Genetic and phylogenetic comparisons of the fast-growing species in genus *Neolamarckia* for breeding and industrial exploitation

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Abstract

The *Neolamarckia* Bosser genus consists of two species: *Neolamarckia cadamba* (Roxb.) Bosser and *Neolamarckia macrophylla* (Roxb.) Bosser, which are highly valued for industrial and medicinal applications in South Asian countries. The two species are sympatric and share several important characteristics in growth, wood quality, phytochemicals, and secondary metabolites. *N. cadamba* has been extensively utilized while *N. macrophylla* is rarely exploited. This article provides an overview of these two species from various aspects, specifically emphasizing their genetic relationships. Based on the organelle genomes, a single gene linked to cellulose synthesis, and molecular markers, the interspecific variation was initially analyzed, revealing a close genetic relationship between the two species. These results highlight the potential for cross-species research and pave the way for further exploration. Their evolutionary divergence and taxonomic positions within the *Rubiaceae* family require further clarification through nuclear genomes. Both species exhibited a moderate level of genetic diversity within populations in terms of nucleotide diversity per site with nrDNA ITS markers (π=0.1185±0.0242) for *N. cadamba* or heterozygosity with SSR markers (0.05~0.29) for *N. macrophylla*. While population genetic structure assayed with molecular markers was generally low in *N. cadamba* (Fst≈3 % in China), it could be high in *N. macrophylla* (Φ_st≈ 55 % in Indonesia). Quantitative genetic differentiation in wood traits was small among provenances of *N. cadamba* but remains to be investigated in *N. macrophylla*. The two species potentially have similar wood properties and low heritability of wood traits. Molecular studies on wood traits in both species are limited, emphasizing the significance and urgency of future research on genetic improvement of wood traits for industrial purposes, prompting action and making progress in this area.

Key words: *Rubiaceae*; *Neolamarckia cadamba*; *N. macrophylla*; phylogenetic relationship; wood property traits; breeding; tropical trees

Introduction

The *Neolamarckia* genus belongs to the Rubiaceae family that together with other four families (Apocynaceae, Gelsemiaceae, Gentianaceae and Loganiaceae) constitute order Gentianales Juss. Ex Bercht. & J. Presl within Lamiids in the Asterids clade (Angiosperm Phylogeny Group 2016). The Rubiaceae family is placed in the core eudicots in angiosperms and forms an evolutionary clade that was early divergent from the other four families in the Gentianales order (https://www.mobot.org/mobot/research/apweb/, accessed on December 27, 2025) (Bremer 1996, Potgieter et al. 2000, Backlund et al. 2000). This family represents an ancient lineage, traceable to the Late Cretaceous, and constitutes a large and phylogenetically complex group. It is one of the most species-rich angiosperm families, with approximately 17,268 species (https://www.gbif.org/species/8798, accessed on December 27, 2025), and is divided into three subfamilies (Cinchonioideae, Ixorioideae, and Rubioideae) with more than 600 genera. The Rubioideae subfamily is much early divergent from Ixorioideae and Cinchonioideae in lineage sorting (Bremer and Eriksson 2009). One notable common feature among five families of the Gentianales order is rich in highly bioactive secondary metabolites, prominently represented by iridoids and monoterpene indole alkaloids. These compounds show great promise for traditional medicine, modern pharmacology, and apiculture, and of great phytomedical and economic values.

Among three sub-families of Rubiaceae, genus *Neolamarckia* was placed in Trib. Naucleeae DC. ex Miq. of the Cinchonioideae subfamily (Luo et al. 1999, Bremer and Eriksson 2009). The Neolamarckia genus is composed of only two species, *N. cadamba* and *N. macrophylla*. *N. macrophylla* can be morphologically distinguished from *N. cadamba* by its more robust and rose-coloured leaves (Haviland 1897). The genus is primarily found in Southeast Asia, South Asia, and Australia. *N. cadamba* has a broader natural distribution in Vietnam, Malaysia, Myanmar, India, Sri Lanka and southern China (e.g., Guangdong, Guangxi, and Yunnan Provinces) (Luo et al. 1999, Tao and Taylor

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2011) (Figure 1). *N. cadamba* has a long history of domestication and cultivation in its native habitats. This species is a pioneer tree that thrives in habitats with high humidity and fertile soil in tropical regions, such as riverbanks, swamps, and periodically waterlogged areas. Unlike *N. cadamba, N. macrophylla* is a threatened species and only distributed in Indonesia although it is sympatric with *N. cadamba* across a broad geographical range (Husna 2021). From the literature, *N. macrophylla* has not been as extensively studied as *N. cadamba*. Whether *N. macrophylla* possesses similar biological properties to *N. cadamba* for industrial and medical applications has not been assessed.

It is recognized that *N. cadamba* is characterized by fast growth and slow aging. *N. cadamba* can achieve annual growth of 2-3 m at 2-5 years old after planting and reach a height of 25 m at 14 years old (Su et al. 2007). *N. cadamba* also possesses high-quality wood with lengthy wood fibers. Its fiber width, cell wall thickness, and stiffness coefficients are comparable to those of *Pinus kesiya* Royle ex Gordon and *Picea abies* (L.) H. Karst. (Lal et al. 2010). The wood has a low lignin content but a high total cellulose content, making it suitable for pulp production. As an ornamental and timber species, *N. cadamba* was artificially introduced to African and Central American regions, exceeding its natural distribution shown in Figure 1 (Julius 1984, Ismaill et al. 1995). More dynamic distributions of *N. cadamba* across years were mapped in detail at GBIF (Global Biodiversity Information Facility) website (https://www.gbif.org/species /2896883, accessed on December 27, 2025).

Another remarkable feature of *N. cadamba* is its long history as a medicinal plant in Southeast and South Asian countries, such as the Philippines and India (Dubey et al. 2011). The extracts from the bark of *N. cadamba* are utilized for treating fever, cough, various wounds, and diabetes. The bark contains multiple flavonoids, alkaloids, and terpenoids, which possess significant medicinal properties, including antioxidants, antidiarrheal, and anti-tumour effects. Several reviews on *N. cadamba* have been conducted from physiological, ecological, phytochemical, and pharmacological perspectives (Pandey and Negi 2016, Singh et al. 2023, Verma et al. 2018, Yadav et al. 2022). *N. cadamba* has been extensively utilized for industrial and medicinal purposes and holds significant economic value in tropical regions. Additionally, the species offers other significant features, such as leaves that serve as animal forage. The flowers are a good source of honey and edible fruits or additives to foods. The tree's straight and cylindrical stem shape makes it suitable for landscaping and economic purposes, earning it the nickname "miracle tree" (Dwivedi et al. 2015). *N. cadamba* is a valuable resource plant with promising development prospects and application values. This review focuses on assessing (1) the genetic similarities and differences between *N. cadamba* and *N. macrophylla* at the species and population levels and (2) their genetic variations in wood traits. The two species have not been concurrently evaluated from these aspects in literature.

Although there are extensive studies on *N. cadamba* in industrial and medicinal applications (Pandey and Negi 2016), few studies are recorded on *N. macrophylla*. Here we review the similarity and differences between these two species and infer their potentially parallel industrial values. Our inferences are based on reviewing their phylogenetic relationships, population genetic structure, genetic variation, and molecular mechanisms related to wood traits. We also explore genetic conservation of *N. macrophylla* due to its endemic to local habitats in Indonesia.

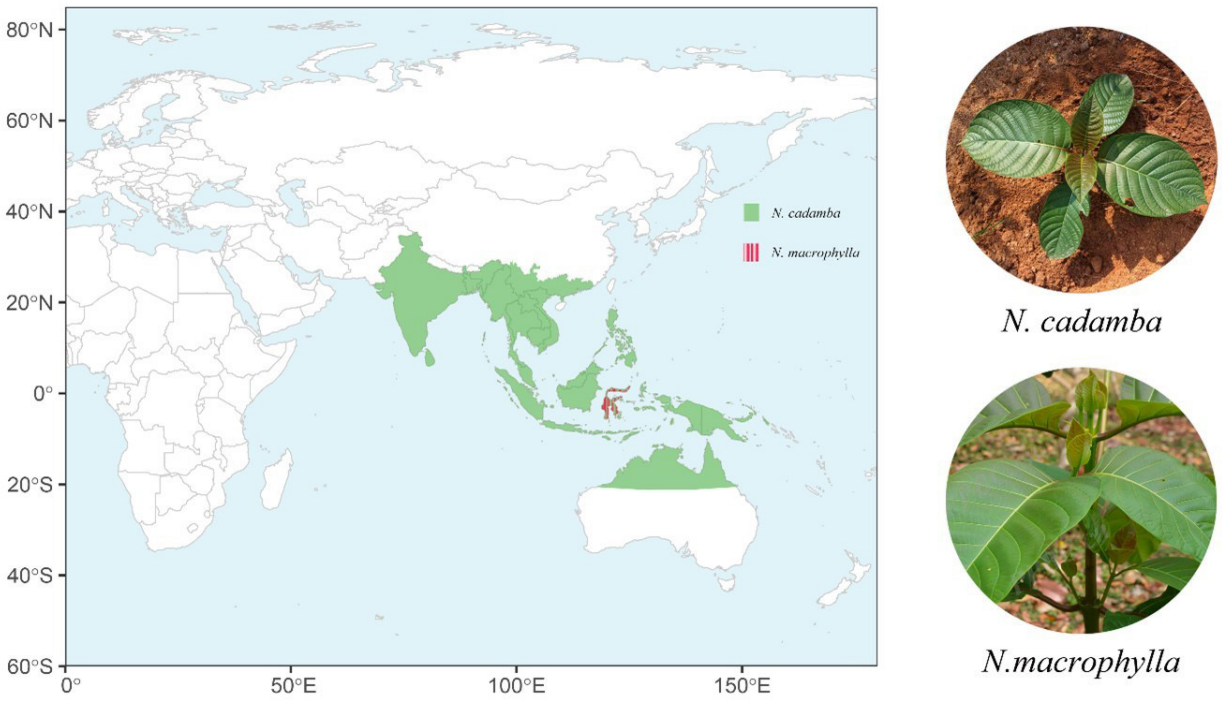

Figure1
Natural distributions of *N. cadamba* and *N. macrophylla*. The regions in green are the distribution areas of *N. cadamba*, and in red vertical lines for the natural distribution areas of *N. macrophylla*. The distribution map was created with R statistical software utilizing the rnaturalearth package v.1.0.1 (South 2023) for spatial data visualization. Image for morphology of *N. macrophylla* (credit: Zhuomin Shen, Plant Photo Bank of China [PPBC ID: 18389809]) was from Xishuangbanna, Yunnan, China, and retrieved from https://ppbc.iplant.cn/tu/18389809, accessed on August 31, 2025). Image for morphology of *N. cadamba* (credit: Chao Wu) was from South China Agricultural University, Guangzhou, China.

Comparison of inter- and intra-specific genetic variation

Species uncertainty in taxonomy

The historical classification of the Rubiaceae family has been a subject of great concern, leading to uncertainty in the taxonomic division of genus *Neolamarckia*. The Rubiaceae family was officially named in 1789 (Anderson 1982) and distinguished by its opposite leaves and stipules, which are significantly different from those of other plant families. According to the GBIF at website (https://www.gbif.org/species/8798, accessed on December 27, 2025), this genus has many synonyms. In terms of taxonomy, this family is most closely related to the Lonicera and Malvaceae families (Nayan et al. 2019, Robbrecht 1988). Initially, the family was divided into two parts based on the number of ovules in the ovary carpel. Later, the Rubiaceae family was further divided into four subfamilies, including Cinchona, Dracaenopsinae, and Coastal Kirinae subfamilies (Bremekamp 1952). Subsequently, four additional subfamilies were identified: Hillioideae, Gleasonioideae, Pomazotoideae, and Urophylloidee. Based on various morphological and anatomical characteristics of the leaves, including dimples, crystals, soft hairs, small tumours, corollas, nuts, outer seed coat, endosperm, and pollen, the Rubiaceae family was classified into four subfamilies: the primitive Ixoroideae subfamily, the evolved Rubiaceae subfamily, and the intermediate transitional Cinchonoideae and Luculioideae subfamilies (Robbrecht 1988). Our current systematic analysis of the Rubiaceae family is based on these four subfamilies. The genus *Neolamarckia* is classified into the Cinchonoideae subfamily, the Naucleeae tribe (Luo et al. 1999, Bremer and Eriksson 2009).

The species names in genus *Neolamarckia* Juss. have undergone multiple changes. According to the Royal Botanic Gardens at Kew (https://powo.sciece.kew.org/; accessed on 10 August 2024) or GBIF at website (https://www.gbif.org/species/2896888, accessed on December 27, 2025), N. cadamba has several synonyms, including *Nauclea cadamba* Roxb., *Anthocephalus cadamba* (Roxb.) Miq., *Sarcocephalus cadamba* (Roxb.) Kurz, *Samama cadamba* (Roxb.) Kuntze, *A. indicus* var. *glabrescens* H.L.Li (Li 1944), *A. indicus* var. *macrophyllus* Pierre ex Pit., *A. morindifolius* Korth., and *N. megaphylla* S. Moore. These homotypic and heterotypic synonyms imply historical uncertainty in nomenclating this species.

Similarly, the name of *N. macrophylla* has also undergone multiple changes. According to the Royal Botanic Gardens at Kew (https://powo.sciece.kew.org/, accessed on 10 August 2024) or GBIF at website (https://www.gbif.org/species/2896884, accessed on December 27, 2025), it had several

homotypic or heterotypic synonyms, including *Nauclea macrophylla* Roxb., *Anthocephalus macrophyllus* (Roxb.) Havil, *Bancalus macrophyllus* (Roxb.) Kuntze, and *N. elegans* Teijsm. & Binn. ex Hassk. Bosser (1984) corrected the genus name and classification that was previously established due to specimen confusion, taxonomic errors in merging, and incomplete information, and established genus *Neolamarckia*. The only two species in the genus, namely *N. macrophylla* and *N. cadamba*, have been used until today (Julius 1984, Wang 2000). These complexities underscore the significance of elucidating the genetic relationships and taxonomic positions of the two species in genus *Neolamarckia* of the Rubiaceae family.

The two species can be identified through leaf morphologic traits and flower structure. According to Ridsdale (1978), the leaves for *N. cadamba* (synonym *A. chinensis*) have distinct petioles. The upper part of ovary is distinctly four-loculed and has four hollow cartilaginous structures. The leaves of *N. macrophylla* (synonym *A. macrophyllus*) are more or less sessile. The upper part of ovary is two-loculed and has four solid small cartilaginous structures.

Phylogenetic relationship

First we evaluate the phylogenetic relationship between *N. macrophylla* and *N. cadamb*a, which is rarely recorded in literature. Chang et al. (2014) compared a cellulose synthase gene between these two species and revealed that *N. macrophylla* and *N. cadamba* were genetically closely related. The sequences of the sucrose synthase gene (*Nmsusy1*) of *N. macrophylla* were highly homologous with gene *Susy1 Coffea arabica* L. (89 %), *Susy1 C. canephora* (86 %) and *Susy2 C. canephora* (88 %) in the same family (Tan et al. 2014). Note that the *Coffea* genus was placed in Trib. Coffeeae of the Ixoroideae subfamily (Bremer and Eriksson 2009). Based on the chloroplast genome, Shi et al. (2020) showed that the two species were genetically closely related, and the genus *Neolamarckia* was close to *Antirhea chinensis* (Champ. Ex Benth.) Benth. & Hook. f. ex. F.B. Forbes & Hemsl. The two species have comparable genome sizes (154,999bp for *N. cadamba* and 155,406bp for *N. macrophylla*). Based on the mitochondrial genome, Xie et al. (2026) showed that *N. macrophylla* and *N. cadamba* were divergent from their ancestral populations at about 6.757 Mya (2.472-12.1107 for 95 % HPD), supporting that the two species were more recently divergent. *N. cadamba* has a larger mitochondrial genome size than *N. macrophylla* (414,980 vs. 289,793 bp) and more tRNA genes. Purifying selection was the dominant process to impede genomic divergence at the protein-coding genes (Xie et al. 2026).

Most studies investigated the phylogenetic relationship between *N. cadamba* and other species in the same or different families. Wang et al. (2021) sequenced mitochondria genome sequences of *N. cadamba* and supported that *N. cadamba* belongs to the Gentianales order and was separated from species in the Apocynaceae family. Based on the nuclear genome sequences (genome size 744.5 Mb in total), Zhao et al. (2022) showed that *N. cadamba* had a close genetic relation to *Coffea canephora* Pierre ex A. Froehner and *Ophiorrhiza pumila* Champ. Ex Benth. of the same family. The *Ophiorrhiza* genus belongs to the Rubioideae subfamily (Bremer and Eriksson 2009). *N. cadamba* was divergent from *O. pumila* at about 41.7 Mya and from *C. canephora* at about 31Mya. It is clear that the divergent time between *N. cadamba* and *N. cadamba* is much less than this magnitude.

One feature is concerned with the evolution of the *LAMT* gene that is relevant to the biosynthesis of cadambine. Only one copy of the *LAMT* gene occurred in *C. canephora* and *O. pumila* genomes. In contrast, the *LAMT* gene in *N. cadamba* was duplicated from the recent whole genome duplication (WGD) event (Zhao et al. 2022). Rai et al. (2021) discovered that three key N-methyltransferases (NMTs) important for caffeine biosynthesis are lost in *N. cadamba* genomes. They are xanthosine methyltransferase (CcXMT), theobromine synthase (7-methylxanthosine methyltransferase, CcMXMT), and caffeine synthase (3,7-dimethylxanthosine methyltransferase, CcDXMT). The key residues Gln161, Ile266, Ser316, and Tyr356 of CcXMT1 were no longer conserved in the amino acid sequences of homologs in *N. cadamba*. This probably explains the inability of *N. cadamba* to synthesize caffeine due to the lack of xanthosine (Zhao et al. 2022). Two emerging questions are: (1) How many copies of the *LAMT* gene are present in *N. macrophylla*? (2) Are there sequence divergences between *N. macrophylla* and *N. cadamba* in genes coding the three NMT enzymes? Given the close phylogenetic relationship between the two species, it is hypothesized that *N. macrophylla* could have more than one copy of the *LAMT* gene and lost the three NMT enzymes. The precise answers to these two questions need strict comparisons of relevant gene sequences.

Molecular population genetic diversity

How their geographical distributions affect the population structure of these two species remains to be fully explored. Their substantial differences in natural distribution could yield distinct patterns of geographical variation. Genetic studies on *N. cadamba* at the population level have explored various aspects, including transcriptomic analysis (Ouyang et al. 2016) and provenance trials (Que et al. 2021). However, studies with molecular markers to examine phylogeographical variation and population genetic structure across the entire range of species are scarce. Ying et al. (2014) employed ISSR (inter-simple sequence repeat) markers to assess genetic differentiation between two artificial populations and among six natural populations in Malaysia. Their findings indicated that most genetic variation was within populations (G_{st}=8.71 % for two artificial populations and G_{st}=20.13 % for six natural populations).

Wang et al. (2021) and Lv et al. (2023) utilized ITS (internal transcribed spacer) sequences from nuclear DNA (nrDNA) and two SNPs (single nucleotide polymorphisms) markers from mtDNA to investigate the population genetic variation of *N. cadamba* in China. Their research covered ten populations (256 individuals) across the natural distribution of the species in China and one population from Indonesia. Their findings indicated that the nucleotide diversity per site was not low for the nrDNA ITS markers (π=0.1185±0.0242) but low for the mtDNA markers (π=0.00038±0.00052). The haplotype diversity for

the mtDNA markers was lower compared with estimates of other angiosperms (Lv et al. 2023). Both marker analyses revealed the absence of phylogeographical structure (G_{st}>N_{st}). Most genetic variation occurred within populations for the nrDNA ITS marker (F_{st}= 2.25 %) but among populations for the mtDNA markers (F_{st}=71.2 %), suggesting that more extensive pollen flow rather than seed flow occurred among populations (the ratio of the migration rate of pollen to the migration rate of seeds was much greater than 1). Moreover, the research concluded that there were no isolation-by-distance (IBD) effects across the natural distribution of *N. cadamba* in China (Lv et al. 2023). A few local populations of *N. cadamba* potentially underwent historical population expansion after bottleneck effects (negative but not significant Tajima's D values; Lv et al. 2023).

Research on *N. macrophylla* has focused on genetic and breeding studies from various aspects, including enhancing seed germination and seedling quality through hormonal and biopriming methods (Yuniarti et al. 2023), as well as inducing genetic variation through gamma irradiation (Larekeng et al. 2022). Preliminary genetic diversity and structure investigations in *N. macrophylla* have been conducted using molecular markers. Arif et al. (2019) utilized 3 SSR (simple sequence repeats) markers to assess genetic diversity in three provenances in South Sulawesi, Eastern Indonesia. The observed heterozygosity (H_e) ranged from 0.05 to 0.29, indicating low genetic diversity. Additionally, it was found that genetic variation was predominantly distributed among populations (ϕst=55%), which is distinct from the population structure of *N. cadamba* (Lv et al. 2023). This pattern also implies that multiple populations should be concerned with conserving genetic resources of *N. macrophylla*.

Generally, research on population genetic variation in these two species is still in its early stages. Each species needs comprehensive overviews on the population's genetic makeup across their natural ranges or countries. A key consideration is to understand the mating system of these species, mainly because the taxa are zoogamous and insects, such as bees, butterflies, and beetles, act as pollinators. The *Neolamarckia* tree produces spherical clusters of flowers, each containing numerous small flowers and measuring approximately 5 cm in diameter (Yadav et al. 2022). The flowers are hermaphroditic, featuring a five-lobed corolla and numerous stamens. The possibility of partial selfing and inbreeding cannot be ruled out, particularly in the case of *N. macrophylla*, which has a limited and fragmented distribution in Indonesia (Arif et al. 2019). Larekeng et al. (2019) investigated mating systems of three natural populations of *N. macrophylla* using three SSRs, showing that the selfing rate was about 23.1 %. Such mixed mating systems provide useful information for us to understand population genetic structure and to develop conservation strategies or breeding programs for *N. macrophylla*. The mating system of *N. cadamba* remains to be scored.

Comparison of variation in wood traits

In this section, we discuss the similarity and differences between the two species in the context of wood traits and properties. It is recognized that *N. cadamba* holds significant industrial importance in various domains (Yadav et al. 2022, Herawati et al. 2024). These include multiple utilizations in woodworking products, such as plywood and particleboard in pulp and paper industry, and in pharmaceuticals, forest ecosystems, horticulture, landscape architecture, and animal forage. Extensive literature reviews have documented its phytochemical profiles, including alkaloids, flavonoids, saponins, terpenoids, and tannins, along with their pharmaceutical uses (Pandey and Negi 2016, Qureshi et al. 2021, Balan et al. 2025). Both species could yield new pharmacologically active compounds, holding great promise for developing new drugs and disease treatments. Our focus in the following two subsections is on research progress in physical properties and genetic variation of wood traits, which are important to meet diverse industrial demands.

Physical properties of wood traits

The fundamental physical and chemical properties of wood play an essential role in determining wood quality for industrial applications (Latib et al. 2014, Cahyono et al. 2016). For example, specific gravity (SG) is a critical factor in veneer production (Lutz 1978). Physical properties typically encompass wood moisture content, specific gravity, density, shrinkage, and swelling. Meanwhile, mechanical properties include static bending, compression parallel to the grain, compression perpendicular to the grain, and compression shear parallel to the grain. Latib et al. (2014) examined the physical and chemical properties of three *N. cadamba* trees with a diameter at breast height (DBH) ranging from 35 to 41cm. They observed that SG decreased from the bottom to the middle to the top portion of the tree but decreased from near bark to middle to near pith. The percentage of moisture content increased from the bottom to the top portion. Notably, the tree portion did not impact cold and hot water solubility, alkali solubility, alcohol-toluene solubility, ash content, and lignin content.

Most studies focused on *N. cadamba* rather than *N. macrophylla*. Mahmud et al. (2017) demonstrated that the moisture content of *N. cadamba* under dry conditions was similar to that of other timber species. At the ninth year (juvenile stage) of plantations, the basic wood density (g/m^3) was lower than that of certain plant species, such as *Azadirachta excelsa* (Jack) Jacobs, *Acacia mangium* Willd., and Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg. (Trockenbrodt et al. 1999). Wood shrinkage and swelling were twice as much in the tangential direction compared to the radial direction. Significant differences in physical properties were noted between the lower and upper portions of the trunk. It was also found that the mechanical properties of oven-dried wood were considerably more robust than air-dried wood's, with variations from the lower to upper portions. Parthiban et al. (2019) compared plywood density, modulus of elasticity (MOE), and modulus of rupture (MOR)

among eight species at 5 to 6 years old, indicating that *N. cadamba* fell within the ranges of different measurements.

Table 1 presents the basic wood properties of *N. cadamba* and *N. macrophylla* obtained at the juvenile phase at eight years old (Cahyono et al. 2016, Que et al. 2022, He 2024) and 3.5 years old (Anna et al. 2020) with samples collected at DBH. Both species showed some differences in basic wood properties, but their comparisons remain to be statistically tested. According to the International Association of Wood Anatomists (IAWA) classification (Wheeler et al. 1989), the fiber lengths (FLs) of both species were medium. It is expected that these closely related species would generally exhibit similar physical properties of wood.

Table 1
Comparison between *N. cadamba* and *N. macrophylla* in basic wood properties

Traits	*N. cadamba* *	*N. cadamba* #	*N. macrophylla* †
Diameter at the breast height (DBH) (cm)	10.56±2.38	11.56±1.38	39-40
Fiber length (FL)(µm)	1411.37±11.81	1183.28±83.87	1546.53 ± 198.8
Fiber diameter (FD)(µm)	32.48±1.19		
Fiber wall thickness (FWT) (µm)	5.32±0.64		5.94 ± 0.76
Vessel length (VL)(µm)	663.17±8.43		
Vessel diameter (VD)(µm)	158.00±5.21		
Microfibril angle (MFA) (°)		11.54±3.56	37.10 ± 8.49
Average density (AD) (g/m3)	0.33±0.18	0.94±0.00	
Sapwood density (SW) (g/m3)	0.336±0.18		
Specific gravity (SG)		0.46±0.02	0.37±0.01~ 0.43±0.02
Air-dried moisture content (%)		13.62±0.37	
Modulus of elasticity (MOE) (kg/cm2)		51006.48±8667.76	
Modulus of rupture (MOR) (kg/cm2)		488.20±72.96	

* References from Que et al. (2022) and He (2024); # Reference from Anna et al. (2020); † Reference from Cahyono et al. (2016)

Latib et al. (2014) demonstrated that *N. cadamba* possesses various chemical properties, with 5.56 % cold water solubility, 6.56 % hot water solubility, and 18.22 % alkali solubility (NaOH), primarily attributed to hemicellulose or degraded cellulose. The wood exhibited 2.45 % solubility in alcohol toluene, 0.62 % ash content, 28.57 % lignin content, and 83.87 % holocellulose solubility in cold and hot water. Amirta et al. (2016) and Rahman et al. (2021) also conducted alkaline treatment studies and obtained similar results. Mukhdlor et al. (2021) investigated the chemical properties of *N. macrophylla* (synonym *A. macrophyllus*) and found 24.04 ± 0.17 % lignin content, 36.06 ± 0.50 % alpha-cellulose, 68.67 ± 0.33 % holocellulose, 0.65 ± 0.03 % ash, 73.22 ± 0.07 % volatile matter, and 17.41 ± 0.06 % fixed carbon. The lignin and holocellulose contents were slightly lower compared with *N. cadamba*, suggesting the need for a more comprehensive comparison with additional experimental data and statistical tests.

Genetic variation of wood traits

Similarly, most studies in literature were on *N. cadamba* to evaluate genetic variation of growth traits in existing populations for genetic improvement, with a few studies on estimating genetic variation in wood traits. For example, Parthiban et al. (2019) conducted an experiment using twenty genotypes of *N. cadamba* at the Forest College and Research Institute, Tamil Nadu Agricultural University, Mettupalayam (11°19'N, 76°56'E), 300 msl, 800 mm, pH 7.1) from 2010 to 2016. They estimated the genetic coefficient of variation (GCV) for height (14.27 %), circumference at breast height (14.04 %), and volume (40.53 %). The moderate heritability values of 0.35 for tree height, 0.50 for circumference at breast height, and 0.51 for volume indicated the potential for further improvement among the twenty genotypes. Sudrajat et al. (2019) also established a provenance-progeny test in Parung Panjang, Bogor District, West Java Province, Indonesia, to assess seedling

growth traits in the nursery and field. However, genetic variation in wood traits remains to be quantified.

Anna et al. (2020) carried out a provenance-progeny trial of *N. cadamba* at the Parung Panjang Research Forest Station in Bogor, Indonesia. The research involved samples from 12 provenances (105 families) in Indonesia. The study focused on assessing variations in growth (height, diameter), pilodyn penetration, and physical wood properties of core samples, as well as characterizing the wood properties. Significant differences among provenances were observed in these traits. Heritability estimates for individual traits were generally low, ranging from 0.025 to 0.181, but moderate for family heritability, ranging from 0.04 to 0.296. Additionally, the study found weak correlations between wood physical properties and growth traits. Among provenances, minor phenotypic variations were observed in MOE, MOR, and fiber length (FL). These results suggested that specific genetic improvement in some wood physical properties could be expected through selection at the family level rather than at the individual level or the provenance level.

The South China Agricultural University (SCAU) research group collected seeds from 73 families across 11 different provenances in China and added a germplasm source from Indonesia in 2012. They conducted a provenance-progeny test at the Jijia Town Forest Farm, Leizhou Forestry Bureau, Leizhou City, Guangdong Province, China (110°21′34″E, 21°10′06″N). The experimental site experiences a humid monsoon climate, with an average annual sunshine duration of 2003.6 hours and an average annual temperature of 22°C. Over the years, the group has examined both growth and wood traits (Que et al. 2022, He 2024).

According to the findings of the provenance-progeny test conducted by Que et al. (2021, 2022), analysis of the experimental data at age five years revealed the following conclusions: (1) Significant differences were observed among provenances in vessel length (VL), vessel diameter (VD), and average density (AD). Similar to the DBH and height traits, these wood characteristics also showed geographical variation. (2) Insignificant differences were found among provinces in fiber length (FL), fiber diameter (FD), the ratio of FL/FD, vessel length (VL), vessel inner diameter, and the degree of crystallinity (Cr). (3) The provenance heritability of wood property traits was estimated as 0.02 for FL, 0.16 for the ratio of FL/FD, 0.07 for VL, 0.45 for AD, and 0.11 for Cr. The genetic coefficient of variation (GCV) ranged from 0.59 % to 2.96 %. Additionally, weak correlations were identified between growth and wood property traits (Que et al. 2022, He 2024). These findings suggest that genetic improvement may be constrained by provenance selection and that simultaneous improvement of both wood property and growth traits would be challenging.

Tchin et al. (2012) identified four and six SNPs from C4H (cinnamyl alcohol dehydrogenase) and CA (cinnamate 4-hydroxylase) genes, respectively, which were significantly associated with wood density. Tiong et al. (2014) identified two SNPs from the xyloglucan endotransglycosylase/hydrolase (*NcXTH1*) gene that were significantly associated with the basic wood density of *N. cadamba*. These SNPs could be potentially used for gene-assisted selection of wood density. Que et al. (2022) and He (2024) conducted GWAS analysis to search for SNPs associated with wood property traits by re-sequencing 108 individuals sampled from 10 provenances. Both found multiple SNPs significantly associated with wood density and vessel diameter (VD) but did not find SNPs associated with FL, FD, FWT, and VL. More samples of resequencing are now undergoing further GWAS analysis.

The aforementioned provenance trials of *N. cadamba* conducted in Indonesia and China suggested small genetic variation among provenances in growth and wood property traits. For the wood property traits with insignificant provenance differentiation, such as FL, FD and VL in Que et al. (2022), they could arise from effects of the similar selection models among provenances (e.g., similar stabilizing or the same directional selection) or from effects of extensive gene flow, as implied from small population genetic structure derived from nrDNA ITS markers (Lv et al. 2023). Whether these wood property traits are neutral or not remains to be determined. For the wood property traits with significant provenance differentiation, such as VL, VD and AD in Que et al. (2022), distinct selection models among provenances could play dominant roles that overcame the homogenizing effects of gene flow. This probably arose from long-term adaptation to habitats with distinct ecological factors. The overall provenance trials imply that genetic improvement should focus on studying the superior family and individuals within the family, emphasizing genomic selection and polyploidization breeding.

Only a few studies are available on wood traits of *N. macrophylla*. A progeny test was carried out in Gowa, South Sulawesi, Indonesia (Aida et al. 2019). This study investigated 108 families collected from 10 seed zones. Initial analysis of the 2-year-old stand revealed a heritability of 0.2337 for height and 0.1873 for DBH at the family level. The genetic correlation between height and DBH was found to be 0.9121. Another progeny test of *N. macrophylla* was carried out in West Seram District, Maluku Province, Indonesia (Suseno et al. 2021), involving 80 families. The results showed significant differences among provenances in height and DBH at four years old. High heritabilities at individual and family levels were observed for height and DBH. However, genetic variations in the physical properties of wood traits remain to be explored in future studies.

Molecular mechanisms of wood properties

We finally review molecular studies on wood property traits of these two species. The physical properties of wood encompass a wide range of traits, which have been the subject of significant research progress in the molecular mechanisms of wood formation in genus *Neolamarckia*, thanks to the application of transcriptomic and genomic sequencing technologies. Through transcriptomic analysis, researchers have identified potential genes linked to wood traits. Ho et al. (2014) identified numerous xylogenesis unigenes from expressed sequence tags (ESTs). Tiong et al. (2014) characterized in silico the cellulose synthase gene (*NcCesA1*) in developing xylem tissues of *N. cadamba*, and Pang et al. (2015) used expressed sequence tag (EST) sequencing of cDNA clones to identify essential

genes involved in xylogenesis and lignin biosynthesis of *N. cadamba* (Huang et al. 2014). These genes include tubulin genes, cellulose synthase (*CesA*), xyloglucan endotransglycosylase (XET), arabinogalactan, cinnamate 4-hydroxylase (*C4H*), caffeoyl coenzyme A O-methyltransferase (*CCoAOMT*), and peroxidase. Further research is necessary to understand the functions of these genes in wood formation.

Specific genes related to wood formation were identified and functionally annotated in *N. cadamba*. Bai (2016) cloned three sucrose transport genes, namely *NcSUT2, NcSUT3*, and *NcSUT4*, from the phloem of *N. cadamba*. These genes were localized in various sub-cellular locations, such as the plasma membrane and chloroplasts (Halawane et al. 2011). Ouyang et al. (2016) utilized transcriptomic data to pinpoint numerous key genes involved in secondary cell wall biosynthesis during the wood formation process of *N. cadamba*, including the *NcCesA* gene responsible for cellulose biosynthesis. Furthermore, Que et al. (2022) identified 6 FBP genes from the genome of *N. cadamba*, which played an important role in photosynthesis and sugar accumulation of the species. Notably, the FBP gene family has shown expansion during historical evolution (Huang et al. 2018). Additionally, Xu et al. (2023) identified 85 WRKY genes from *N. cadamba*, which are involved in growth, development, and response to hormonal and abiotic stresses. Upon treatment with methyl jasmonate, the expression of genes *NcWRKY64* and *NcWRKY74* was significantly upregulated, leading to increased cadambine accumulation.

The genetic transformation system of *N. cadamba* has not yet been successfully developed. One possible approach is to isolate the target genes from *N. cadamba* and verify their functions in model plants. Ouyang et al. (2016) successfully cloned the *AcEXPA8* gene from *N. cadamba*, which was highly expressed in vascular cambium. When this gene was overexpressed in *Arabidopsis thaliana* (L.) Heynh, it promoted secondary growth, morphogenesis and growth of leaves. Li et al. (2017) demonstrated that the *NcEXPA8* gene was also highly expressed in cambium region of *N. cadamba*. Overexpression of this gene in *Arabidopsis* increased the plant diameter and height but did not affect the cellulose content in cell walls. Li et al. (2019) investigated the *NcCSE* gene, isolated from *N. cadamba*, and its role in lignin biosynthesis with *Arabidopsis* Heynh. The gene completely restored lignin reduction in *Arabidopsis CSE-2* mutant plants, while the *NcHCT* gene only partially restored lignin. Downregulation of *NcCSE* expression through gene editing technology reduced the lignin content, enhancing biomass saccharification efficiency and improving animal nutritional uptake (Ouyang 2013).

Huang et al. (2018) used various analytical tools, including GeNorm, NormFinder, BestKeeper, and RefFinder, to identify the most stable reference genes using RNA-seq data under different experimental conditions. The study revealed *NcSAMDC* as the most stable gene and *NcRPL10A* as the gene with the highest expression stability across diverse tissues of *N. cadamba*. These findings provide valuable groundwork for future research to understand gene functions related to wood traits.

Conclusions and prospectives

The two species in the *Neolamarckia* genus, *N. cadamba* and *N. macrophylla*, belong to Trib. Naucleeae of the Cinchonioideae subfamily of the Gentianales order. These species are notable for fast-growing and high-quality wood for industrial applications and are also rich in bioactive secondary metabolites for medicinal values in tropical and subtropical regions. This review discussed the research progress in taxonomic division and phylogenetic relationship, physical properties and genetic variation of wood traits, and molecular mechanisms of wood property traits of these two species. Specific conclusions are summarized below:

(1) Phylogenetic analyses with organelle genomes and molecular markers of nuclear genomes indicated that *N. cadamba* and *N. macrophylla* were more recently divergent and have a closely genetic relationship. Purifying selection was the dominant process to impede evolutionary divergence of mitochondrial genomes between the two species.

(2) Population genetic differentiation was smaller for *N. cadamba* than for *N. macrophylla* in terms of nuclear markers. A mixed mating system (predominant outcrossing with a certain level of self-fertilization) was evidenced in *N. marcophylla* but remains to be scored in *N. cadamba*.

(3) Physical properties of wood traits were generally different between the two species. Strict comparisons are needed to statistically test their differences with more experimental data.

(4) Provenance trials indicated that differentiation among provenances was significant for a few wood property traits (e.g., VL, VD and AD), but genetic coefficients of variation (GCV) of all wood property traits were generally small among provenances in *N. cadamba*. Genetic variation of wood property traits has rarely been assessed in *N. macrophylla*. Breeding should primarily focus on selection at the family and individual levels, and hence, genomic selection would show great promise.

(5) Correlations between wood property and growth traits were weak in *N. cadamba* but unknown in *N. macrophylla*, implying a challenge for simultaneously improving growth and wood quality traits in *N. cadamba*.

(6) Several genes related to wood property traits were identified only in *N. cadamba* and a few gene functions were tested using model plants. Generally, molecular mechanisms of wood traits remain to be investigated in both species.

Apart from the concerns aforementioned for further studies, the following two questions are emphasized. The first question is concerned with lineage sorting of these two sympatric species. The evolutionary divergence between the two species needs further clarification using nuclear genomes, including detection of gene introgression. The second question concerns breeding or genetic improvement for modern industry. The SCAU research group is currently working on breeding programs through genomic selection for excellent

genotypes and polyploidization for improving resistance of *N. cadamba* to adverse environments (cold and insects).

Besides, one conventional breeding scheme is artificial hybridization although natural hybridization between these two species in sympatry is not recorded in literature. Introgressive hybridization is a significant process in genetic improvement, facilitating the transfer of adaptive genes between species. It enables the incorporation of beneficial traits from one species into another, enhancing genetic diversity and evolutionary potential. Goulet et al. (2017) have shown that hybridization and subsequent introgression can increase local adaptation by introducing novel alleles. This process also enables transgressive segregation and promotes rapid evolutionary change in plant populations (Goulet et al. 2017). How this process is applied to the two species is of significance because *N. macrophylla* is endemic to local habitats and restrictively distributed.

While direct research on the potential hybridization between *N. macrophylla* and *N. cadamba* is currently lacking, the possibility of such hybridization under controlled conditions is intriguing. Given that these species belong to the same genus and are genetically related based on the organelle genomes, there is a clear need for further research on this topic. Cross-breeding experiments and molecular studies could provide more insights into this exciting possibility.

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Author Contributions

CW wrote the draft of article; CW, HX and ZHH participated in literature collection; FCY reviewed and revised the article; XSH revised and finalized the article. All authors read and approved submission of this article.

Competing Interests

The authors declare no competing interests.

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