frontiers | Frontiers in Ecology and Evolution

TYPE Data Report
PUBLISHED 30 January 2026
DOI 10.3389/fevo.2026.1751419

OPEN ACCESS

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RECEIVED 28 November 2025
REVISED 19 December 2025
ACCEPTED 02 January 2026
PUBLISHED 30 January 2026

CITATION
Fadilah A, Hikmat A, Karlinasari L, Dwiyanti FG, Pratama R, Maulana F, Kamal I, Syaputra D and Siregar IZ (2026) Complete chloroplast genome assembly of *Rubroshorea leprosula* wood from Indonesia for phylogenetic and conservation studies.
Front. Ecol. Evol. 14:1751419.
doi: 10.3389/fevo.2026.1751419

Complete chloroplast genome assembly of *Rubroshorea leprosula* wood from Indonesia for phylogenetic and conservation studies

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KEYWORDS

chloroplast genome, dipterocarp, Illumina, phylogenetic, *Rubroshorea*

1 Introduction

Red meranti is considered a primary commercial product in the timber trade, recognized as the leading roundwood commodity with a total volume of 653.49 thousand m^3 in 2020 (BPS, 2021). This type of wood is characterized by its straight, cylindrical trunk and is primarily sourced from natural forests. There are also efforts to cultivate red meranti through sustainable forest management practices (Wistara et al., 2016). Previous reports indicated that the survival rate of the red meranti exceeds 67%, with a Mean Annual Diameter Increment (MADI) above 1.7 cm/year (Widiyatno et al., 2020).

As a member of the Dipterocarpaceae family, red meranti comprises approximately 75 species found in the lowland tropical rainforests of the Indo-Malayan region (van Steenis, 1983). *Rubroshorea leprosula* (Miq.) P. S. Ashton and J. Heck, a synonym for *Shorea leprosula* Miq (Ashton and Heckenhauer, 2022), is locally known as meranti tembaga. It is also internationally traded as part of the light red meranti timber group (Ng et al., 2021). Typically, *R. leprosula*

grows up to 1.000 m above sea level and has an estimated extent of occurrence (EOO) of over 2 million km^2. This species is native to Southeast Asia, with a natural distribution that includes Singapore, Peninsular Malaysia, Peninsular Thailand, the Indonesian islands of Java, Sumatra, and Borneo (Kalimantan, Brunei Darussalam, Sabah, and Sarawak) (Pooma and Newman, 2024).

R. leprosula is a timber tree known for its high economic value and significant presence in both regional and international tropical timber markets (Harahap et al., 2018). It is traded and utilized as raw material for various applications, including light and heavy construction, furniture, flooring, and plywood (Purwaningsih and Kintamani, 2018; Alex et al., 2023). This species is a key product of lowland tropical rainforests and serves as symbols of these ecosystems (Yu et al., 2021). The harvested timber of *R. leprosula* shows promising prospects, as it is classified as commercial wood class 1 (Djarwanto et al., 2017), with a strength class of III (Wahyudi and Sitanggang, 2016) and durability class of III-IV (Kartasujana and Martawijaya, 1973). However, the high value of *R. leprosula* has led to overexploitation and unsustainable harvesting under the Timber Forest Product Utilization Permit (Izin Usaha Pemanfaatan Hasil Hutan Kayu – Hutan Alam, IUPHHK-HA), as well as illegal logging and trade. Logging activity continues to be reported in Gunung Leuser National Park, where loggers specifically target *R. leprosula* due to its accessibility and ease of processing compared to other species (Harnelly et al., 2016). Moreover, *R. leprosula* typically occurs in late successional stages and is considered a climax species in lowland dipterocarp forests, characterized by low regeneration rates (Nurfatma et al., 2017). It also shows low natural regeneration in degraded habitats such as Tesso Nilo National Park (Kusumo et al., 2016). Consequently, it has low dominance in protected forests like Bukit Barisan Selatan National Park (Prayoga et al., 2019). These ecological characteristics render the species highly vulnerable to habitat disturbance and overexploitation, especially in concentrated areas such as the now-abandoned PT. Patriadi concession. As a result, the population of *R. leprosula* has been declining due to the conversion of forest land into agricultural and industrial plantation areas (Gaveau et al., 2016; Harahap et al., 2018), which has contributed to a continuous decrease in its global population. According to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, this species is globally classified as Near Threatened (NT) and has undergone a 20–29% reduction over the past three generations (approximately 210 years) (Pooma and Newman, 2024). Indonesia is known as a wood-producing country that exported timber products, including those from illegal logging, to partner countries such as China and Japan from 2001 to 2010, with volumes estimated at 11,000 m^3 and 12,000 m^3 Roundwood Equivalent (RWE), respectively (Ji et al., 2018). In 2013, about 80 million m^3 of RWE was illegally produced across nine countries, with approximately 50% of this illegal supply originating from Indonesia (Hoare, 2015). However, only 3,829 m^3 of illegal wood was seized in 2017 (Ministry of Environment and Forestry, 2019). This situation highlights the urgent need for conservation efforts to protect and sustain the existing populations of *R. leprosula*. Identifying the species and origin of illegal wood is challenging without reliable identification methods. The most established method for wood identification is the study of wood anatomy, which characterizes species based on their internal structure. However, this method can sometimes be challenging in distinguishing wood species, particularly within meranti species, leading to the development of other methods, such as chemical and genetic methods. However, genetic methods are currently considered more accurate for identifying wood species and their origins (Finkeldey et al., 2009; Lowe and Cross, 2011) through genomic information.

Unlocking genomic data for *R. leprosula* is vital for enhancing wood identification and developing genetic conservation strategies. Among various genomic resources, the chloroplast genome is particularly valuable, as it provides crucial insights into genetic variation among closely related species. In plants, the chloroplast genome or plastome is a semi-autonomous structure enclosed in double membranes, housing independent genetic material (Dobrogojski et al., 2020; Daniell et al., 2021). These organelles possess molecular machinery that regulates gene expression (Chevigny et al., 2020) and play a vital role in various physiological processes within plants (Mahapatra et al., 2021). The chloroplast genome is a valuable tool for genetic studies due to its slow evolutionary rate, maternal inheritance in most angiosperms, and its conserved structure and gene sequences (Zulfahmi et al., 2015; Song et al., 2019). In angiosperms, the chloroplast genome typically ranges from 107 kb to 218 kb and encodes 120 to 130 genes crucial for transcription, translation, and photosynthesis (Daniell et al., 2016; Li et al., 2024). Due to its conservation, the chloroplast genome serves as a reliable resource for molecular identification, genetic diversity assessment, and phylogenetic studies (Chew et al., 2023; Kim et al., 2024). The genome of *Rubroshorea leprosula* from Malaysia has been sequenced using the Illumina HiSeq platform to study comparative genomics and molecular dating of the evolution of the Dipterocarpaceae family, highlighting the role of drought in a seasonal tropical rainforests (Ng et al., 2021). Another *Rubroshorea leprosula* genome from China was sequenced by Yu et al. (2021) using the Illumina NovoSeq 6000 platform to conduct a comprehensive evolutionary analysis of chloroplast genomes from 20 species of Dipterocapoideae and to identify barcoding loci for species identification. However, data on the genomic resources for *R. leprosula* from Indonesia are still limited, as the Indonesian population may harbor unique genetic characteristics. This lack of information poses a significant challenge to advancing research on developing chloroplast DNA (cpDNA) markers, which are essential for genetic conservation efforts. Therefore, this study aims to assemble and characterize the complete chloroplast genome of *Rubroshorea leprosula* from Indonesia, generated from short-read sequencing, and to analyze its phylogenetic relationship with other species. This study enhances understanding of the genetics of *R. leprosula* from Indonesia and contributes to wood identification and conservation efforts. It represents a vital step toward preserving this species and enriching the knowledge of plant genetics.

2 Method

2.1 Plant material, DNA extraction, and sequencing

The plant material used in this study consisted of silica-gel dried cambium sample collected from *Rubroshorea leprosula* from Bukit Tigapuluh National Park, Riau Province on Sumatra Island, Indonesia (-0.814669° S, 102.528702° E), specifically from one individual mature tree with a stem diameter at the breast height of 50.8 cm and total height approximately 21 m with straight stem (Figure 1) to ensure the quality and consistency of the samples obtained. The cambium sample was scraped with a stainless-steel scalpel blade to form a sawdust-like material. The sawdust was then ground again with a Qiagen TissueLyser II. A total of 100 mg of the cambium powder sample was used for genomic DNA extraction and isolation following the modified Cetyltrimethylammonium Bromide (CTAB) protocol (Doyle and Doyle, 1990). Specifically, the modifications involve two incubations: 65°C for 60 min and 37°C for 30 min, with an additional 20 µL of Proteinase K before the first incubation and 20 µL of RNase A before the second. The initial quantification and assessment of genomic DNA purity were conducted using a Nanodrop 2000 spectrophotometer (Thermo Scientific), which exhibited a concentration of 300.3 ng/µL, A260/280 of 1.81, and A260/230 of 1.18, and was visualized via 1% Tris-Borate-EDTA (TBE) agarose gel electrophoresis. To achieve accurate DNA quantification, Qubit dsDNA HS Assay Kits (Thermo Scientific) were utilized. The genomic DNA samples of *R. leprosula* exhibited a concentration of 13.1 ng/µL and a total amount of 458.5 µg. The high-molecular-weight genomic DNA extracted from *R. leprosula* was subsequently used for library preparation to facilitate subsequent short-read sequencing. Libraries were prepared according to the protocol provided by Novogen AIT, Singapore, for the Illumina NovaSeq 6000. The sequencing was done through PT. Genetika Science Indonesia, resulting in a data output of 3 GB. Short-read sequencing has been selected for this study due to its well-established application in the reconstruction of chloroplast genomes. Its high accuracy and coverage facilitate reliable assembly and annotation of the chloroplast genome, while also offering cost-effective solutions for study purposes (Wang et al., 2018). All data analysis was conducted at the Forest Genetics and Molecular Forestry Laboratory within the Department of Silviculture, Faculty of Forestry and Environment at Institut Pertanian Bogor (IPB) University in Bogor, West Java, Indonesia.

2.2 Chloroplast genome assembly and annotation

Raw reads of the *Rubroshorea leprosula* from Illumina NovaSeq 6000 sequencing (Fastq) were uploaded to the Galaxy web platform, specifically the public server at usegalaxy.org v25.0.4.dev0 (https://usegalaxy.eu/) for analysis (Afgan et al., 2016). Quality control was conducted to evaluate the quality of reads. The quality of raw short-reads was assessed using FastQC v0.12.1 (Andrews, 2010), and clean reads were filtered with Fastp v0.24.0 (Chen et al., 2018) using

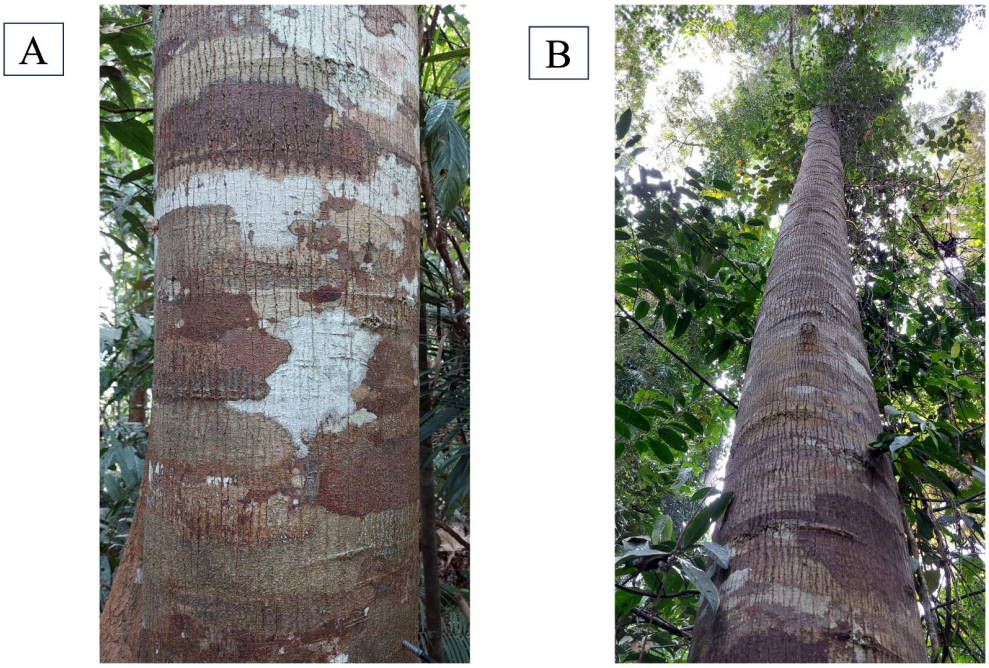

FIGURE 1
The *Rubroshorea leprosula* tree studied in Bukit Tigapuluh National Park, characterized by its **(A)** bark and **(B)** upright trunk.

default parameters. Clean reads were assembled using SPAdes v3.15.3 (Bankevich et al., 2012) and GetOrganelle v1.7.7.1 (Jin et al., 2020), both with default parameters. SPAdes v3.15.3 uses an adaptive multi–k-mer strategy by default. This approach was considered appropriate for the high-quality Illumina short-read data employed in this study and has been widely applied in chloroplast genome assembly. To improve accuracy, the assembled contigs were polished using Pilon v1.20.1 (Walker et al., 2014). These contigs were then mapped to the reference plastome of *Shorea leprosula*, a synonym of *Rubroshorea leprosula* (GenBank accession: MZ160997.1). The assembly results were then annotated using GeSeq (https://chlorobox.mpimp-golm.mpg.de/geseq.html) (Tillich et al., 2017). The fully annotated circular genome was visualized using OrganellarGenomeDRAW (OGDRAW) v1.3.1 accessible through the MPI-MP Chlorobox platform (Greiner et al., 2019).

2.3 Phylogenetic tree construction

In order to evaluate the phylogenetic position of the reconstructed chloroplast relative to those of closely related organisms and to assess the possible effects of these differences, a phylogenetic analysis was conducted. A total of 20 chloroplast genomes of taxa closely related to *Rubroshorea leprosula* (from the Dipterocarpaceae family) were downloaded from GenBank (the National Center for Biotechnology Information/NCBI) and aligned with the obtained plastomes. A complete list of the accessions used is given in Supplementary Table 1. *Neolamackia cadamba* (NC_041149.1) was included and used as an outgroup. The sequences were processed in Mega X v12.1.1 (Kumar et al., 2018) and aligned with MAFFT v7.526 (Katoh and Standley, 2013) using default parameters. A maximum likelihood (ML) phylogenetic tree was inferred with the IQ-TREE Web Server (Trifinopoulos et al., 2016), applying 1,000 bootstrap replicates. The phylogenetic tree was visualized using iTOL (Letunic and Bork, 2024).

3 Result

Short-read sequencing of *Rubroshorea leprosula* generated a total of 20,499,674 reads, equivalent to 3 gigabase pairs (Gbp) of raw data. The mean read length was 150 bp, and the mean read quality score of the raw data was recorded at 36. After filtering, all reads passed the quality assessment with the same score. The complete chloroplast genome of *R. leprosula* has been successfully assembled using short-read (Illumina NovaSeq 6000) sequencing data to resolve structural regions. The *Rubroshorea leprosula* chloroplast genome exhibits a typical quadripartite structure (Figure 2a) with a total length of 150,691 bp. The genome consists of a Small Single-copy Region (SSC: 19,917 bp) and a Large Single-copy Region (LSC: 83,740 bp), separated by a pair of inverted repeat regions: Inverted Repeat A (IRA: 23,517 bp) and Inverted Repeat B (IRB: 23,517 bp) (Figure 2a). The GC content of the *R. leprosula* sequence is 34.2%. This finding is nearly comparable in size to the *Shorea leprosula* syn. *Rubroshorea leprosula* chloroplast genome reported by Yu et al. (2021), which is 152,100 bp. Furthermore, similar chloroplast genome sizes were also found in *Shorea macrophylla* syn. *Rubroshorea macrophylla*, at 150,778 bp (Chew et al., 2023), and *Rubroshorea johorensis*, at 149,968 bp (Nugroho et al., 2025). These results indicate that the chloroplast genome size in the Sumatran population of *Rubroshorea leprosula* is relatively conserved and consistent within the *Rubroshorea* or *Shorea* group, at around 150 kb. The *Rubroshorea leprosula* chloroplast genome contains a total of 115 genes, including 80 protein-coding genes, 30 transfer RNA (tRNA) genes, and 4 ribosomal RNA (rRNA) genes (Supplementary Table 2). These genes

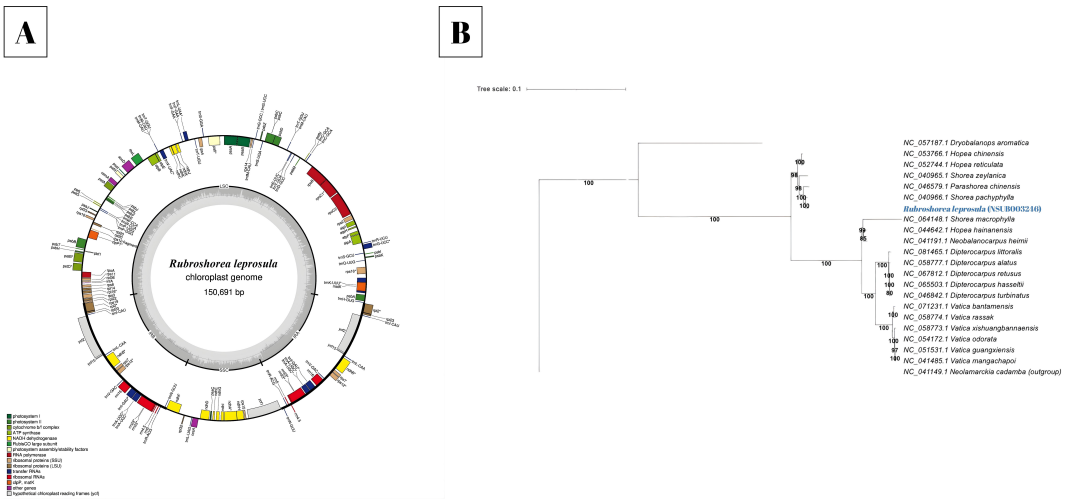

FIGURE 2
Chloroplast genome and phylogenetic relationships of *Rubroshorea leprosula*: **(A)** Chloroplast genome map and **(B)** Phylogenetic tree based on chloroplast genome.

are categorized into four functional groups: self-replicating genes, photosynthetic genes, genes with other functions, and genes of unknown function (Supplementary Table 2). In the *Rubroshorea leprosula* chloroplast genome, of the total identified genes, 19 contain introns, suggesting that RNA processing events may play a crucial role in gene expression and regulation, as further detailed in Supplementary Table 2.

Similar to other plant chloroplasts, *R. leprosula* likely exhibits high levels of recombination and structural rearrangements, traits characteristic of plant chloroplast genomes that contribute to genome plasticity. However, variations in gene content and intron presence may indicate species-specific adaptations that could be linked to environmental factors or evolutionary history. The results of chloroplast genome sequencing of *R. leprosula* indicated that, although the assembled genome remains limited, it can be used for further population genetic studies, providing essential data for designing conservation strategies for this species. This underscores the need for further research in this area. Conducting additional comparative genomic studies may provide deeper insights into the functional implications of these genomic features in *R. leprosula*.

The phylogenetic tree of *R. leprosula* based on the complete chloroplast genome showed that the studied *R. leprosula* was in the same clade as other species within the same genus, specifically *Shorea pachyphylla* (NC_040966.1) syn. *Rubroshorea pachyphylla*, with a bootstrap value of 100% (Figure 2b). Additionally, *R. leprosula* forms a monophyletic clade with *Parashorea chinensis* (NC_046579.1), *Shorea zeylanica* (NC_040965.1) syn. *Doona zeylanica*, *Hopea reticulata* (NC_052744.1), and *Hopea chinensis* (NC_053766.1), emphasizing the intricate evolutionary connections among these taxa. This finding contrasts with the study by Yu et al. (2021), which reported that the phylogenetic tree of the genus *Rubroshorea* was not monophyletic. The present study provides an updated phylogenetic analysis of *R. leprosula*, contributing to a deeper understanding of the evolutionary dynamics that characterize *R. leprosula* and its related species.

Data availability statement

The datasets presented in this study are available in online repositories. The names of the repository/repositories and accession number(s) can be found in the DNA Data Bank of Japan (DDBJ) under the Bioproject number PRJDB20739 (https://ddbj.nig.ac.jp/search/entry/bioproject/PRJDB20739). The Bio-sample number for Rubroshorea leprosula is SAMD01779978 (https://ddbj.nig.ac.jp/search/entry/biosample/SAMD01779978).

Author contributions

AF: Writing – review & editing, Investigation, Software, Writing – original draft, Visualization, Formal analysis. AH: Supervision, Writing – review & editing. LK: Writing – review & editing, Supervision. FGD: Writing – review & editing, Investigation, Methodology, Data curation. RP: Formal analysis, Writing – review & editing, Data curation. FM: Writing – review & editing. IK: Data curation, Writing – review & editing. DS: Data curation, Writing – review & editing. IZS: Supervision, Funding acquisition, Conceptualization, Writing – review & editing, Resources.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This study was funded by the Directorate General of Higher Education, Research, and Technology, Ministry of Education, Culture, Research, and Technology, Indonesia on Masters Education towards Doctorate for Excellent Graduates (PMDSU) research scheme under the Research Implementation Program Contract for 2025 (No. 006/C3/DT.05.00/PL/2025, dated 28 May 2025) and World Resources Institute's (WRI) Forest Program grant (Project Code: R4586) entitled "Indonesian-based Wood Identification Program" awarded by Norwegian Agency for Development Cooperation (NORAD) to corresponding Author.

Acknowledgments

The authors are grateful to the Directorate General of Natural Resources and Ecosystem Conservation at the Ministry of Environment and Forestry of the Republic of Indonesia for granting the Genetic Resources Access Permit for Rubroshorea leprosula (No. SK.192/KSDAE/SET.3/KSA.2/10/2022) and Bukit Tigapuluh National Park for granting entry permits and access for the collection of Rubroshorea leprosula samples. The authors also thank the Riau Natural Resources Conservation Agency for providing transport permits for genetic material from the study site to Institut Pertanian Bogor (IPB) University. Additionally, the authors appreciate Mr. Tugio, a local botanist, for his valuable assistance during field sample collection.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2026.1751419/full#supplementary-material

References

Afgan, E., Baker, D., van den Beek, M., Blankenberg, D., Bouvier, D., Čech, M., et al. (2016). The galaxy platform for accessible, reproducible and collaborative biomedical analyses: 2016 update. *Nucleic Acids Res.* 44, W3–W10. doi: 10.1093/nar/gkw343

Alex, T., Winarni, B., Suryadi, S., Yuniati, Y., Salsabila, P. P., Pratiwi, S., et al. (2023). Clay impregnation on strength of red meranti wood (*Shorea leprosula*). *Glob J. Res. Agric. Life Sci.* 3, 1–6. doi: 10.5281/zenodo.10013885

Andrews, S. (2010).FastQC: A quality control tool for high throughput sequence data. Available online at: https://www.bioinformatics.babraham.ac.uk/projects/fastqc/ (Accessed November 16, 2025).

Ashton, P. S., and Heckenhauer, J. (2022). Tribe Shoreae (Dipterocarpaceae subfamily Dipterocarpoideae) finally dissected. *Kew Bull.* 77, 885–903. doi: 10.1007/s12225-022-10057-w

Badan Pusat Statistik (2021). *Statistics of Forest Concession Establishment 2020* (Jakarta: Badan Pusat Statistik).

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., et al. (2012). SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *J. Comput. Biol.* 19, 455–477. doi: 10.1089/cmb.2012.0021

Chen, S., Zhou, Y., Chen, Y., and Gu, J. (2018). Fastp: An ultra-fast all-in-one FASTQ preprocessor. *Bioinformatics.* 34, i884–i890. doi: 10.1093/bioinformatics/bty560

Chevigny, N., Schatz-Daas, D., Lotfi, F., and Gualberto, J. M. (2020). DNA repair and the stability of the plant mitochondrial genome. *Int. J. Mol. Sci.* 21, 328. doi: 10.3390/ijms21010328

Chew, I. Y. Y., Chung, H. H., Lim, L. W. K., Lau, M. M. L., Gan, H. M., Wee, B. S., et al. (2023). Complete chloroplast genome data of *Shorea macrophylla* (Engkabang): Structural features, comparative and phylogenetic analysis. *Data Br.* 47, 109029. doi: 10.1016/j.dib.2023.109029

Daniell, H., Jin, S., Zhu, X. G., Gitzendanner, M. A., Soltis, D. E., and Soltis, P. S. (2021). Green giant—a tiny chloroplast genome with mighty power to produce high-value proteins: history and phylogeny. *Plant Biotechnol. J.* 19, 430–447. doi: 10.1111/pbi.13556

Daniell, H., Lin, C.-S., Yu, M., and Chang, W.-J. (2016). Chloroplast genomes: diversity, evolution, and applications in genetic engineering. *Genome Biol.* 17, 134. doi: 10.1186/s13059-016-1004-2

Djarwanto,, Damayanti, R., Balfas, J., Basri, E., Jasni,, Sulastiningsih, I. M., et al. (2017). *Pengelompokan Jenis Kayu Perdagangan Indonesia (Classification of Species of Indonesian Trade Wood).* (Bogor (ID: Forda Press).

Dobrogojski, J., Adamiec, M., and Luciński, R. (2020). The chloroplast genome: a review. *Acta Physiol. Plant* 42, 1–13. doi: 10.1007/s11738-020-03089-x

Doyle, J. J., and Doyle, J. L. (1990). Isolation of plant DNA from fresh tissue. *Focus (Madison).* 12, 13–15.

Finkeldey, R., Leinemann, L., and Gailing, O. (2009). Molecular genetic tools to infer the origin of forest plants and wood. *Appl. Microbiol. Biotchenol.* 85, 1251–1258. doi: 10.1007/s00253-009-2328-6

Gaveau, D. L. A., Sheil, D., Husnayaen,, Salim, M. A., Arjasakusuma, S., Ancrenaz, M., et al. (2016). Rapid conversions and avoided deforestation: Examining four decades of industrial plantation expansion in Borneo. *Sci. Rep.* 6, 32017. doi: 10.1038/srep32017

Greiner, S., Lehwark, P., and Bock, R. (2019). OrganellarGenomeDRAW (OGDRAW) version 1.3.1: Expanded toolkit for the graphical visualization of organellar genomes. *Nucleic Acids Res.* 47, W59–W64. doi: 10.1093/nar/gkz238

Harahap, N. N., Siregar, I. Z., and Dwiyanti, F. G. (2018). Root architecture and its relation with the growth characteristics of three planted *Shorea* species (Dipterocarpaceae). *IOP Conf Ser. Earth Environ. Sci.* 203, 1–11. doi: 10.1088/1755-1315/203/1/012016

Harnelly, E., Iqbar,, Fauziah,, Sara, A., Fathiya, N., and Amelia, R. (2016). Dipterocarpaceae inventory at Ketambe Research Station, Gunung Leuser National Park. *J. Trop. Silvic.* 7, S83–S85. doi: 10.29244/j-siltrop.7.3.s83-s85

Hoare, A. (2015). "Tackling illegal logging and the related trade," in *What Progress and Where Next?* (Chatham House, the Royal Institute of International Affairs: London). Available online at: https://www.chathamhouse.org/sites/default/files/publications/research/20150715IllegalLoggingHoareFinal.pdf (Accessed February 9, 2025).

Ji, Y., Ranjan, R., and Truong, C. (2018). Determinants of illegal logging in Indonesia: An empirical analysis for the period 1996–2010. *J. Sustain For.* 37, 197–220. doi: 10.1080/10549811.2017.1369436

Jin, J. J., Yu, W.B., Yang, J. B., Song, Y., Depamphilis, C. W., Yi, T. S., et al. (2020). GetOrganelle: A fast and versatile toolkit for accurate *de novo* assembly of organelle genomes. *Genome Biol.* 21, 1–31. doi: 10.1186/s13059-020-02154-5

Kartasujana, I., and Martawijaya, A. (1973). *Commercial Woods of Indonesia, Their Properties and Uses* (Bogor (ID: Forest Products Research Institute). Pengumuman No. 3 1973.

Katoh, K., and Standley, D. M. (2013). MAFFT Multiple Sequence Alignment Software Version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. doi: 10.1093/molbev/mst010

Kim, J. E., Kim, K. M., Kim, Y. S., Chung, G. Y., Che, S. H., and Na, C. S. (2024). Chloroplast genomes of *Vitis flexuosa* and *Vitis amurensis*: Molecular structure, phylogenetic, and comparative analyses for wild plant conservation. *Genes (Basel).* 15, 1–15. doi: 10.3390/genes15060761

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Mol. Biol. Evol.* 35, 1547–1549. doi: 10.1093/molbev/msy096

Kusumo, A., Nur Bambang, A., and Izzati, M. (2016). Struktur vegetasi kawasan hutan alam dan hutan terdegradasi di Taman Nasional Tesso Nilo. *J. Ilmu Lingkung.* 14, 19–26. doi: 10.14710/jil.14.1.19-26

Letunic, I., and Bork, P. (2024). Interactive Tree of Life (iTOL) v6: recent updates to the phylogenetic tree display and annotation tool. *Nucleic Acids Res.* 52, W78–W82. doi: 10.1093/nar/gkae268

Li, L. F., Yang, M., Qi, Y., Gao, P. H., Yang, S. W., Zhao, Y. T., et al. (2024). Chloroplast genome of four *Amorphophallus* species: genomic features, comparative analysis, and phylogenetic relationships among Amorphophallus species. *BMC Genomics* 25, 1122. doi: 10.1186/s12864-024-11053-z

Lowe, A. J., and Cross, H. B. (2011). The application of dna methods to timber tracking and origin verification. *IAWA J.* 32, 251–262. doi: 10.1163/22941932-90000055

Mahapatra, K., Banerjee, S., De, S., Mitra, M., Roy, P., and Roy, S. (2021). An Insight into the mechanism of plant organelle genome maintenance and implications of organelle genome in crop improvement: an update. *Front. Cell Dev. Biol.* 9. doi: 10.3389/fcell.2021.671698

Ministry of Environment and Forestry (2019). *The State of the Indonesia's Forests 2018.* Eds. S. Nurbaya, Efransjah, and S. A. Awang (Jakarta: Ministry of Environment and Forestry, Republic of Indonesia).

Ng, K. K. S., Kobayashi, M. J., Fawcett, J. A., Hatakeyama, M., Paape, T., Ng, C. H., et al. (2021). The Genome of *Shorea leprosula* (Dipterocarpaceae) highlights the ecological relevance of drought in aseasonal tropical rainforests. *Commun. Biol.* 4, 1166. doi: 10.1038/s42003-021-02682-1

Nugroho, A., Rustam, E., Widyani, N., Indriani, F., Sudrajat, D. J., Salim, M. A., et al. (2025). Complete assembly of the organellar genome of *Rubroshorea johorensis* utilizing advanced long-read sequencing technologies. *Front. Genet.* 16. doi: 10.3389/fgene.2025.1574266

Nurfatma, N., Pamoengkas, P., and Heriansyah, I. (2017). Analisis tipologi tutupan vegetasi sebagai dasar penyusunan strategi restorasi di area IUPHHK-RE PT REKI. *J. Pengelolaan Sumberd Alam dan Lingkung.* 7, 41–50. doi: 10.19081/jpsl.2017.7.1.41

Pooma, R., and Newman, M. F. (2024). Shorea leprosula (amended version of 2017 assessment). *IUCN Red List Threat Species*, 8235. doi: 10.2305/IUCN.UK.2024-1.RLTS.T33123A254583583.en

Prayoga, R., Indriyanto,, and Riniarti, M. (2019). Pola distribusi jenis meranti merah (*Shorea* spp.) di Resort Pemerihan, Taman Nasional Bukit Barisan Selatan. *J. Hutan Trop.* 7, 225–232. Available online at: https://ppjp.ulm.ac.id/journal/index.php/jht/article/view/7326/5693 (Accessed June 27, 2024).

Purwaningsih,, and Kintamani, E. (2018). The diversity of Shorea spp. (Meranti) at some habitats in Indonesia. *IOP Conf Ser. Earth Environ. Sci.* 197, 12034. doi: 10.1088/1755-1315/197/1/012034

Song, Y., Chen, Y., Lv, J., Xu, J., Zhu, S., and Li, M. (2019). Comparative chloroplast genomes of *sorghum* species: sequence divergence and phylogenetic relationships. *BioMed. Res. Int.* 2019, 1–11. doi: 10.1155/2019/5046958

Tillich, M., Lehwark, P., Pellizzer, T., Ulbricht-Jones, E. S., Fischer, A., Bock, R., et al. (2017). GeSeq - Versatile and accurate annotation of organelle genomes. *Nucleic Acids Res.* 45, W6–W11. doi: 10.1093/nar/gkx391

Trifinopoulos, J., Nguyen, L. T., von Haeseler, A., and Minh, B. Q. (2016). W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Res.* 44, W232–W235. doi: 10.1093/nar/gkw256

van Steenis, C. G. G. J. (1983). *Flora Malesiana. Series I, Spermatophyta* Vol. 9 (London: DR W. Junk Publisher the Hague).

Wahyudi, I., and Sitanggang, J. J. (2016). Wood quality of cultivated red meranti (*Shorea leprosula* miq.). *Jurnal Ilmu Pertanian Indonesia.* 21, 140–145. doi: 10.18343/jipi.21.2.140

Walker, B. J., Abeel, T., Shea, T., Priest, M., Abouelliel, A., Sakthikumar, S., et al. (2014). Pilon: An integrated tool for comprehensive microbial variant detection and genome assembly improvement. *PloS One* 9, 1–14. doi: 10.1371/journal.pone.0112963

Wang, W., Schalamun, M., Morales-Suarez, A., Kainer, D., Schwessinger, B., and Lanfear, R. (2018). Assembly of chloroplast genomes with long- and short-read data: a comparison of approaches using *Eucalyptus pauciflora* as a test case. *BMC Genomics* 19, 977. doi: 10.1186/s12864-018-5348-8

Widiyatno,, Hidayati, F., Hardiwinoto, S., Indrioko, S., Purnomo, S., Jatmoko,, et al. (2020). Selection of dipterocarp species for enrichment planting in a secondary tropical rainforest. *For. Sci. Technol.* 16, 206–215. doi: 10.1080/21580103.2020.1831620

Wistara, N. J., Sukowati, M., and Pamoengkas, P. (2016). The properties of red meranti wood (*Shorea leprosula* Miq) from stand with thinning and shade free gap treatments. *J. Indian Acad. Wood Sci.* 13, 21–32. doi: 10.1007/s13196-016-0161-y

Yu, Y., Han, Y., Peng, Y., Tian, Z., Zeng, P., Zong, H., et al. (2021). Comparative and phylogenetic analyses of eleven complete chloroplast genomes of Dipterocarpoideae. *Chin. Med. (United Kingdom).* 16, 1–15. doi: 10.1186/s13020-021-00538-8

Zulfahmi,, Mahfira, U. O., Siregar, U. J., Siregar, I. Z., and Yunanto, T. (2015). Comparison of levels of chloroplast DNA diversity of two *Shorea* species with contrasting geographical distribution. *Asia-Pacific J. Mol. Biol. Biotechnol.* 23, 291–302. doi: 10.21307/APJMBB-2015-009