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Review

Advances in Sexual and Asexual Propagation of *Toxicodendron vernicifluum*: Mechanisms, Bottlenecks, and Industrialized Breeding Perspectives

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Abstract

Toxicodendron vernicifluum is an economically important lacquer-producing tree endemic to East Asia; propagation bottlenecks severely restrict elite clone industrialization. This review summarizes 20 years of the domestic and international literature on seed propagation, root cutting, stem cutting, grafting, and tissue culture of lacquer tree, compares technical performance among China, Japan, Vietnam, and Mediterranean *Rhus* species, and quantitatively summarizes germination/rooting rates across protocols. Sexual propagation has low rooting efficiency; tissue culture faces high cost and browning obstacles; molecular regulatory mechanisms remain poorly characterized. We propose an integrated breeding framework combining molecular mechanism dissection, low-cost vegetative propagation optimization, and standardized plantlet production. Future directions including multi-omics analysis, gene-edited easy-rooting germplasm, and bioreactor micropropagation are highlighted to support large-scale elite clonal stock production in Qinba Mountain regions.

Keywords: *Toxicodendron vernicifluum*; seed dormancy; vegetative propagation; grafting; tissue culture; browning inhibition; elite clone breeding; industrial micropropagation

1. Introduction

Natural lacquer tree (*Toxicodendron vernicifluum* (Stokes) F.A. Barkley, syn. *Rhus verniciflua*), a woody species endemic to East Asia, produces unique biogenic lacquer widely recognized as a premium sustainable natural coating material, alongside multiple economic values including seed oil, timber production, and mountain ecological restoration [1]. China hosts the origin and largest germplasm resource bank of *T. vernicifluum*, with the Qinba-Wuling Mountain zones across Shaanxi, Sichuan and Hubei Provinces contributing over 40% of national raw lacquer output. Beyond China, Japan and Vietnam have introduced local lacquer tree populations and developed regionally adapted breeding systems targeting wax harvest and resin yield, respectively. In contrast, Mediterranean countries mainly study *Rhus coriaria*, a closely related sumac species with distinct horticultural applications, whose propagation techniques cannot be directly transferred to lacquer-producing *T. vernicifluum* due to interspecific physiological divergence [2–5].

Propagation technology forms a foundational bottleneck, restricting the scaled cultivation of elite high-lacquer clones of *T. vernicifluum*. This species exhibits dioecy and allogamy, resulting in severe phenotypic segregation among seed-derived plantlets, which causes unstable lacquer yield and weakens the uniformity of commercial plantations. Conventional vegetative propagation approaches, including root layering, stem cuttings and

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grafting, suffer from low and inconsistent survival rates, limiting the large-scale supply of uniform elite plantlets. In vitro tissue culture, regarded as a promising industrialized breeding strategy, has gained increasing research attention globally, yet persistent technical obstacles such as severe explant browning, microbial contamination and high production costs hinder its widespread adoption at mountain nurseries [6–8].

Over the past two decades, substantial experimental efforts have been dedicated to seed dormancy release, adventitious root regulation, graft compatibility screening and micropropagation optimization for lacquer trees, generating scattered but valuable technical datasets across China, Japan, Vietnam and European laboratories. However, a systematic cross-regional synthesis integrating sexual and asexual propagation progress, quantitative comparison of technical efficiency, and in-depth analysis of unresolved physiological and molecular barriers remains scarce in the existing literature [7,9,10].

This review aims to fill the above research gaps by: (1) systematically summarizing recent research progress on seed dormancy release and vegetative propagation regulation of *T. vernicifluum* and related Rhus species; (2) quantitatively comparing the efficiency, advantages and limitations of sexual propagation, root layering, stem cuttings, grafting and tissue culture via integrated summary tables; (3) dissecting unresolved physiological and molecular obstacles restricting stable, large-scale plantlets breeding; and (4) proposing a hierarchical research roadmap integrating multi-omics mechanism dissection, low-cost vegetative propagation optimization and standardized industrial micropropagation systems. The integrated synthesis presented herein provides theoretical references and technical guidance for elite lacquer plantlets cultivation in Qinba Mountain regions and other East Asian lacquer-producing zones, and offers comparative insights for propagation research on other hard-to-root woody oil and economic tree species.

2. Sexual Propagation of *Toxicodendron vernicifluum*

Sexual propagation via seed sowing is the most traditional and low-cost breeding system for *T. vernicifluum*. It features high propagation coefficients, well-developed taproot systems, and strong stress tolerance of plantlets, making it suitable for constructing large-scale ecological shelterbelts and low-yield raw lacquer plantations. Nevertheless, this method suffers from two irreparable intrinsic defects for elite cultivation: severe phenotypic segregation of progeny and triple-layer deep seed dormancy. Without dedicated scarification and stratification, fresh lacquer seeds exhibit extremely low germination rates (<5%) under natural conditions and require 2–3 consecutive years to complete uneven emergence, severely limiting annual plantlets output [11,12]. Over the past two decades, global research has focused on revealing dormancy mechanisms, optimizing pre-germination protocols, and comparing seed performance among temperate, tropical, and wax-oriented Toxicodendron and Rhus germplasms.

2.1. Triple-Layer Seed Dormancy Mechanisms

The deep dormancy of *T. vernicifluum* seeds arises from combined physical, mechanical, and physiological barriers, which jointly restrict water uptake, gas exchange, and radicle protrusion and elongation (Figure 1).

First, a thick waxy cuticle covers the seed surface, forming a hydrophobic physical barrier that blocks imbibition of water and gas exchange. Main local cultivars in the Qinba Mountains, such as ‘Dahongpao’ and ‘Gabachi’, have a 1000-seed weight of merely 38.6 g, with intact wax layers leading to natural germination rates below 42.7% [11,12]. Second, the dense, lignified endocarp exerts mechanical resistance to radicle protrusion, even after full hydration of embryonic tissues [8,12,13]. Third, hormonal imbalance creates physiological dormancy: mature seeds accumulate high endogenous abscisic acid (ABA) while bioactive

gibberellins (GA3) remain at low concentrations, and a high ABA/GA_3 ratio suppresses embryonic cell elongation and germination initiation [8,14].

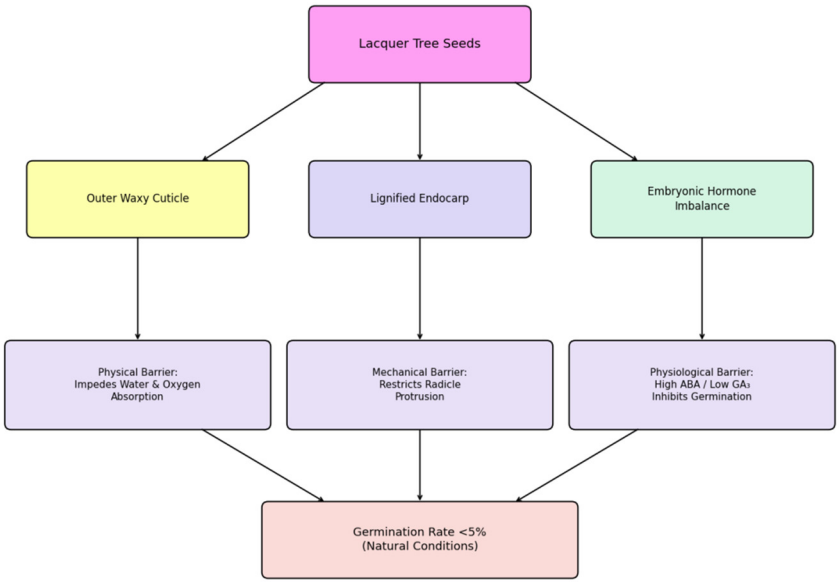


Figure 1. Schematic diagram of triple dormancy barriers in *Toxicodendron vernicifluum* seed. (1) Outer waxy cuticle: hydrophobic physical barrier blocking water and oxygen imbibition; (2) lignified endocarp: mechanical constraint inhibiting radicle protrusion; (3) embryonic hormonal imbalance: high ABA and low GA_3 maintain physiological dormancy.

Additional extrinsic factors further reduce seed viability and the subsequent germination. *T. vernicifluum* is dioecious with unbalanced male–female ratios across natural stands. Cold and rainy spring weather inhibits pollinator activity, leading to unstable annual seed yields with obvious alternate bearing cycles; national seed production in low-yield years can decline by more than 50% relative to bumper years. Embryo immaturity is another widespread issue: viability tests indicate over half of harvested seeds contain incompletely developed embryos, which cannot germinate even after full dormancy release. These compound barriers lead to unstable seed supply and low effective plantlet emergence in nursery production [12,15].

2.2. Optimized Pre-Germination Treatments for Dormancy Release

2.2.1. Alkali Rubbing and Cold Stratification

This low-cost chemical-free composite protocol is widely adopted in mountain nurseries. Seeds are soaked in 85 °C hot water for 3–5 min, then fully rubbed with plant ash and soda powder to strip surface wax. After 5–7 days of warm water soaking to soften lignified endocarps, seeds undergo cold sand stratification for 14–18 months. This integrated treatment elevates germination rates to 72%–78%, and high-quality elite germplasm can reach a maximum germination percentage above 82% [11]. The primary disadvantage is the ultra-long stratification cycle, which occupies nursery storage space for over one year.

2.2.2. Acid Etching Combined with GA3 Priming

Concentrated sulfuric acid short-term etching physically disrupts the rigid endocarp, followed by GA3 soaking and short-period cold stratification. Single acid scarification only achieves germination rates below 5%; sequential acid etching + GA3 + stratification raises this value to 22%–35%. Supplementary density sorting to remove shrunken, empty seeds further increases the final germination rate to approximately 47%. This method requires

strict acid safety operation and is more appropriate for small-batch elite seed pretreatment rather than mass plantlet production [1].

2.2.3. Mechanical Abrasion

For household-scale plantlet cultivation without chemical reagents, seeds are mixed with coarse sand and mechanically rubbed to abrade the waxy coat, followed by cellar stratification over winter. Although the operation threshold is low, the overall germination performance is inferior to chemical composite treatments, limiting its application in standardized commercial nurseries [1,16].

2.3. Standardized Field Sowing and Plantlets Management Protocols

Uniform field cultivation workflows have been established for *T. vernicifluum* across Southwest and Qinba Mountain producing regions. Ripe seeds are collected in autumn, dewaxed, and stored in moist sand over winter, then sown in drills the following spring with a covering soil depth of 1–2 cm. Upon germination routine plantlets management includes precision water and nutrient regulation, plus integrated green pest control targeting lacquer rust and aphids. Plantlets require 2–3 years of field cultivation before outplanting for forestation [7,17,18].

Despite mature agronomic management, the genetic segregation defect cannot be eliminated via cultivation regulation. Plantlet populations display continuous variation in lacquer yield, cold resistance, and disease tolerance, rendering sexual plantlets unsuitable for high-uniformity elite lacquer plantations that pursue stable commercial output.

2.4. Global Comparative Analysis of Seed Propagation in Related Taxa

Seed dormancy and germination performance vary drastically among East Asian lacquer trees, tropical Vietnamese germplasm, *Rhus coriaria*, and Mediterranean *Rhus coriaria*. *Rhus coriaria* was selected as a comparative taxon for its close phylogenetic affinity to *Toxicodendron* within Anacardiaceae, its contrasting economic use (spice/tannin vs. lacquer), and shared propagation challenges (seed dormancy, low regeneration), enabling meaningful cross-species protocol comparison [2]. Cross-species dormancy characteristics and required pretreatment cycles are visualized in Figure 2.

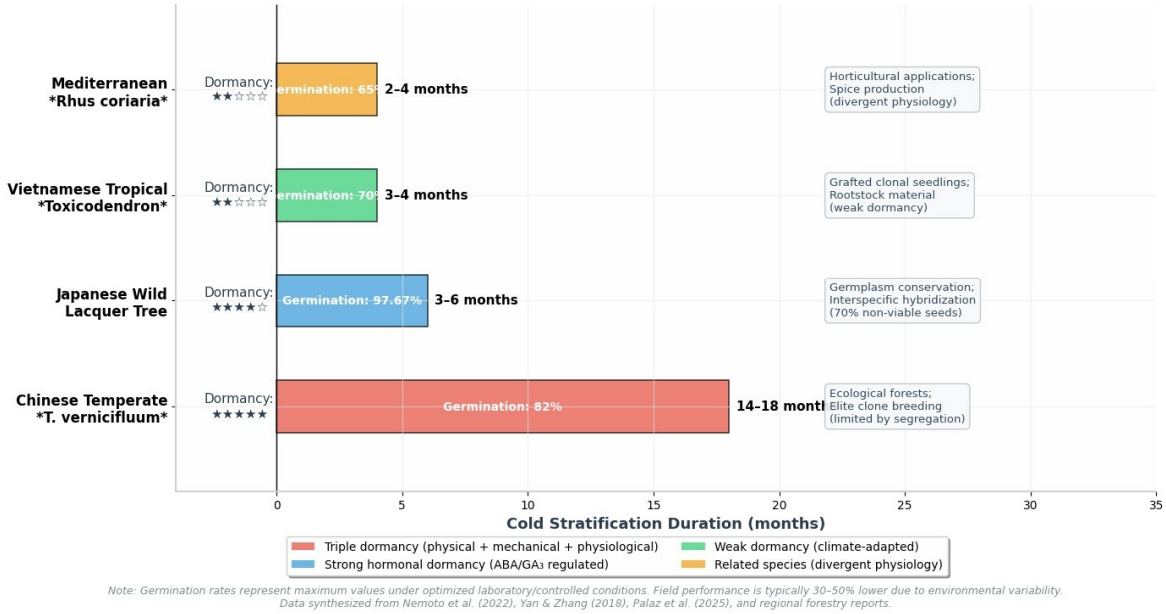


Figure 2. Cross-species comparison of seed dormancy intensity, stratification requirements, and germination performance among *Toxicodendron vernicifluum* and related taxa. Dormancy intensity is

rated on a five-star scale based on the number and severity of barriers (physical, mechanical, and physiological). Cold stratification duration represents the optimized pretreatment cycle required to break dormancy under controlled conditions. Maximum germination rates reflect laboratory-optimized protocols: Chinese temperate *T. vernicifluum* requires 14–18 months of alkali scarification plus cold stratification (72%–82%); Japanese wild lacquer tree achieves 97.67% under acid etching + GA3 priming but suffers from severe pistil abortion; Vietnamese tropical germplasm exhibits weak dormancy (3–4 months); Mediterranean *Rhus coriaria* shows divergent physiological regulation unsuitable for direct technical transfer. Field germination performance is typically 30%–50% lower than laboratory values due to environmental variability [1,2,11].

2.4.1. Japanese Wild Lacquer Tree

Japanese breeding programs prioritize seed wax extraction rather than raw lacquer production. Its seed dormancy regulatory pathway shares high similarity with Chinese *T. vernicifluum*, with ABA/GA_3 ratio acting as the core switch for dormancy release. A standardized protocol combining acid etching, cold stratification, and GA_3 priming has been reported to achieve a laboratory germination rate of up to 97.67% under optimized conditions [13,15,19]. However, this value represents the maximum achievable under controlled experimental settings; typical germination rates under standard nursery conditions are considerably lower and more variable. The Japanese population is believed to have originated from eastern China, with phylogeographic studies revealing a clear east–west genetic break across Chinese populations corresponding to stepped landforms: western clades are restricted to high mountains and plateaus, while eastern clades occupy lower hills and plains. This biogeographic history has resulted in significantly lower genetic diversity in Japanese populations compared to their Chinese counterparts, suggesting a founder effect associated with human introduction or dispersal across the East China Sea–land bridge during glacial periods. These genetic and environmental differences between Chinese and Japanese *T. vernicifluum* may contribute to observed variations in propagation behavior and should be considered when interpreting or transferring protocols between regions. Severe pistil abortion causes over 70% of seed-bearing trees to produce non-viable seeds; thus, seed propagation is only used for germplasm conservation and interspecific hybridization, not commercial plantlets supply [1,8,20].

2.4.2. Vietnamese Tropical Lacquer Tree

Tropical *T. vernicifluum* exhibits far weaker dormancy than temperate Chinese populations, requiring only 3–4 months of cold pretreatment to break dormancy. Local forestry institutions have screened optimal stratification durations and plant growth regulator concentrations to maximize emergence. Nevertheless, Vietnamese nurseries rely predominantly on grafted clonal plantlets for commercial plantations, with sexually propagated seeds merely used as rootstock material [11].

2.4.3. Mediterranean *Rhus coriaria*

European research focuses on *Rhus coriaria*, a tannin and oil-producing sumac species with a single physical wax-imposed dormancy layer. Researchers adopt organic solvent degreasing combined with density sorting and cold stratification to establish standardized pre-germination pipelines. However, large physiological interspecific differences between *R. coriaria* and lacquer-producing *T. vernicifluum* prevent direct transplantation of these protocols to East Asian lacquer tree breeding systems [2].

2.5. Core Limitations Restricting Large-Scale Application of Sexual Propagation

Three inherent drawbacks constrain the utilization of seed propagation for elite lacquer clone industrialization:

(1) Irreversible genetic segregation: Sexual progeny lose stable high-lacquer and stress-resistant traits of superior mother trees, making plantlet stands unsuitable for high-yield commercial lacquer plantations.
(2) Cumbersome dormancy release and unstable seed supply: Long stratification cycles increase nursery time costs, while alternate bearing and pollination limitations create annual fluctuations in viable seed availability.
(3) Low effective embryo quality: Over half of harvested seeds contain underdeveloped embryos. Routine viability screening—e.g., flotation-based sorting or X-ray inspection—should therefore be performed prior to stratification to discard non-viable seeds, thereby conserving nursery resources and improving germination efficiency [1,15].

3. Sexual Propagation of *Toxicodendron vernicifluum*

This section objectively summarizes the technical performance, advantages, and inherent limitations of all major propagation pathways for *Toxicodendron vernicifluum*, based on experimental evidence reported in the literature. Quantitative comparisons are presented in Table 1 (sexual propagation) and Table 2 (asexual propagation). The goal is to provide a factual foundation, without speculative interpretation, for the subsequent discussion and future research proposals [6,8,10].

Table 1. Comparison of seed germination performance under different dormancy-breaking treatments for *Toxicodendron vernicifluum* [12].

Pretreatment Combination	Core Operation Steps	Stratification Duration	Maximum Germination Rate	Advantages	Disadvantages
Alkali rubbing + cold stratification	85 °C hot water soaking, ash/soda wax removal, warm water softening	14–18 months	14–18 months	Low chemical risk, fit for large mountain nurseries	Extraordinarily long storage cycle
Acid etching + GA_3 priming	H_2SO_4 scarification, GA_3 soaking, short cold stratification + seed density	3–6 months	22%–47%	Short stratification	Corrosive chemical
Mechanical abrasion + cellar stratification	Coarse sand rubbing to remove wax, over winter cellar storage	8–10 months	<40%	No chemical input, easy operation for small households	Low germination rate, unstable emergence uniformity

Table 2. Comparative bottlenecks of three traditional asexual propagation methods for *T. vernicifluum* [17,18,21].

Propagation Method	Core Scalability Defect	Core Scalability Defect	Practical Industrial Restriction
Root layering	Extremely low multiplication rate limited by maternal root biomass	Each mature tree only supplies 20–50 usable root segments annually	Cannot support large standardized lacquer plantation plantlets demand
Hardwood/softwood cutting	Unstable rooting performance sensitive to field microclimate	Open-air nursery rooting rate drops by 30%–50% without automatic mist irrigation	Fluctuating transplant survival rate restricts commercial plantlets batch supply
Grafting	Scion–rootstock incompatibility and persistent wound gummosis	15%–30% graft failure rate; surviving grafts show premature senescence after 3–5 years in field	No standardized anti-gummosis post-grafting management system for mass application

3.1. Seed Dormancy and Pre-Germination Treatments

Freshly harvested seeds exhibit extremely low germination rates (<5%) under natural conditions due to combined physical (waxy seed coat impermeability), mechanical (lignified

endocarp constraint), and physiological (high ABA/low GA_3 hormonal imbalance) barriers. Over the past two decades, various pre-germination protocols have been developed to relieve dormancy:

(1) **Chemical scarification**: Alkali dewaxing combined with concentrated sulfuric acid etching significantly increases water uptake, but treatment duration and concentration require precise control to avoid embryo damage.
(2) **Cold stratification**: Prolonged moist chilling at 4–5 °C for 3–18 months is the most commonly applied method to break physiological dormancy. However, stratification efficacy varies markedly across provenances and seed lots.
(3) **Compound hormone treatments**: Exogenous GA_3 application partially counteracts ABA inhibition, yet optimal concentrations differ among genotypes.

Despite these interventions, germination performance remains inconsistent, with reported rates ranging from 30% to 75% depending on seed quality, treatment regime, and environmental conditions. No single protocol has achieved stable, high germination (>80%) across multiple provenances and collection years.

3.2. Field Sowing and Plantlets Management

Standardized field cultivation protocols have been established in major Chinese production regions (Qinba, Sichuan, Hubei). Ripe seeds collected in autumn undergo dewaxing and moist sand stratification over winter, followed by drill sowing in spring at 1–2 cm depth. Routine management includes precision irrigation, nutrient regulation, and integrated pest control targeting lacquer rust and aphids. Plantlets typically require 2–3 years of nursery cultivation before outplanting.

3.3. Key Limitations

(1) **Phenotypic segregation**: Seed-derived populations exhibit continuous variation in lacquer yield, cold hardiness, and disease resistance, making them unsuitable for high-uniformity commercial plantations that require stable output quality.
(2) **Long and unstable dormancy release cycles**: Stratification periods of 3–18 months, combined with alternate bearing and incomplete embryo development in many seeds, reduce annual nursery efficiency and increase land and labor costs.
(3) **High seed wastage**: Over half of harvested seeds contain underdeveloped embryos, leading to wasted inputs and reduced overall multiplication efficiency.

4. Conventional Asexual Propagation Methods

Vegetative propagation techniques—root layering, stem cuttings, and grafting—are the primary means of preserving elite genotype traits, as they bypass the segregation problem of sexual reproduction. However, each method suffers from distinct technical limitations that restrict scalability (Table 2).

4.1. Root Layering

Root layering involves using root segments from donor trees to generate new plants. This method is operationally simple and requires minimal equipment. However, it is severely limited by the finite root biomass of mature donor trees: each tree provides only 20–50 usable root segments annually, yielding an extremely low multiplication rate. This constraint makes root layering incapable of supporting large-scale nursery demands.

4.2. Stem Cuttings (Hardwood and Softwood)

Cutting propagation has been extensively studied, with protocols optimized for IBA concentration, substrate composition, and greenhouse conditions. Under optimal environ-

ments (automatic mist irrigation, controlled temperature), rooting rates can reach 60%–70%. However, under open-air nursery conditions typical of mountain production zones, rooting rates drop sharply by 30%–50% due to fluctuating temperature, humidity, and wound phenolic oxidation.

The primary physiological barrier is the exudation of urushiol phenolics from wounded tissues, which oxidizes into toxic quinones that inhibit cambial cell division and root primordia initiation. Exogenous hormone application partially mitigates this inhibition, but cannot fully eliminate genotype-dependent variability. Elite cultivars ('Dahongpao', 'Gabachi'), triploid germplasm, and wild provenances display divergent rooting capacities, and no universal protocol achieves consistently high rooting across all genotypes.

4.3. Grafting

Grafting offers the advantage of combining superior scion traits with robust rootstock systems. However, it is plagued by two major problems: (1) scion–rootstock incompatibility, leading to graft failure rates of 15%–30%; and (2) persistent wound gummosis, a pathological condition characterized by abnormal sap exudation that corrodes cambial tissue and impairs long-term vigor. Even successful grafts often show premature senescence after 3–5 years in field cultivation. Systematic screening for compatible, gummosis-resistant rootstock–scion combinations is currently lacking.

4.4. In Vitro Tissue Culture

Tissue culture is theoretically the most powerful clonal propagation pathway, offering high multiplication rates, independence from seasonal constraints, and the potential for large-scale production of selected genotypes. Yet, its practical application in mountain producing regions is severely hindered by high costs and technical obstacles.

4.4.1. Technical Obstacles

(1) **Explant browning**: Phenolic compounds in excised tissues oxidize rapidly upon wounding, causing necrosis and preventing in vitro establishment. Anti-browning agents (activated charcoal, antioxidants like PVP and ascorbic acid) must be added to the medium, significantly raising material costs.

(2) **Microbial contamination**: Surface sterilization and endophytic contamination control are genotype-dependent. While protocols exist for specific diploid cultivars, many wild germplasms and triploid materials maintain contamination and browning rates above 20%, reducing subculture efficiency [22].

(3) **Acclimatization:** In vitro-derived plantlets possess weak stomatal regulation and require carefully controlled shading, misting, and humidity control during greenhouse acclimatization. Most rural nurseries lack the necessary facilities, leading to substantial plantlet loss during the ex vitro transfer stage.

4.4.2. Cost Constraints

The combined costs of anti-browning medium formulation, sterile equipment, skilled labor, and greenhouse facilities make tissue culture approximately 3–5 times more expensive than conventional cutting propagation per surviving plantlet. This economic barrier prevents widespread adoption, particularly in less-developed mountain lacquer-producing areas.

4.5. Genotype-Dependent Response Variability

Across all propagation methods—seed germination, cutting rooting, grafting compatibility, and tissue culture establishment—strong genotype-dependent responses have been consistently documented. Elite cultivars, triploid selections, and wild provenances

each respond differently to standard protocols. This variability implies that no "one-size-fits-all" protocol currently exists, and protocol optimization must be performed on a genotype-specific basis.

4.6. Absence of Unified Technical Standards

China, Japan, and Vietnam each employ isolated operational procedures for seed pretreatment, cutting management, grafting, and tissue culture [19,23]. Even within China's major producing regions (Qinba, Sichuan, Hubei), large discrepancies exist in dewaxing techniques, stratification duration, hormone concentrations, and graft binding practices. No comprehensive local or national standards cover the entire chain from seed harvest to outplanting. Quantitative grading criteria—such as root collar diameter, plantlets height, fibrous root number, and early yield potential—are undefined, hindering commercial evaluation and market regulation of elite clonal stock.

4.7. Summary: A Multi-Layered Constraint System

The limitations described above reveal that *T. vernicifluum* propagation faces not a single isolated bottleneck but a multi-layered constraint system: intrinsic genetic and physiological traits constitute the root cause; conventional vegetative techniques suffer from inherent scalability defects; tissue culture is limited by high industrial costs; molecular knowledge remains insufficient for targeted improvement; and the absence of unified standards leads to disordered plantlets production. These interrelated constraints mutually reinforce each other, forming a closed causal chain that collectively prevents stable, cost-effective, large-scale supply of uniform elite seedlings. The following Discussion interprets the underlying causes of these limitations, and Section 4 proposes targeted solutions to break this constraint chain.

5. Future Research Perspectives

Based on the technical limitations identified in Section 3 and the mechanistic interpretations in Section 5, this section proposes a phased research roadmap that balances short-term field applicability, mid-term standardization, and long-term fundamental breakthroughs.

5.1. Phase I: Fundamental Molecular Dissection of Key Traits (Long-Term Foundational)

The root cause of propagation barriers lies in insufficient understanding of species-specific physiological and molecular networks. This phase should establish a molecular framework to guide all subsequent breeding and technical optimization [19,23].

First, multi-omics combined analysis should be performed to clarify the ABA–GA hormone balance pathway controlling triple seed dormancy. Dynamic changes in gene expression and endogenous metabolites during cold stratification need to be tracked to identify hub transcription factors that switch dormancy release. Comparative omics analysis among Chinese temperate *T. vernicifluum*, Japanese wax lacquer trees, and Mediterranean *Rhus coriaria* can reveal conserved and species-specific dormancy regulatory modules, supporting cross-species technical reference [24].

Second, wound-induced urushiol biosynthesis and phenolic browning pathways require in-depth mining. Key enzyme genes driving quinone toxic substance accumulation after cutting and grafting wounding should be knocked out or overexpressed to verify their inhibitory effects on cambial cell division and root primordia initiation. Such work will fundamentally resolve the low rooting bottleneck caused by endogenous phenolic compounds [3,4].

Third, molecular markers tightly linked to high germination, high rooting, and anti-browning traits should be screened via genome-wide association studies (GWAS). Developed simple sequence repeat (SSR) or single-nucleotide polymorphism (SNP) markers

can be applied to molecular-assisted selection (MAS), accelerating the breeding of new germplasm with weak dormancy and strong rooting capacity [23–25].

5.2. Phase II: Optimization of Low-Cost, Field-Adaptable Asexual Propagation Protocols (Short-Term Implementation)

Conventional vegetative propagation (root layering, cuttings, grafting) dominates nursery production in mountain lacquer-producing regions. Future research should focus on simplifying operation procedures, reducing facility investment, and stabilizing survival rates without relying on high-end greenhouse equipment [16,26].

5.2.1. Compound Low-Cost Root-Promoting Formulations and Open-Air Cutting Facilities

Environment-friendly compound regulators mixed with plant-derived extracts instead of single chemical growth regulators should be developed to alleviate phenolic inhibition on rooting. Portable low-cost shading and intermittent mist devices suitable for scattered mountain nurseries need to be designed to reduce water evaporation and maintain wound humidity, stabilizing open-air cutting rooting rates above 70%. Meanwhile, substrate mixing ratios using local agricultural waste (crop straw, forest humus) should be screened to replace commercial river sand and peat, cutting nursery material costs significantly.

5.2.2. Screening of Compatible, Gum-Resistant Rootstock and Standardized Grafting Workflow

Systematic reciprocal grafting tests between local wild Toxicodendron provenances and high-yield scion cultivars (‘Dahongpao’, ‘Gabachi’) should be carried out to select rootstock materials with strong wound gummosis resistance and long-term field compatibility. Standardized protocols including optimal grafting windows, waterproof wrapping materials, and wound anti-oxidation coating agents need to be formulated to lower graft failure rates and eliminate premature senescence of grafted plantlets.

5.2.3. Simplified Root Layering Clonal Multiplication Technology

To raise the multiplication coefficient of root segment propagation, research on root rejuvenation cultivation of young donor trees should be conducted to increase the yield of thick, high-activity root cuttings annually. Graded root segment classification and targeted exogenous hormone soaking schemes can further improve the emergence uniformity of root-derived plantlets.

5.3. Phase III: Construction of an Integrated Hybridization–Clonal Micropropagation Breeding Pipeline (Medium-Term)

Sexual seed propagation and asexual clonal propagation have complementary advantages: plantlet populations provide abundant variation for elite individual selection, while vegetative propagation stably inherits superior agronomic traits. An integrated breeding system combining sexual hybridization and industrial micropropagation should be established as the core long-term breeding route for lacquer tree elite clones [8].

First, controlled intraspecific hybridization between high-lacquer, drought-resistant, and disease-resistant parent trees should be implemented to construct segregating populations. Superior single plants with stable high yield and strong stress tolerance are screened from hybrid plantlets groups via multi-year field trait identification.

Second, the selected superior individuals are used as explant donors for tissue culture rapid propagation. Optimized low-cost micropropagation media (cheap organic carbon sources substituting sucrose) can reduce the unit cost of tissue-cultured plantlets. The pipeline unifies germplasm innovation and mass plantlets supply, overcoming the respective defects of single sexual breeding or asexual propagation modes [27].

5.4. Phase IV: Formulation of Cross-Regional Unified Technical Standards for Plantlets Production (Medium-Term)

The lack of standardized operating specifications across lacquer-producing regions leads to uneven plantlet quality and hinders the commercial circulation of elite clones. Future collaborative research among China, Japan, and Vietnam should focus on establishing unified industry-wide technical specifications covering the whole breeding chain.

(1) Full-process operating standards: Formulate uniform technical regulations for seed collection, dewaxing, scarification, cold stratification, sowing, cutting pretreatment, grafting management, and in vitro disinfection and subculture, adapting to temperate, subtropical, and tropical lacquer tree cultivation zones.
(2) Quantitative plantlets grading standards: Establish clear classification thresholds based on root collar diameter, plantlets height, fibrous root number, and early lacquer yield potential, separating qualified commercial plantlets from inferior individuals and standardizing market trading evaluation indicators.
(3) Field technical operation manuals oriented to mountain smallholder nurseries: Simplify complex laboratory protocols into operable field guidance documents to lower the technical threshold for grassroots growers.

5.5. Phase V: Development of Automated Bioreactor Micropropagation for Industrial Plantlets Supply (Long-Term Industrial)

Traditional solid medium tissue culture relies on intensive manual labor and limited subculture efficiency. Automated liquid culture systems represented by temporary immersion bioreactors are the key direction to realize large-scale, low-cost factory plantlet production in the future [28,29].

First, temporary immersion bioreactor culture systems should be optimized for lacquer tree explants. Adjustable immersion frequency, nutrient solution composition, and light quality regulation schemes can simultaneously improve proliferation coefficients and rooting efficiency, shortening the micropropagation cycle by 30%–50% compared with solid medium culture.

Second, low-cost light-emitting diode (LED) spectrum regulation technology should be matched with liquid culture to strengthen plantlets lignification during the rooting stage, reducing mortality during greenhouse acclimatization.

Third, miniaturized, low-price bioreactor equipment suitable for county-level medium-sized nurseries should be developed to break the high-facility-input barrier restricting the popularization of tissue culture technology in remote mountain lacquer production zones.

5.6. Integrated Roadmap Summary

This phased approach ensures that (a) nurseries receive near-term improvements, (b) scientific research addresses fundamental questions, and (c) industrial-scale production becomes progressively feasible. It avoids the risk of over-investing in laboratory-only solutions that cannot be transferred to production settings, while maintaining a clear trajectory toward genetic-level breakthroughs.

6. Conclusions

This review provides the first comprehensive, cross-regional synthesis of sexual and asexual propagation research in *Toxicodendron vernicifluum*, integrating quantitative comparisons across China, Japan, Vietnam, and Mediterranean Rhus species. The following main conclusions emerge:

Seed propagation suffers from triple-layer dormancy (physical, mechanical, and physiological) and irreversible genetic segregation. Although optimized pre-germination proto-

cols (alkali rubbing + cold stratification) achieve 72%–82% germination, the long stratification cycle (14–18 months) and unstable seed supply limit industrial applicability.

Conventional asexual propagation methods—root layering, stem cuttings, and grafting—preserve elite genotypes but each faces distinct scalability constraints: low multiplication rates, genotype-dependent rooting variability (30%–70% under optimal conditions, dropping 30%–50% in open-field nurseries), and graft incompatibility/gummosis (15%–30% failure rate).

Tissue culture offers the highest theoretical multiplication potential but is constrained by explant browning, genotype-dependent contamination, high costs (3–5× conventional methods), and insufficient acclimatization infrastructure in mountain nurseries.

A central cost–uniformity dilemma characterizes T. vernicifluum propagation: no single method simultaneously satisfies genetic uniformity, scalability, and low cost, creating a structural barrier to industrialization.

Key knowledge gaps include the lack of validated molecular mechanisms for dormancy release and wound-induced rooting inhibition, absence of multi-omics studies, and insufficient long-term field performance data for clonal plantlets.

Future priorities should focus on: (a) molecular dissection of dormancy and rooting regulatory networks using multi-omics approaches; (b) optimization of low-cost, field-adaptable vegetative protocols; (c) establishment of cross-regional unified technical standards; and (d) development of automated bioreactor systems for industrial micropropagation [29].

This integrated framework provides theoretical guidance for elite lacquer plantlet production in the Qinba Mountains and other East Asian lacquer-producing regions, and offers comparative insights for propagation research on other hard-to-root woody economic species.

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Abbreviations

ABA—Abscisic acid; DNA—Deoxyribonucleic acid; GA3—Gibberellic acid; GA—Gibberellin; GWAS—Genome-wide association study; LED—Light-emitting diode; MAS—Marker-assisted selection; RNA—Ribonucleic acid; SNP—Single-nucleotide polymorphism; SSR—Simple sequence repeat.

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