickory orchards in Lin'an showed that surface-soil pH ranged from 4.6 to 8.2, with more than 40% of sites having a pH below 6. In most orchards, available nitrogen was substantially higher than available phosphorus and potassium, indicating that despite considerable variation in baseline soil conditions among sites, long-term production had commonly resulted in soil acidification and asynchronous N-P-K supply (Zhang et al., 2011). Soil acidification itself should not be simply described as directly causing dry rot or root rot, but it can alter ionic balance in the rhizosphere, nutrient availability, and the root-growth environment. When soils remain acidic over long periods, the buffering effect of base cations such as Ca and Mg declines, while phosphorus fixation, aluminum activation, and changes in micronutrient availability may occur simultaneously, exposing Chinese hickory roots to prolonged nutritional and chemical stress.

A major problem in Chinese hickory plantations is therefore the pronounced imbalance in nutrient supply. A 2013 survey of 189 Chinese hickory plantation soils across seven townships in Lin'an found a mean soil pH of only 5.2, with 75% of sites below pH 5.5. Available nitrogen exceeded 80 mg/kg in 91% of the sites, whereas available phosphorus was below 10 mg/kg in 63% and available potassium was below 80 mg/kg in 51% of the sites (Ma et al., 2016). These findings have direct production implications. When trees show chlorosis, weak growth, or declining fruiting performance, continued application of N-rich compound fertilizers alone may further intensify soil acidification and nutrient imbalance without necessarily resolving limitations related to P, K, or the rhizosphere environment. From a disease-development perspective, such nutrient imbalance is more appropriately regarded as a predisposing factor, increasing the likelihood of successful pathogen colonization by weakening fine-root renewal, tissue repair, and defense metabolism.

5.3 Understory vegetation removal, soil erosion, and microclimatic change

Traditional production practices often maintain relatively bare plantation floors to facilitate manual nut collection and reduce competition from understory vegetation. However, understory plants also perform important ecological functions by intercepting rainfall, reducing slope runoff, providing carbon inputs through roots and litter, and buffering fluctuations in soil-surface temperature and moisture. Experiments involving understory vegetation conversion in Chinese hickory plantations showed that, compared with continuous understory removal, the establishment of woody and herbaceous vegetation significantly increased active soil carbon and nitrogen pools and improved soil carbon storage functions (Gao et al., 2024). Understory vegetation is therefore not merely a group of "weeds" competing with Chinese hickory for water and nutrients; root turnover, surface cover, and litter inputs are also important components maintaining rhizosphere soil structure and nutrient cycling. When these inputs are interrupted over long periods, surface soils are more likely to experience organic matter depletion, reduced structural stability, and weaker buffering of soil moisture.

A meta-analysis of understory removal experiments in Chinese forests showed that removing understory vegetation increased soil temperature on average, while reducing soil moisture, organic carbon, total nitrogen, pH, and microbial biomass, with negative effects generally becoming stronger as treatment duration increased (Zhang et al., 2022). A global-scale analysis similarly showed that understory removal reduced soil C and N stocks, available K, microbial biomass carbon, and fine-root biomass (Xiong et al., 2024). Under such conditions, slope runoff and erosion may intensify during the rainy season, while surface warming and evaporation increase during dry periods, accompanied by reduced organic matter inputs and fewer fine-root interactions. For root rot and tree decline, these changes collectively create an environmental background that is unfavorable for long-term root stability but may favor disease expression.

5.4 Rhizosphere microbial disturbance and loss of soil biological resilience

A multi-site comparative study in 2026 showed that increasing management intensity in Chinese hickory plantations was associated with reductions in rhizosphere bacterial diversity and network stability, while changes in soil nutrients and enzyme activities were important drivers of microbial community reorganization. In contrast, reduced management intensity promoted recovery of microbial network complexity and key taxa (Fang et al., 2026). Assessing whether a Chinese hickory plantation is "healthy" should therefore not depend solely on whether a particular pathogen is detected, but should also consider whether the rhizosphere network retains sufficient structural complexity and functional redundancy. A community with many species but weak interactions and limited functional diversity does not necessarily possess strong disease-suppressive capacity. In contrast, combinations of functional groups that stably participate in C, N, and P cycling, resource competition, and pathogen antagonism may be more important for limiting disease expansion. Integrating the evidence from long-term management, soil degradation, and rhizosphere changes, disease susceptibility in Chinese hickory can be conceptualized as a continuous process of "management pressure-soil degradation-rhizosphere ecological destabilization-increased host susceptibility" (Figure 2).

Spatial studies of Chinese hickory root rot further support this interpretation. Analyses of rhizosphere and non-rhizosphere soils at different distances from diseased trees showed that available potassium, phosphatase

activity, and soil pH were negatively correlated with root rot incidence. As disease pressure changed, bacterial α-diversity at some locations recovered to levels approaching those of healthy soils, but community composition itself did not fully recover, indicating that "recovery of diversity" does not necessarily mean "recovery of ecological function" (Xing et al., 2022). Although rhizosphere microbial networks were generally more stable than those in non-rhizosphere soil, they showed lower resistance to disease-associated disturbance.

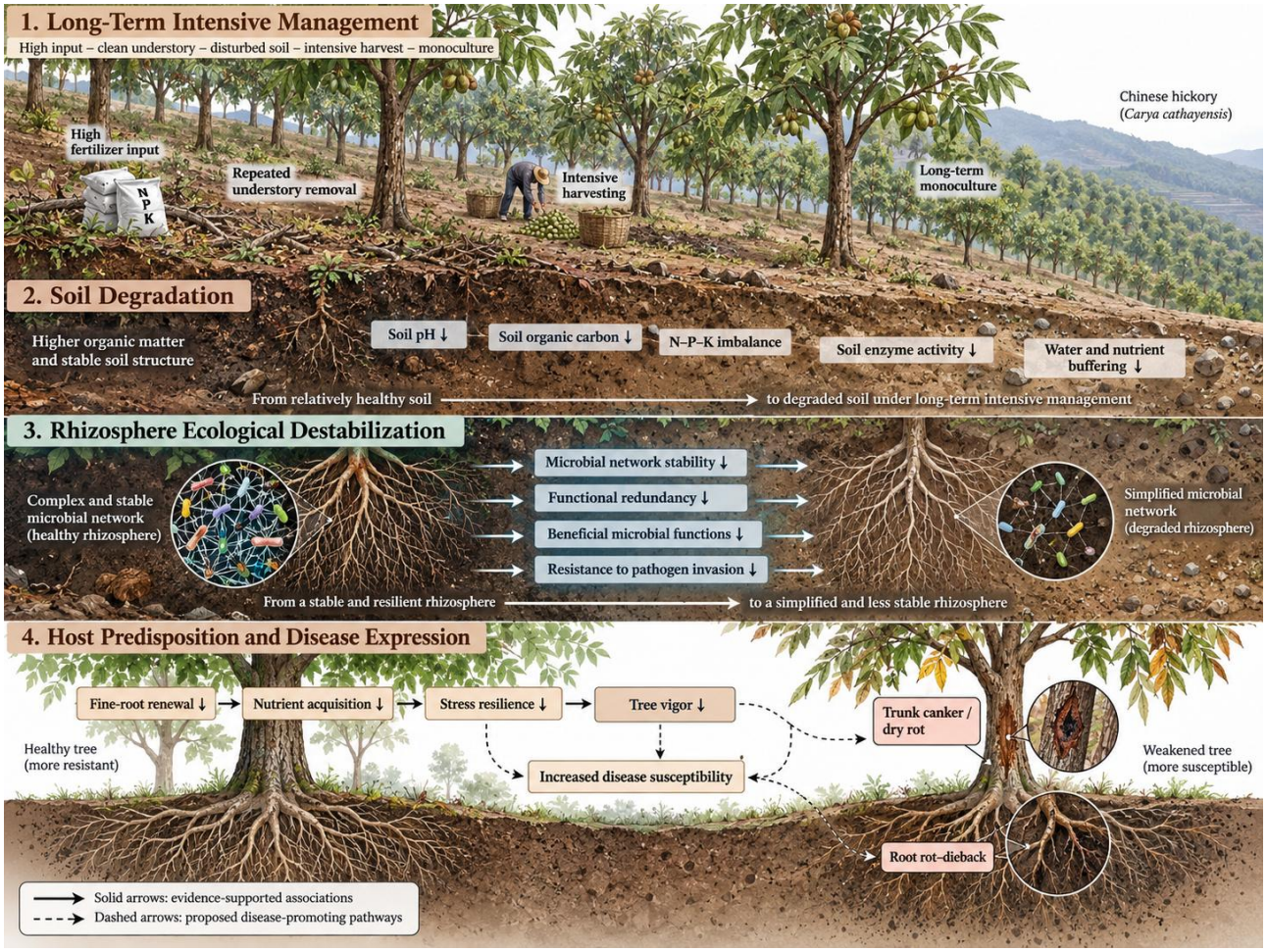


Figure 2 Ecological pathways linking long-term intensive management to disease susceptibility in chinese hickory plantations

5.5 Climate, tree age, wounds, and other predisposing factors

In addition to long-term soil degradation, short-term climatic stress often determines whether a latent infection develops into visible disease. Direct evidence for drought-pathogen interactions is available in Chinese hickory. Drought treatment significantly increased the susceptibility of Chinese hickory to *Botryosphaeria dothidea*, while also increasing H_2O_2 and the accumulation of proline, leucine, and isoleucine in the phloem and reducing non-structural carbohydrate concentrations. Some of these amino acids were further shown to promote asexual reproduction of the pathogen or enhance its tolerance to oxidative stress (Wang et al., 2023). The commonly observed field sequence of "preceding drought-declining tree vigor-rapid disease expression following subsequent rainfall" should therefore not be interpreted solely as a consequence of water shortage. Drought may already have altered host carbon reserves and tissue metabolism in ways that facilitate subsequent pathogen expansion. Extreme drought, prolonged high temperature, heavy rainfall, and waterlogging are therefore better regarded as triggers of disease expression rather than as independent primary causes.

Wounding and host condition further determine whether such environmental stress can be translated into tissue infection. Artificial inoculation studies in Chinese hickory showed that *B. dothidea* produced conspicuous black lesions in cortical tissues approximately 5 d after wound inoculation, after which hyphae progressively extended into deeper cortical tissues and the xylem; by 15 d, both lesion development and tissue colonization had increased

substantially (Yang et al., 2024). Wounded tissues can therefore markedly shorten the pathway by which the pathogen enters woody tissues. Botryosphaeriaceae in perennial woody plants are also well known as latent and stress-associated pathogens, with disease expression frequently occurring together with drought, frost injury, mechanical damage, waterlogging, or other factors that weaken host trees. By contrast, tree age itself should not be treated simply as an independent risk indicator, because increasing age is often accompanied by cumulative wounding, changes in fruiting load, root senescence, and a longer history of intensive management.

6 Sustainable Management Strategies for Major Diseases of Chinese Hickory

6.1 Plantation sanitation, canopy management, and inoculum reduction

For perennial trunk and branch diseases of Chinese hickory, reducing the initial pathogen pressure within plantations remains the first line of integrated disease management. A systematic survey conducted from 2016 to 2018 in six townships of the major production area of Lin'an recovered 97 Botryosphaeriaceae isolates from Chinese hickory cankers and identified five species. *Botryosphaeria dothidea* was overwhelmingly dominant, although other *Botryosphaeria* species and *Lasiodiplodia theobromae* were also present, indicating that morphologically similar trunk cankers in the field are not necessarily associated with a single pathogen (Zhuang et al., 2021). Chinese hickory dry rot generally begins to develop in late March and may persist until late November, while the pathogen is capable of overwintering. Trees 10-30 years old were reported to show relatively greater disease severity, whereas plantations with better site conditions and routine management generally exhibited less severe disease (Zhang et al., 2013). In production plantations, visibly dead branches, severely cankered branches, and chronically necrotic tissues should therefore be identified and managed preferentially from late winter to early spring, while unnecessary bark and branch injuries should be minimized during harvesting, pruning, and mechanical operations. Notably, previous field surveys found lower disease severity in stands with relatively greater canopy closure. Canopy management should therefore focus on removing diseased, weak, and crossing branches while maintaining appropriate canopy structure and tree vigor rather than pursuing excessive canopy opening.

In 2020, *Colletotrichum fructicola*-associated foliar disease was widely observed within an approximately 2.6 km² survey area in Huzhou, Zhejiang Province, and artificial inoculation followed by reisolation confirmed that the fungus could produce leaf lesions on Chinese hickory (Ma et al., 2023a). *Pestalotiopsis mangiferae* has likewise been confirmed as a causal agent of leaf spot and leaf blight in Ningguo, Anhui Province, and surrounding areas (Liu and Huang, 2018). In heavily affected plantations and nurseries, visibly diseased leaves, shoots, and plant debris should therefore be removed in conjunction with field disease surveys, while large accumulations of infected residues should be avoided within the plantation. Disinfection of pruning tools, reduction of mechanical injuries, and timely removal of dead branches may further reduce opportunities for pathogen movement among trees. In this sense, plantation sanitation should shift from simple "orchard cleaning" toward a broader objective of reducing high-risk diseased tissues, protecting healthy woody tissues, and maintaining stable tree vigor.

6.2 Soil restoration, balanced nutrition, and understory vegetation management

Comparisons among different management regimes showed that the disease index of dry rot was only 3.3 ± 3.35 in ecologically managed Chinese hickory plantations but reached 81.9 ± 1.27 under excessive management. Soil pH values in the two systems were 6.64 ± 0.06 and 5.80 ± 0.04, respectively, accompanied by marked differences in available N, P, and K and in bacterial community composition (Zhang et al., 2018b). These findings indicate a close association among long-term high-input management, changes in soil chemical properties, and disease severity. Between 2008 and 2018, reduced inorganic fertilizer input combined with soil-improvement measures in the major Chinese hickory-producing regions was associated with partial recovery of mean soil pH and soil organic carbon, together with a decline in available nitrogen, suggesting that management adjustments can reshape plantation soil fertility over longer time scales (Jin et al., 2021). A survey of 153 paired soil-nut samples further found that more than 60% of sites simultaneously exhibited low available phosphorus and low pH, while boron deficiency was particularly common; soil available P, B, and Zn were also clearly associated with the spatial distribution of nutrients in the nuts (Fu et al., 2022). Simulated acidification experiments showed that

nitrogen application and aluminum stress inhibited Chinese hickory uptake of P, K, Ca, Mg, Cu, B, and Zn and altered stress-related metabolites such as chlorogenic acid and catechins (Cao et al., 2024). In practical management, pH correction and balanced N-P-K and micronutrient supply should therefore be based on soil testing rather than continued reliance on increased nitrogen inputs.

A four-year grass-cover experiment in the major Chinese hickory-producing area showed that, compared with clean cultivation, treatments with rapeseed, ryegrass, and Chinese milk vetch increased soil organic carbon by approximately 23.1%-24.7%, microbial biomass carbon by 138.6%-159.7%, and water-soluble organic carbon by 56.2%-69.5%, while also increasing soil microbial functional diversity (Wu et al., 2014b). A long-term cover-cropping experiment conducted from 2011 to 2021 further showed that rapeseed, Chinese milk vetch, and their mixed cover increased soil C and N stocks, potential enzyme activities, and labile nutrient pools, with the legume-crucifer mixture producing the strongest improvement in soil multifunctionality (Hu et al., 2023). In addition to cover vegetation, the recycling of Chinese hickory husks also has local production value. After one year, husk mulching and biochar treatments increased soil pH by 0.33 and 1.71 units, respectively, while mulching, carbonization, and organic-fertilizer treatments all increased soil organic carbon and available nutrients (Liu et al., 2023). A long-term survey published in 2026 further showed that, compared with traditional beating harvest and stronger surface disturbance, 2-7 years of net harvesting combined with understory vegetation retention was associated with higher particulate, dissolved, and microbial biomass carbon, as well as a higher soil carbon pool management index (Zhou et al., 2026). Soil restoration in Chinese hickory disease management should therefore involve soil-test-based balanced fertilization, reduced dependence on long-term clean cultivation and herbicides, retention of appropriate understory cover, increased return of organic materials, and reduced surface disturbance on sloping land. The ultimate goal is not to directly eliminate a particular pathogen, but to restore a soil environment that supports root growth and long-term tree resilience.

6.3 Biological control and rhizosphere microbial regulation

Paenibacillus polymyxa CF05 can inhibit *B. dothidea* in vitro, and its spores formulated in a CMC/PVA carrier maintained good stability for up to 12 months. In two consecutive years of field trials, the formulation reduced both newly formed and pre-existing canker lesions, with control efficacy comparable to that of thiophanate-methyl. CF05 treatment also increased PAL, PPO, and POX activities and enhanced phenolic accumulation in Chinese hickory trunks, indicating that its effects involve not only direct antagonism but also induction of host defense (Xu et al., 2018). *Streptomyces hygroscopicus* LYJ637, which produces rapamycin, has also shown strong activity against *B. dothidea*. Its metabolites had EC50 values of only 5.1×10^{-3} and 5.5×10^{-2} μg/mL against mycelial growth and spore germination, respectively, lower than those of thiophanate-methyl under the same experimental conditions. A formulated preparation of the strain also reduced both new and existing cankers in three consecutive years of field trials and achieved control efficacy comparable to that of chemical fungicides (Jiang et al., 2021). These long-term field results indicate that biological control agents in perennial woody crops such as Chinese hickory have progressed beyond laboratory antagonism screening toward formulation development and practical plantation application.

Belowground diseases further shift the concept of biological control from “one strain against one pathogen” toward regulation of the rhizosphere community. *Bacillus amyloliquefaciens* subsp. *plantarum* CGMCC 11640, isolated from Chinese hickory, and its fermentation supernatant strongly inhibited *B. dothidea*, with mycelial growth inhibition ranging from 75.8% to 94.3% depending on the proportion of supernatant. Scanning electron microscopy showed shrinkage, collapse, and structural damage in fungal hyphae and spores (Cheng and Xu, 2017). For root rot, *Bacillus velezensis* TCS001 not only inhibited *Phytophthora cinnamomi* ST402 and achieved a disease control efficacy of 71%, but also significantly altered rhizosphere bacterial richness and co-occurrence networks and promoted the recruitment of several beneficial microorganisms associated with disease resistance (Xie et al., 2025). For practical production, a more realistic approach is therefore to combine validated *Bacillus*, *Paenibacillus*, or actinomycete-based products with organic matter inputs, cover vegetation, and soil improvement so that introduced beneficial microorganisms can establish suitable ecological niches in the rhizosphere.

6.4 Disease-resistant rootstocks, germplasm resources, and grafting-based disease management

Long-term trials initiated in 2005 at Tuankou and Longgang showed that Chinese hickory grafted onto pecan (*Carya illinoinensis*) rootstocks had only 2.52 ± 0.76 and 3.25 ± 0.35 canker lesions per tree, respectively, in 2017, compared with 35.65 ± 3.15 and 31.65 ± 3.06 lesions in self-grafted Chinese hickory controls. Fresh nut yield per tree in the grafted treatments was approximately 9.74 and 9.78 kg, respectively, also higher than the corresponding 6.13 and 5.56 kg recorded in self-grafted controls (Yao et al., 2019). Subsequent comparisons incorporating *C. hunanensis* as a rootstock showed that self-grafted Chinese hickory suffered the most severe disease, whereas combinations using *C. hunanensis* displayed greater resistance than those using pecan. More resistant graft combinations showed less phloem and xylem injury, higher phenolic contents and PAL/PPO activities, and stronger expression of phenylpropanoid-related genes such as PAL, C4H, and CHS (Zhou et al., 2023). These findings indicate that rootstock effects are not limited to stronger root systems but may also reduce the progression of trunk canker by altering systemic defense status.

However, rootstock utilization should not be interpreted simply as large-scale replacement of existing planting material with an introduced *Carya* species. Perennial economic plantations require simultaneous consideration of rootstock-scion compatibility, tree growth, disease resistance, nut yield and quality, root adaptation, and long-term stability across different site conditions. Interregional movement of nursery stock may itself introduce new pathogen risks. The discovery of *Phytophthora cathayensis* in declining Chinese hickory plantations, together with its potential association with pecan-related material, makes this concern particularly relevant. Although the pathogen has been hypothesized to be associated with movement of *Carya* germplasm or nursery stock, its exact origin and transmission pathway remain unresolved (Morales-Rodríguez et al., 2020). The deployment of disease-resistant rootstocks should therefore preferably follow an integrated strategy combining long-term multi-site evaluation, production of pathogen-free planting material, pathogen detection, and nursery quarantine.

6.5 Early diagnosis, disease monitoring, and rational chemical intervention

B. dothidea is characterized by a pronounced latent infection phase. A real-time quantitative PCR assay targeting its EF1 gene can directly quantify pathogen DNA in Chinese hickory tissues and is 100 times more sensitive than conventional PCR, providing a technical basis for detecting pathogen load before obvious symptoms develop (Zhu et al., 2016). For belowground disease, a LAMP assay developed for *P. cinnamomi* ST402 specifically detects this pathogen without generating positive reactions to *P. cathayensis*, *Fusarium oxysporum*, or other tested oomycetes and fungi. Its performance in field soil samples also showed high agreement with conventional baiting and isolation methods (Tong et al., 2021). In production systems, the greatest value of these techniques lies in supporting pathogen surveillance by regional plant-protection agencies, nurseries, and key disease areas. Targeted sampling can be conducted in planting material for newly established plantations, local decline hotspots, and sites at high risk of root rot, after which decisions regarding isolation, soil treatment, or further chemical intervention can be based on diagnostic results, thereby reducing broad preventive pesticide applications. Based on the evidence summarized above, disease management in Chinese hickory can be further integrated into a sustainable plantation health management system centered on plantation sanitation, soil and understory ecological restoration, biological and rhizosphere regulation, disease-resistant rootstocks, early diagnosis, and risk-based intervention (Figure 3).

When fungicide use is necessary, application timing and resistance management are more important than simply increasing the number of sprays. Screening of 17 fungicides against Chinese hickory trunk canker showed that difenoconazole, tebuconazole, and prochloraz strongly inhibited mycelial growth of *B. dothidea*, while trifloxystrobin had an EC50 of 1.78 ± 0.61 mg/L against spore germination. Three-year application-program trials conducted at two field sites further showed that, under the specific experimental conditions, treatments initiated on March 10 provided significantly better control than those initiated on March 20, indicating that the timing of the first intervention is an important determinant of control efficacy. However, this specific date reflects particular experimental years and plantation conditions in Zhejiang and should not be converted mechanically into a fixed spray calendar for all production areas (Dai et al., 2017). The same study also evaluated the sensitivity of 107 single-spore isolates to trifloxystrobin, with EC50 values ranging from 0.29 to 8.38 mg/L, providing a baseline for

future monitoring of sensitivity shifts. Sustainable management therefore does not require the complete exclusion of fungicides, but rather places chemical intervention at the downstream end of the overall disease-management system. High-risk windows should be identified on the basis of pathogen monitoring, local phenology, and weather conditions; treatment should be prioritized for key diseased trees and high-risk plantations; and fungicides with different modes of action should be rotated appropriately. Ultimately, a hierarchical management system should be established in which plantation sanitation reduces the initial inoculum load, soil and vegetation management restore tree vigor, microbial regulation strengthens ecological disease suppression, resistant rootstocks reduce long-term susceptibility, and monitoring guides targeted fungicide use. In this framework, chemical intervention shifts from a long-term dominant measure to a supplementary tool used only when necessary.

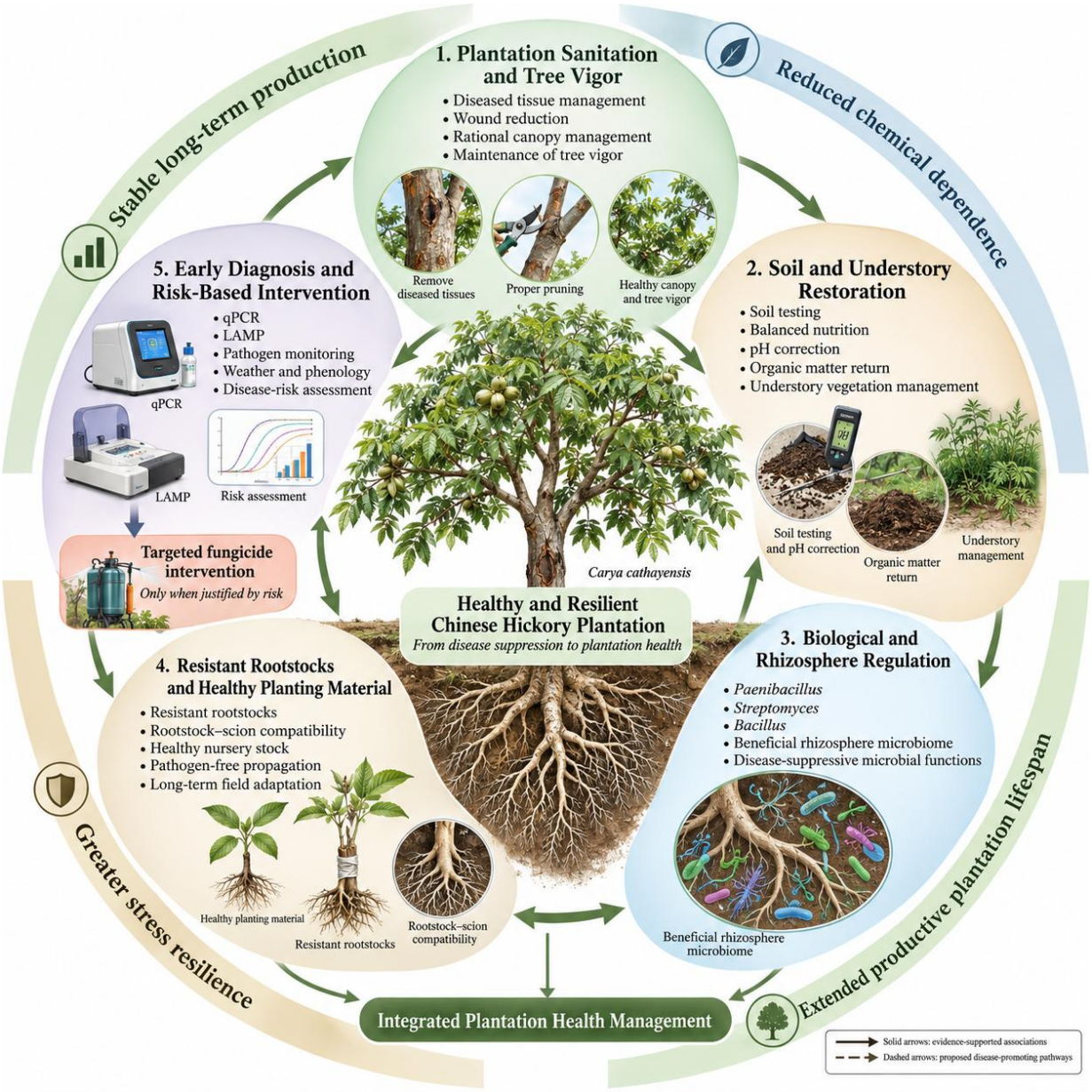


Figure 3 A sustainable plantation health management framework for Chinese hickory

7 Current Challenges and Future Directions in Chinese Hickory Disease Research

7.1 From single-pathogen diagnosis to disease-complex identification

A major priority for the next stage of Chinese hickory disease research is to clarify the pathogen composition underlying similar disease symptoms and to determine the causal relationships among the microorganisms involved. Trunk canker, root rot, and tree decline may each involve multiple fungal or oomycete groups, but the

simultaneous detection of several microorganisms in diseased tissues does not automatically demonstrate that they collectively constitute a disease complex. Conventional tissue isolation, morphological identification, and fulfillment of Koch's postulates for individual pathogens remain fundamental for establishing pathogenicity. However, in perennial woody plants, where latent infection, secondary colonization, and the coexistence of multiple pathogens are common, analyses based on a single isolate are often insufficient to explain the entire disease process. Modern plant disease diagnosis is progressively expanding from targeted PCR toward high-throughput sequencing, pathobiome analysis, image-based diagnosis, and multisource data integration. These approaches are particularly valuable for distinguishing complex diseases that produce similar symptoms but involve different pathogen assemblages (Cubero et al., 2024).

Future studies of disease complexes in Chinese hickory should establish an evidence chain based on "detection-quantification-localization-combined validation." First, fine roots, the root collar, phloem, xylem, and leaves should be sampled separately from healthy, early-stage diseased, severely diseased, and dead trees, and metabarcoding, metagenomic approaches, or targeted multiplex assays should be used to characterize changes in pathogen abundance across disease progression. Second, in situ tissue detection and pathogen quantification are needed to determine the temporal sequence of pathogen occurrence rather than relying only on endpoint comparisons between healthy and diseased trees. Finally, single-pathogen and multi-pathogen co-inoculation experiments should be used to distinguish synergistic interactions, antagonism, and secondary colonization. Current research on multi-pathogen plant diseases has clearly shown that different pathogens within the same host may compete, coexist, or act synergistically, and that "co-detection" and "joint pathogenicity" represent different levels of evidence (Priyadarshi et al., 2026). Ultimately, the proposed "root rot-dieback complex" of Chinese hickory should be defined by experimental evidence of causality rather than by simply accumulating a list of detected pathogens.

7.2 Long-term epidemiological monitoring and climate-responsive disease forecasting

A second major challenge is to transform the current disease information, which is dominated by single-site, single-year, and case-based surveys, into long-term, continuous, and comparable epidemiological datasets. Chinese hickory trunk canker already provides a useful foundation for this transition. Long-term field spore trapping and meteorological monitoring in Lin'an showed relatively stable temporal relationships among disease symptoms, airborne spore release, and seasonal temperature variation during 2011-2018. On this basis, the disease cycle was divided into latent, onset, epidemic, and relatively stable phases (Liang et al., 2025). Such results are highly valuable, but multi-year monitoring from a single region is insufficient to establish predictive models applicable across the entire production area. Chinese hickory plantations from northwestern Zhejiang to southern Anhui differ considerably in elevation, slope aspect, soil conditions, water availability, stand age, and management intensity. Future studies should therefore establish permanent monitoring plots and standardize the recording of disease incidence, disease severity, spore load, soil moisture, temperature and humidity, rainfall, tree phenology, and management practices so that data can be meaningfully compared across years and regions.

Disease forecasting should further advance from simple correlations between weather and disease toward integrated models incorporating host phenology, pathogen biology, and climatic conditions. Studies of fruit-tree diseases have shown that the effects of climate change are not simply expressed as greater disease pressure under higher temperatures, because temperature and rainfall simultaneously alter flowering, budbreak, and periods of tissue susceptibility, thereby shifting pathogen infection windows. In peach systems, the integration of phenological and disease models has already enabled assessment of synchronous changes in host development and fungal disease risk under different climate scenarios (Vanalli et al., 2024). For Chinese hickory, a more practical approach would be to model different risk components separately, such as spring rainfall in relation to trunk-canker spore release, summer heat and drought in relation to tree stress, and prolonged soil wetness in relation to *Phytophthora* root rot, and then integrate these components into regional low-, medium-, and high-risk categories. What growers ultimately need is simplified early-warning information that can answer practical questions: during which period, in which type of plantation, which disease poses the greatest risk, and whether intervention is warranted.

7.3 Disease-suppressive soils and beneficial rhizosphere microbiomes

A third major research priority should move beyond simply "screening more biocontrol strains" toward understanding why some soils can suppress disease over long periods. Plant pathology increasingly emphasizes the concept of disease-suppressive soil, in which disease remains limited even when a susceptible host and pathogen are both present because microbial competition, antagonism, resource limitation, and induction of host immunity restrict disease development. Such suppressiveness may arise through long-term interactions among root exudates, host genotype, and specific microbial communities. Plants under pathogen attack may also actively enrich protective microorganisms, generating a persistent "soil-borne legacy" (Spooren et al., 2024). This concept is particularly relevant to perennial Chinese hickory, whose roots remain in the same location for many years while rhizosphere microbial communities may be progressively assembled or depleted under long-term fertilization, weed control, management disturbance, and disease pressure.

Future studies should therefore move beyond asking which microbial genera are more abundant around healthy or diseased trees and instead identify the core microbial groups and functional combinations that actually determine disease suppression. Potentially suppressive soils could first be identified in plantations that remain healthy despite being adjacent to severely diseased stands. Soil-transfer experiments, sterilization and microbiome-restoration assays, community reconstruction, and pathogen-challenge experiments could then be used to determine whether suppressiveness is transferable. Subsequently, key microbial taxa could be assembled into synthetic communities with complementary functions, including resource competition, antimicrobial production, nutrient transformation, and induced resistance. Current Synthetic Community (SynCom) research is already progressing from simple mixtures of several beneficial microorganisms toward standardized strain collections, reference communities, and reproducible community-assembly systems to improve the reliability of translating greenhouse results into field applications (Northen et al., 2024). For Chinese hickory, the more meaningful objective is to develop locally adapted disease-suppressive microbial consortia capable of remaining stable in acidic mountain soils and perennial root environments.

7.4 Optimization of disease-resistant germplasm and rootstock-scion combinations

As a perennial nut tree, Chinese hickory may remain in production for several decades once a rootstock-scion combination is established. Evaluation criteria should therefore simultaneously include disease resistance, graft compatibility, root vigor, tree growth, nut yield and quality, and adaptation to abiotic stresses such as high temperature, drought, and acidic soils. Recent research showed that Chinese hickory grafted onto *Carya hunanensis* or pecan (*C. illinoinensis*) rootstocks maintained higher net photosynthetic rates and stomatal conductance under temperatures of 35-40 °C and exhibited relatively stable hormonal regulation and transcriptional responses. These results indicate that rootstock effects extend beyond disease resistance alone and also influence whole-tree environmental adaptation (Huang et al., 2024). This finding highlights the need to shift future rootstock selection from "resistance to a specific disease" toward improvement of long-term integrated resilience.

A superior rootstock does not necessarily confer the same performance to every scion, and the interaction among rootstock × scion × environment should become a central unit of future research. Studies of Chinese hickory grafting have shown that auxin transport and genes associated with PIN, ABCB, and AUX/LAX are closely involved in graft-union healing and vascular reconstruction (Saravana Kumar et al., 2018), demonstrating that graft compatibility has a clear physiological and molecular basis. Broader experience from rootstock breeding in nut trees likewise indicates that an ideal rootstock must integrate resistance to diseases and soil stresses with effects on tree size, yield, nut quality, water and nutrient uptake, and graft compatibility (Vahdati et al., 2021). Future Chinese hickory research could establish multi-location rootstock-scion trials in which trunk diseases, root rot, extreme-temperature tolerance, yield, and nut quality are continuously evaluated for at least 5-10 years, while molecular markers and early physiological indicators are incorporated to shorten the selection cycle for disease-resistant rootstocks.

7.5 From disease suppression to integrated plantation health management

Chinese hickory plantations represent long-lived soil-root-tree-microbiome-pathogen systems, in which trunk diseases, root rot, and tree decline should not be regarded as completely independent problems. Current plant-health research increasingly emphasizes interactions among intensive management, soil degradation, microbial homogenization, climatic stress, and pathogen invasion. Soils with lower biodiversity and simplified microbial networks are generally more vulnerable to pathogen invasion, indicating that pathogen surveillance should be integrated with assessments of soil and microbial health (Delgado-Baquerizo et al., 2025). For Chinese hickory, this means that future monitoring should gradually extend beyond lesion development and pathogen abundance to include soil pH, organic carbon, nutrient balance, root vitality, canopy condition, microbial network characteristics, and records of extreme weather events. At this higher level of assessment, the central question becomes not merely "whether a particular pathogen is present," but "whether the tree and plantation system remain healthy."

At the production level, a tiered management framework can be established. In healthy plantations, priority should be given to protecting soil quality and tree vigor while minimizing pathogen introduction. Low-risk plantations should emphasize surveillance and plantation sanitation. Where soil degradation or localized disease has already appeared, nutritional adjustment, understory vegetation restoration, and biological regulation should be prioritized to rebuild ecological resilience. Targeted chemical treatment should be introduced only when clearly defined disease-risk thresholds are reached and should be guided by pathogen detection. Recent syntheses of non-chemical disease control have likewise emphasized that cultural practices, biological control, natural products, microbiome engineering, and precision technologies should not be treated as separate alternatives, but rather integrated into management systems capable of reducing chemical inputs while improving overall system stability (Adkar-Purushothama et al., 2025). Ultimately, Chinese hickory disease research should develop a long-term plantation health management model based on "accurate diagnosis-risk forecasting-healthy soil-stable rhizosphere-resilient rootstock-scion combinations-targeted intervention when necessary." Evaluation criteria should likewise expand beyond short-term disease-control efficacy to include stable long-term production, reduced chemical inputs, improved tree resilience, and extension of the productive lifespan of Chinese hickory plantations.

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Conflict of Interest Disclosure

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