

Review Article

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From Leaves to Roots: Mapping the Full Genome of Trees and Decoding Their Functions

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Abstract The advent of high-throughput sequencing technologies has revolutionized the field of tree genomics, enabling comprehensive mapping and functional analysis of tree genomes. This study synthesizes recent advancements in tree genomics, highlighting the integration of genomic, phenotypic, and environmental data to understand tree biology and improve forest health. Key findings include the development of standardized genome-wide function prediction tools, such as GOMAP, which facilitate comparative functional genomics across multiple species. Resources like PhyloGenes provide phylogenetic trees and experimentally validated gene functions, aiding in the functional inference of uncharacterized genes. This study also discusses the genomic studies of hardwood trees, which have linked genes to ecological and developmental traits, and the use of genomic prediction models for breeding. Additionally, the application of genome-wide association studies (GWAS) and joint-GWAS approaches in Eucalyptus has identified significant genetic associations with growth traits, enhancing tree breeding efforts. This study underscores the importance of integrating genomic data with environmental and phenotypic data through advanced cyberinfrastructure and databases to improve forest health and productivity. Emerging technologies and methodologies, such as RADseq and KEGG mapping tools, are also explored for their potential to uncover hidden features in tree genomes and facilitate large-scale genomic studies. This study provides a roadmap for future research in tree genomics, emphasizing the need for collaborative efforts and advanced analytical tools to decode the complex biology of trees.

Keywords Tree genomics; Comparative functional genomics; GWAS; Genomic prediction; Cyberinfrastructure

1 Introduction

Understanding the full genome of trees is crucial for advancing modern botany and ecology. Trees play a pivotal role in ecosystems, providing habitat, maintaining biodiversity, and influencing climate through carbon sequestration. Comprehensive genomic analysis allows researchers to uncover the genetic basis of traits that are vital for tree survival and adaptation, such as resistance to biotic and abiotic stresses, growth patterns, and reproductive strategies (Neale et al., 2017; Müller et al, 2018). This knowledge is essential for conservation efforts, especially in the face of climate change, as it can inform strategies to preserve genetic diversity and enhance the resilience of forest ecosystems (Holliday et al., 2017; Cortés et al., 2020).

Recent advancements in sequencing technologies have significantly accelerated the pace of tree genomic research. High-quality reference genomes have been assembled for several tree species, revealing insights into their unique genetic features and evolutionary histories (Neale et al., 2017; Wang et al, 2023). For instance, the genome of *Quercus dentata* has been sequenced, providing valuable information on the genetic regulation of leaf color transition and other adaptive traits (Wang et al, 2023). Genome-wide association studies (GWAS) have identified genes linked to important growth traits in species like Eucalyptus, enhancing our understanding of genetic variation and its impact on phenotypic traits (Müller et al., 2018).

However, tree genomic research faces several challenges. Trees often have large and complex genomes, long generation times, and outcrossing reproductive systems, which complicate genetic studies (Holliday et al., 2017; Cortés et al., 2020). Additionally, the number of sequenced tree genomes still lags behind those of other plant species, limiting the scope of comparative genomic analyses (Neale et al., 2017). Despite these challenges, ongoing efforts in genome sequencing and the development of new analytical methods continue to push the boundaries of our knowledge in this field (Hug et al., 2016; Osborne et al., 2022).

This study provides a comprehensive overview of the current state of tree genomic research, highlighting key achievements and identifying ongoing challenges. By synthesizing findings from recent studies, this study maps the full genome of trees and decodes their functions from leaves to roots. This includes exploring the genetic basis of traits related to growth, adaptation, and resistance, as well as understanding the ecological and evolutionary implications of these traits. Ultimately, this study seeks to inform future research directions and applications in tree breeding, conservation, and ecosystem management, contributing to the sustainable management of forest resources in a changing world.

2 Technological Advances in Tree Genome Sequencing

2.1 Evolution of sequencing technologies: from sanger to next-generation sequencing

The journey of sequencing technologies began with the advent of Sanger sequencing in the 1970s, which revolutionized the field by allowing the complete sequencing of genomes for the first time. Sanger sequencing, also known as the chain termination method, dominated the field for over three decades due to its accuracy and reliability (Dijk et al., 2018; Sharma et al., 2018). However, the need for higher throughput and cost-effective solutions led to the development of next-generation sequencing (NGS) technologies.

NGS technologies, often referred to as the second-generation sequencing, brought about a paradigm shift by enabling massively parallel sequencing of millions of DNA fragments simultaneously. This leap significantly reduced the cost and time required for sequencing, making it accessible for large-scale genomic studies (Bansal et al., 2018; Levy and Boone, 2018). Key NGS platforms include Illumina's sequencing by synthesis and Ion Torrent's semiconductor sequencing, both of which are characterized by short-read lengths but high accuracy (Kumar et al., 2019; Hu et al., 2021).

The limitations of short-read sequencing, such as difficulties in resolving repetitive regions and large genomic rearrangements, paved the way for third-generation sequencing technologies. These long-read sequencing methods, exemplified by Pacific Biosciences and Oxford Nanopore technologies, offer much longer read lengths, which are crucial for accurate genome assembly and detecting complex structural variations (Dijk et al., 2018; Hu et al., 2021). Despite initial concerns about accuracy, recent advancements have significantly improved the precision of long-read sequencing (Hu et al., 2021).

2.2 Impact of high-throughput sequencing on tree genomic studies

The introduction of high-throughput sequencing has had a profound impact on tree genomic studies. NGS technologies have enabled comprehensive genomic analyses of various tree species, facilitating the discovery of genetic variations, gene functions, and evolutionary relationships (Bansal et al., 2018; Satam et al., 2024). The ability to sequence entire genomes rapidly and cost-effectively has accelerated research in areas such as tree breeding, conservation genetics, and understanding tree responses to environmental changes (Sharma et al., 2018).

High-throughput sequencing has also enhanced transcriptomic studies, allowing researchers to investigate gene expression patterns and regulatory mechanisms in trees. This has provided insights into complex traits such as growth, disease resistance, and adaptation to abiotic stresses (Satam et al., 2024). Moreover, the application of NGS in metagenomics has expanded our understanding of tree-microbe interactions, which are critical for tree health and productivity (Sharma et al., 2018).

The integration of high-throughput sequencing data with advanced bioinformatics tools has further amplified the impact of these technologies. Sophisticated algorithms and computational pipelines have been developed to handle the vast amounts of data generated, enabling accurate assembly, annotation, and analysis of tree genomes (Bansal et al., 2018; Satam et al., 2024).

2.3 Future prospects: emerging technologies and their potential

The future of tree genome sequencing looks promising with the continuous evolution of sequencing technologies. Emerging methodologies, such as single-molecule sequencing and nanopore-based approaches, are expected to overcome current limitations and provide even greater accuracy and efficiency (Anderson, 2018; Kumar et al.,

2019). These technologies hold the potential to detect all types of genomic variations, including single nucleotide polymorphisms (SNPs), indels, copy number variations, and chromosomal rearrangements, with high precision (Anderson, 2018).

Advancements in in situ nucleic acid sequencing and microscopy-based sequencing are also on the horizon, offering new avenues for spatially resolved genomic analyses. These techniques could provide detailed insights into the spatial organization of genomes within tree tissues, enhancing our understanding of gene regulation and cellular differentiation (Kumar et al., 2019).

Furthermore, the development of more efficient and scalable sequencing platforms will likely reduce costs and increase accessibility, enabling broader applications in tree genomics. This includes the potential for real-time sequencing in the field, which could revolutionize tree breeding programs and conservation efforts by providing immediate genetic information (Anderson, 2018; Kumar et al., 2019).

3 Genomic Diversity Across Tree Species

3.1 Comparative genomic analysis of broadleaf and conifer trees

Comparative genomic analysis between broadleaf and conifer trees reveals significant differences in their genomic structures and evolutionary adaptations. For instance, spruces, which are coniferous trees, possess very large and repetitive genomes that complicate comparative analysis. However, recent studies have provided more contiguous genome assemblies for various spruce species, such as Engelmann spruce, Sitka spruce, and white spruce. These genomes exhibit structural similarities but also show distinct patterns of gene family expansions and rapidly evolving genes, which are linked to ecological adaptations (Figure 1) (Gagalova et al., 2022). In contrast, broadleaf trees like European beech (*Fagus sylvatica*) have been studied for their phenology-related genes, revealing significant SNP diversity associated with local adaptations to climatic variables (Meger et al., 2021). This comparative approach underscores the unique evolutionary paths and adaptive strategies of broadleaf and conifer trees.

Gagalova et al. (2022) focuses on the genomic mapping and hybrid analysis of various spruce species, specifically examining the genetic composition and evolutionary relationships within the *Picea* genus. By integrating genetic maps and genome assemblies, researchers achieved high synteny across different spruce species, validating the accuracy of the genomic scaffolding process. The study also confirmed the hybrid nature of the interior spruce genotype PG29, revealing predominant contributions from white spruce, along with significant genetic input from Engelmann and Sitka spruces. These findings are essential for understanding the complex hybridization events and genetic diversity in spruce species, providing valuable insights for tree breeding, conservation strategies, and the broader study of conifer genomics.

3.2 Insights into genetic variability and its ecological significance

Genetic variability within tree species is crucial for their adaptation to changing environments. The GenTree project, for example, has documented extensive intra- and interspecific leaf trait variability in seven European tree species, including both conifers and broadleaves. This variability is linked to resource acquisition and conservation, highlighting the ecological significance of genetic diversity in response to environmental gradients (Benavides et al., 2021). Additionally, studies on European beech have shown that genetic variation closely mirrors geographic distribution, with adaptive variation involving thousands of sequence variants across the genome. This polygenic architecture is essential for predicting future maladaptation under climate change conditions. Such insights into genetic variability are vital for understanding how tree species can maintain ecosystem stability and resilience.

3.3 Case studies: unique genomic adaptations in tree species

Several case studies illustrate unique genomic adaptations in tree species. For instance, the subtropical oak *Quercus acutissima* has shown significant genomic and phenotypic differentiation between eastern and western populations. This differentiation is associated with environmental factors such as precipitation, indicating local adaptation (Gao et al., 2020). Another example is the development of a high-throughput SNP array for *Araucaria*

angustifolia, a subtropical conifer. This SNP array has provided a comprehensive look at the genetic diversity and structure of the species, revealing a major north-south genetic cline and enabling more accurate assessments of regional differentiation (Silva et al., 2020). These case studies highlight the diverse adaptive strategies employed by different tree species to thrive in their respective environments.

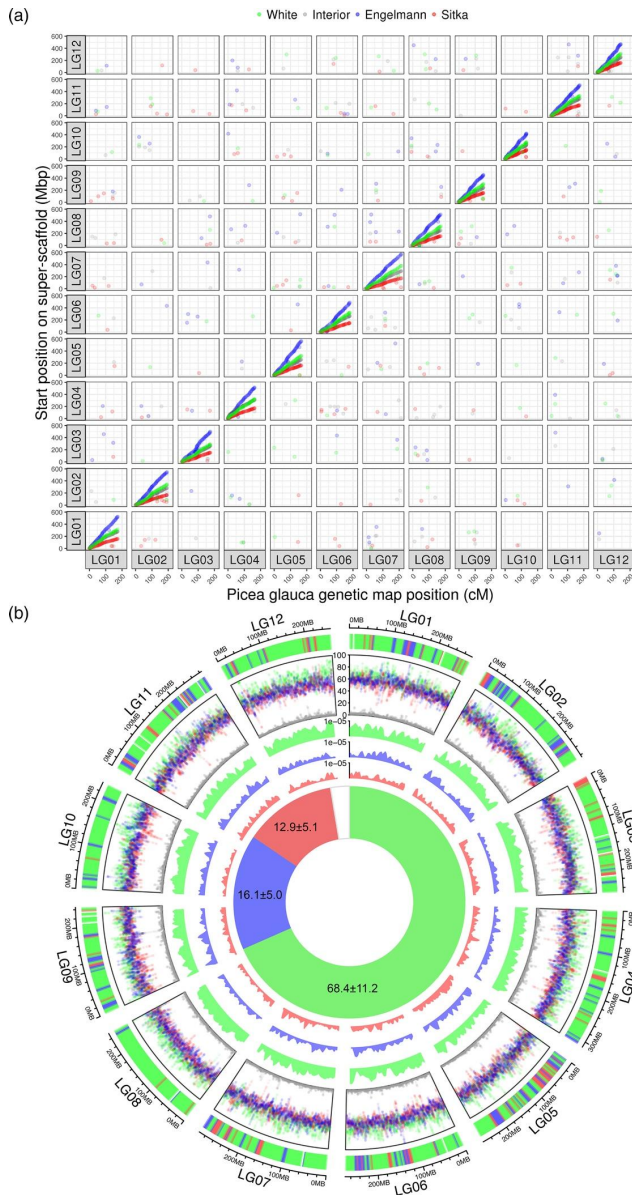


Figure 1 Genomic structure and hybrid composition in spruce species (Adapted from Galalova et al., 2022)

Image caption: (a) Collinearity between super-scaffolds and the genetic map for spruce species. Mapped cDNAs were aligned to each species' genome assembly, identifying the best matching scaffolds. These scaffolds were ordered according to the genetic map, forming super-scaffolds representative of each of the 12 chromosomes. The plot shows the alignment of cDNA start positions against their genetic map positions. (b) Shared SNP composition in the hybrid interior spruce genotype PG29. For each PG29 linkage group super-scaffold, the proportion of SNPs unique to interior spruce (gray) and those shared with Sitka (red), Engelmann (blue), and white spruce (green) were plotted. The ideograms depict regions with the highest shared SNP densities. Base genome contributions were estimated to be approximately 68.4% from white spruce, 16.1% from Engelmann spruce, and 12.9% from Sitka spruce, with unassigned portions indicated in light gray (Adapted from Galalova et al., 2022)

4 Functional Genomics: Decoding Gene Functions in Trees

4.1 Strategies for annotation and characterization of tree genomes

Functional annotation of tree genomes is a critical step in understanding the biological roles of genes and their contributions to growth, development, and stress responses. Various strategies have been developed to annotate

and characterize tree genomes effectively. One such approach involves the use of automated function prediction (AFP) algorithms, which leverage multi-omics data, including transcriptomics, protein-DNA, and protein-protein interaction data, to provide high-confidence functional annotations. This method has been successfully applied to *Arabidopsis thaliana*, resulting in the functional annotation of a significant proportion of previously unknown genes (Depuydt and Vandepoele, 2021). Another strategy involves the use of tools like eggNOG-mapper, which provides functional annotation based on precomputed orthology assignments and is optimized for large-scale genomic datasets (Cantalapiedra et al., 2021). Additionally, workflows for rapid functional annotation, such as those developed for arthropod genomes, can be adapted for tree genomes to produce Gene Ontology and pathway information, facilitating the understanding of complex biological systems (Saha et al., 2021).

4.2 Functional verification of critical genes related to growth, development, and stress response

Functional verification of critical genes in trees involves experimental validation to confirm the predicted functions. This can be achieved through various methods, including gene knockout or overexpression studies, RNA interference, and CRISPR-Cas9 gene editing. For instance, the functional roles of genes involved in flower and root development, defense responses to pathogens, and phytohormone signaling have been elucidated through such experimental approaches in *Arabidopsis thaliana* (Depuydt and Vandepoele, 2021). Comparative functional genomics, using standardized genome-wide function prediction pipelines like GOMAP, can also aid in identifying and verifying critical genes across multiple species, providing insights into conserved and species-specific gene functions (Fattel et al., 2021). Furthermore, machine learning algorithms have emerged as powerful tools for predicting gene functions by integrating large datasets and identifying patterns that may not be apparent through traditional methods (Mahood et al., 2020).

4.3 Integration of transcriptomic and proteomic data to enhance functional understanding

Integrating transcriptomic and proteomic data is essential for a comprehensive understanding of gene functions in trees. Transcriptomics provides information on gene expression levels, while proteomics offers insights into protein abundance, modifications, and interactions. By combining these datasets, researchers can gain a holistic view of the dynamic genome and its regulation. For example, multi-omics approaches have been used to annotate unknown genes in *Arabidopsis thaliana*, revealing their roles in various developmental processes and stress responses (Depuydt and Vandepoele, 2021). Additionally, the integration of transcriptomic and proteomic data has been shown to enhance the functional annotation of microbial genomes, suggesting its potential application in tree genomics (Mendler et al., 2018). The use of advanced technologies and systematic efforts to collect and organize functional genomics data, as described in various studies, underscores the importance of multi-omics integration in advancing our understanding of tree biology (Webber, 2020; Carpenter and Conlan, 2021).

5 Root-to-Leaf Communication: Genetic and Molecular Interactions

5.1 Mechanisms of belowground-aboveground signaling in trees

The communication between roots and leaves in trees involves a complex network of signaling pathways that integrate various environmental and physiological cues. Root-secreted chemicals, such as (-)-loliolide, play a crucial role in mediating both belowground defense mechanisms and aboveground reproductive processes. For instance, (-)-loliolide has been shown to delay flowering in tobacco by upregulating flowering suppressors and downregulating flowering stimulators, highlighting its role in root-to-shoot signaling (Li et al., 2022). Additionally, experimental techniques like split-root systems, grafting, and girdling have been instrumental in studying these long-distance signaling mechanisms. These methods help in understanding how nutrients and signals are transported between roots and shoots, and how they influence plant development and stress responses (Torres et al., 2021).

5.2 Role of root genes in nutrient uptake and signal transduction

Root genes are pivotal in nutrient uptake and signal transduction, influencing the overall health and growth of trees. Root exudates, which are secreted by roots, play a significant role in nutrient acquisition by altering the soil environment. These exudates can mobilize soil nutrients through processes like acidification and chelation, thereby enhancing nutrient availability (Figure 2) (Ma et al., 2022). Moreover, root traits such as specific root

length and root tissue density have been linked to variations in soil microbial biomass and community composition, which in turn affect nutrient cycling and plant growth (Wan et al., 2021). The interactions between root morphology, root exudation, and mycorrhizal symbioses are essential for a holistic understanding of soil nutrient acquisition strategies (Wen et al., 2021).

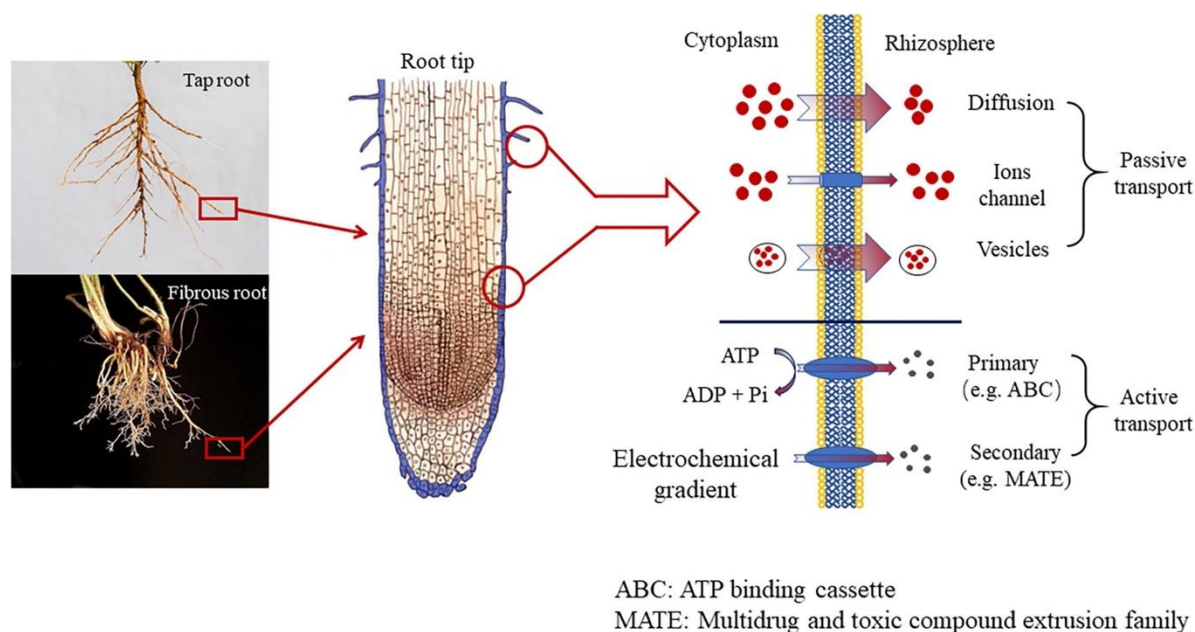


Figure 2 The mechanism of root exudation (Adapted from Ma et al., 2022)

Image caption: The mechanisms of root exudation in tap roots and fibrous roots, focusing on the processes at the root tip. Root exudation occurs through both passive and active transport mechanisms. Passive transport includes diffusion, ion channels, and vesicle transport, which facilitate the release of low-molecular-weight compounds driven by concentration gradients and membrane permeability. Active transport involves ATP-binding cassette (ABC) proteins and H^+/Na^+ gradient-dependent transporters (e.g., MATE), responsible for the release of primary and secondary metabolites. Primary metabolites support plant growth and development under stress, while secondary metabolites enhance environmental adaptation by modifying the surrounding rhizosphere. The image highlights the complex interplay between these mechanisms in regulating root exudation and its significance in plant physiology (Adapted from Ma et al., 2022)

5.3 Influence of leaf genes on photosynthesis and energy production

Leaf genes significantly influence photosynthesis and energy production, which are critical for the growth and survival of trees. Aboveground traits, such as specific leaf area and leaf dry matter content, are often consistent with the leaf economics spectrum and are influenced by soil moisture conditions (Asefa et al., 2022). These traits are crucial for optimizing photosynthetic efficiency and energy production under varying environmental conditions. Additionally, electrical signaling between leaves of different plants can induce systemic physiological changes, including alterations in photosynthetic activity. This type of aboveground plant-to-plant communication demonstrates the interconnectedness of leaf functions and their impact on overall plant health (Szechyńska-Hebda et al., 2022).

6 Case Studies: Gene Discovery and Functional Analysis

6.1 Novel gene identification in diverse tree families

Recent advancements in genomic technologies have significantly enhanced our ability to identify novel genes in various tree families. For instance, a study on Norway spruce demonstrated the use of microsatellite loci to genotype over four hundred unique accessions, leading to the identification of a highly diverse core collection set (Kelblerová et al., 2022). Similarly, genome-wide association studies (GWAS) have been employed to uncover genes associated with growth traits in *Eucalyptus*, revealing significant associations with tree height and other phenotypic traits (Figure 3) (Müller et al., 2018). These studies underscore the importance of leveraging diverse genetic resources and advanced genomic tools to uncover novel genes that contribute to important traits in forest trees.

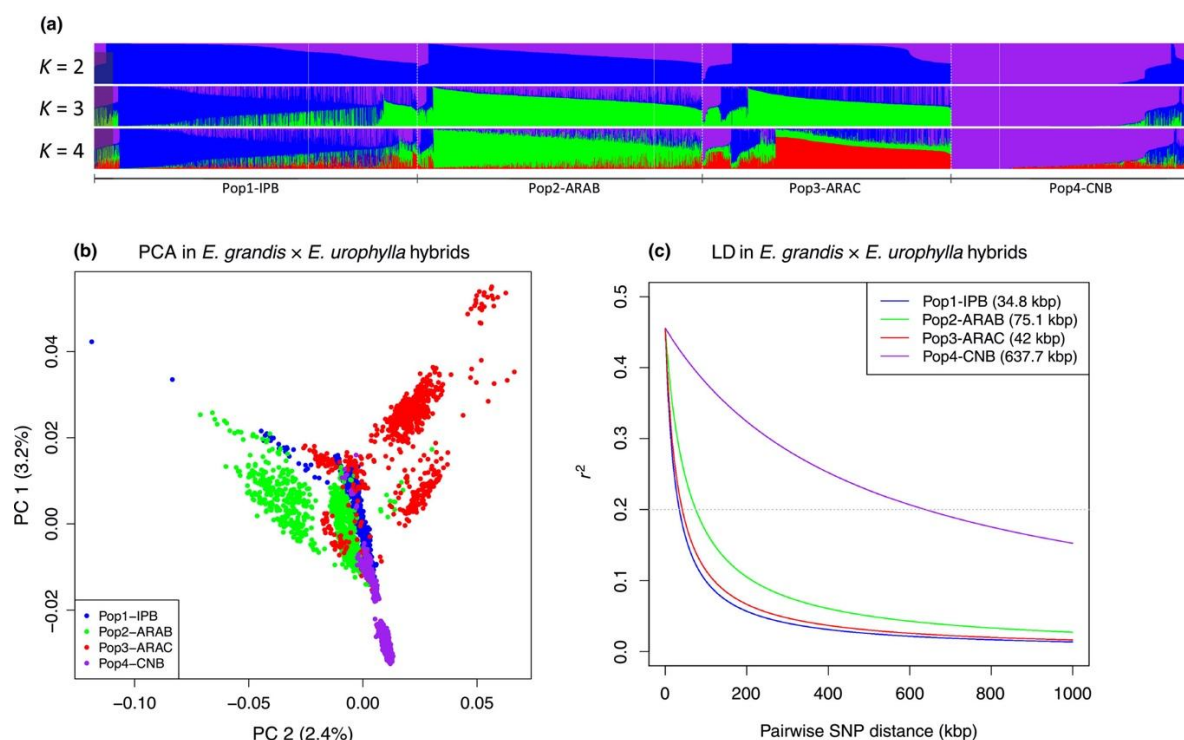


Figure 3 Population structure, PCA, and LD decay in *Eucalyptus grandis* × *E. urophylla* hybrid breeding populations (Adapted from Müller et al., 2018)

Image caption: (a) Bar plots showing the population structure of four unrelated *Eucalyptus grandis* × *E. urophylla* hybrid breeding populations with the number of clusters (K) ranging from 2 to 4. (b) Principal Component Analysis (PCA) displaying the first two principal components (PC 1 and PC 2) for the combined dataset. (c) Genome-wide linkage disequilibrium (LD) decay, represented by the correlation coefficient (r^2), plotted against pairwise single nucleotide polymorphism (SNP) distances up to 1 Mbp. The dashed line at $r^2 = 0.2$ marks the threshold commonly used to determine usable LD in genomic studies (Adapted from Müller et al., 2018)

Müller et al. (2018) investigates the genetic diversity and population structure of *Eucalyptus grandis* × *E. urophylla* hybrids using SNP genotyping. With over 46 000 SNPs retained after filtering, the research identifies distinct subpopulations within the hybrids, varying from K = 2 to K = 5 depending on the population. The analysis emphasizes the importance of accounting for population stratification in genomic studies, as it affects the accuracy of GWAS and heritability estimates. Linkage disequilibrium (LD) patterns reveal that more advanced breeding populations, like Pop4-CNB, exhibit slower LD decay, reflecting the impact of selective breeding. The study underscores the necessity of integrating genetic structure understanding into breeding programs to optimize selection and improve genetic gains.

6.2 Experimental approaches for functional validation in controlled and natural environments

Functional validation of identified genes is crucial for understanding their roles in tree biology and adaptation. Various experimental approaches have been employed to achieve this. For example, the use of quantitative trait loci (QTL) mapping in Scots pine has enabled the identification of QTL linked to complex traits, with validation conducted across multiple environments to account for genotype-by-environment interactions (Calleja-Rodriguez et al., 2019). Additionally, the application of genomic selection (GS) in tree breeding has shown promise in accelerating breeding cycles and improving the accuracy of breeding values by integrating genomic and multi-environment data (Grattapaglia et al., 2018). These approaches highlight the importance of combining controlled experiments with natural environment studies to validate gene functions comprehensively.

6.3 Applications of gene discovery in tree breeding and conservation efforts

The discovery of novel genes and their functional validation have significant implications for tree breeding and conservation. For instance, maximizing genetic diversity through strategic breeding programs, as demonstrated in the Norway spruce case study, can enhance ecosystem resilience and stability (Kelblerová et al., 2022). Moreover, predictive genomic approaches, such as those discussed in the context of forest tree adaptation to climate change,

can inform conservation strategies by identifying allelic variants that contribute to local adaptation (Cortés et al., 2020). The integration of GWAS and genomic selection techniques in tree breeding programs also holds potential for improving wood properties and other economically important traits, thereby supporting sustainable forestry practices (Du et al., 2018). These applications underscore the critical role of gene discovery in advancing tree breeding and conservation efforts.

7 Implications of Genomic Research for Forestry Management

7.1 Enhancing tree health and productivity through genomic insights

Genomic research has significantly advanced our understanding of tree health and productivity, providing tools to address the challenges posed by climate change, pests, and diseases. For instance, genomic selection has been utilized to accelerate breeding programs aimed at improving tree health and productivity. This approach allows for the identification of genetic markers associated with desirable traits, such as disease resistance and growth rates, thereby enabling the selection of superior genotypes for breeding programs (Isabel et al., 2019; Cappa et al., 2022). Additionally, the integration of genomic information with productivity and climate-adaptability traits has been shown to enhance tree breeding programs, ensuring the development of resilient and sustainable forests (Cappa et al., 2022). The use of genomic tools has also facilitated the identification of genes involved in pathogen response, which is crucial for developing strategies to mitigate the impact of pests and diseases on forest ecosystems (Naidoo et al., 2019; Lu et al., 2023).

7.2 Genetic contributions to forest diversity and ecosystem services

Genetic diversity plays a critical role in maintaining forest ecosystem services and resilience. Studies have shown that promoting genetic diversity within tree populations can enhance ecosystem stability and productivity, particularly in the face of climate change and other environmental stressors (Jactel et al., 2018; Kelblerová et al., 2022). For example, a case study on Norway spruce demonstrated that maximizing genetic diversity through strategic breeding programs can improve the resilience of forest ecosystems to climate change and pest outbreaks (Kelblerová et al., 2022). Furthermore, research has highlighted the positive relationship between tree species diversity and forest productivity, with mixed-species stands showing higher productivity and carbon sequestration compared to monocultures (Huang et al., 2018; Jactel et al., 2018). This underscores the importance of incorporating genetic and species diversity into forest management practices to enhance ecosystem services and mitigate the impacts of climate change.

7.3 Strategies for sustainable management and conservation of forest resources

Sustainable forest management and conservation efforts can greatly benefit from genomic research. By understanding the genetic basis of adaptation and resilience, forest managers can develop strategies that promote the conservation of genetic resources and the sustainable use of forest ecosystems. For instance, predictive genomic approaches can improve the accuracy of adaptive selection and shorten generation intervals, aiding in the conservation and improvement of forest tree species (Cortés et al., 2020). Additionally, the application of epigenetics in forest management offers new avenues for enhancing tree phenotypic plasticity and adaptive responses to environmental changes (Amaral et al., 2020). The integration of genomic information with traditional breeding and conservation practices can lead to the development of more resilient forest ecosystems capable of withstanding the challenges of the 21st century (Isabel et al., 2019; Amaral et al., 2020; Cortés et al., 2020). Moreover, the use of genomic tools to study the genetic diversity and adaptive capacity of forest trees can inform policies and practices aimed at preserving forest biodiversity and ecosystem services (Lu et al., 2023).

8 Future Directions in Tree Genomic Research

8.1 Unexplored areas and the need for interdisciplinary approaches

The field of tree genomic research has made significant strides, yet several unexplored areas remain that could benefit from interdisciplinary approaches. For instance, the integration of comparative genomics with fields such as cell and evolutionary biology, ecology, and conservation biology is essential for a comprehensive understanding of tree genomes and their functions (Stephan et al., 2022). This interdisciplinary collaboration can help address the complex multifactorial inheritance of traits in forest trees, which has posed challenges for

traditional genetic dissection approaches (Grattapaglia et al., 2018). Additionally, predictive genomic approaches that merge heterogeneous genomic and ecological datasets using machine learning are becoming imperative to enhance the accuracy of adaptive selection and to understand the genomic potential for adaptation to different environments (Cortés et al., 2020).

8.2 Potential for global collaborations in tree genomic studies

Global collaborations are crucial for advancing tree genomic research. Projects like the Darwin Tree of Life Project demonstrate the potential for large-scale, high-quality genome sequencing through international cooperation between biodiversity organizations and genomics institutes. Such collaborations can facilitate the collection, identification, and sequencing of specimens, thereby generating valuable genomic data that can be openly shared with the global scientific community. Furthermore, the success of genomic selection (GS) in tree breeding, which has shown promise in accelerating breeding cycles and improving the accuracy of breeding values, underscores the need for collaborative efforts to optimize prediction models and integrate multi-environment data (Grattapaglia et al., 2018; Grattapaglia, 2022). These global initiatives can also help address the technical, scientific, and social constraints that currently limit the application of genomics in tree breeding and conservation.

8.3 Funding and resource allocation for future genomic initiatives

Adequate funding and resource allocation are critical for the continued advancement of tree genomic research. The implementation of genomic technologies in genebanks, for example, requires fundamental changes in management, organization, and funding to fully realize their potential (Wambugu et al., 2018). Increased collaboration between genebank managers and the user community is also recommended to enhance the utility of plant genetic resources. Additionally, the establishment of breeder-friendly and cost-effective genotyping platforms, as well as methods based on low-pass whole genome sequencing with imputation, can further reduce genotyping costs and make advanced tree breeding more accessible (Grattapaglia, 2022). Large-scale programs like the US Precision Medicine Initiative and the UK Biobank Initiative provide exemplary models of how interdisciplinary and well-funded efforts can bring the promise of genomics to fruition (Musunuru et al., 2018). These initiatives highlight the importance of strategic, logistical, and financial planning in optimizing the adoption of genomic selection and other advanced genomic methods in tree breeding and conservation.

9 Concluding Remarks

The journey from leaves to roots in tree genome mapping has been marked by significant advancements and challenges. Initially, efforts focused on understanding the genetic basis of tree species through phylogenomics, which aimed to construct evolutionary trees from genomic sequences. This approach has evolved to include landscape genomics, which links genetic variations to environmental factors, providing insights into tree conservation strategies under changing climates. The Darwin Tree of Life Project exemplifies the ambition to sequence the genomes of all eukaryotic life, including trees, to support biodiversity and conservation efforts. Additionally, innovative methods like genotyping-by-sequencing have enabled the mapping of root systems, revealing the intricate belowground architecture of trees. These efforts have been complemented by advances in quantitative genetics and genomics, which have accelerated tree breeding by predicting complex phenotypes and improving breeding cycles. Collectively, these studies have provided a comprehensive understanding of tree genomes from their leaves to their roots, highlighting the complexity and adaptability of tree species.

This study has synthesized key findings from various studies, highlighting the multifaceted approaches used in tree genomic research. By integrating phylogenomics, landscape genomics, and high-throughput sequencing techniques, we have provided a holistic view of tree genome mapping. The study underscores the importance of reconciling gene trees with species networks to understand complex evolutionary events. It also emphasizes the role of landscape genomics in tree conservation, particularly in predicting genetic responses to climate change. The Darwin Tree of Life Project's contributions to high-quality genome sequencing and its implications for biodiversity conservation have been highlighted. Furthermore, the development of scalable methods for mapping root systems and the convergence of quantitative genetics and genomics in tree breeding have been discussed,

showcasing the advancements in understanding tree genetics and improving breeding practices. This study thus serves as a valuable resource for researchers, providing a comprehensive overview of the current state of tree genomic research and its applications.

Future research should focus on several key areas to further advance tree genomic research and its applications. First, there is a need for more comprehensive studies that integrate aboveground and belowground genomic data to provide a complete picture of tree biology. Second, the development of more efficient and scalable sequencing methods will be crucial for large-scale genomic projects like the Darwin Tree of Life Project. Third, landscape genomics should be further explored to understand the genetic basis of tree adaptation to changing environments, which will be essential for developing effective conservation strategies. Additionally, the integration of genomic data with phenotypic and environmental data will enhance the accuracy of genomic selection in tree breeding, leading to more resilient and productive tree populations. Policymakers should support these research efforts by funding large-scale genomic projects and promoting the use of genomic data in conservation and breeding programs. By addressing these recommendations, future research can continue to unravel the complexities of tree genomes and contribute to the sustainable management and conservation of tree species.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Reference

- Amaral J., Ribeyre Z., Vigneaud J., Sow M., Fichot R., Messier C., Pinto G., Nolet P., and Maury S., 2020, Advances and promises of epigenetics for forest trees, *Forests*, 11(9): 976.
<https://doi.org/10.3390/f11090976>
- Anderson M., 2018, Emerging next-generation sequencing technologies, In: Netto G., and Schrijver I. (eds.), *Genomic applications in pathology*, Springer, New York, USA, pp.19-29.
https://doi.org/10.1007/978-1-4939-0727-4_2
- Asefa M., Worthy S.J., Cao M., Song X., Lozano Y.M., and Yang J., 2022. Above and belowground plant traits are not consistent in response to drought and competition treatments, *Annals of Botany*, 130(7): 939-950.
<https://doi.org/10.1093/aob/mcac108>
PMid:36001733 PMCID:PMC9851322
- Bansal G., Narta K., and Teltumbade M., 2018, Next-generation sequencing: technology, advancements, and applications, In: Shanker A. (ed.), *Bioinformatics: sequences, structures, phylogeny*, Springer, Singapore, pp.15-46.
https://doi.org/10.1007/978-981-13-1562-6_2
PMCID:PMC5750229
- Benavides R., Carvalho B., Bastias C., López-Quiroga D., Mas A., Cavers S., Gray A., Albet A., Alía R., Ambrosio O., Aravanopoulos F., Auñón F., Avanzi C., Avramidou E., Bagnoli F., Ballesteros E., Barbas E., Bastien C., Bernier F., Bignalet H., Bouic D., Brunetto W., Buchovska J., Cabanillas-Saldaña A., Cheval N., Climent J., Corréard M., Cremer E., Danusevičius D., Dauphin B., Caño F., Denou J., Dokhelar B., Dourthe R., Farsakoglou A., Fera A., Fonti P., Ganopoulos I., Barrio J., Gilg O., González-Martínez S., Graf R., Grivet D., Gugerli F., Hartleitner C., Heer K., Hollenbach E., Hurel A., Issehuth B., Jean F., Jorge V., Jouineau A., Kappner J., Kärkkäinen K., Kesälahti R., Knutzen F., Kujala S., Kumpula T., Labriola M., Lalanne C., Lambert J., Lascoux M., Provost G., Liesebach M., Malliarou E., Marchon J., Mariotte N., Martínez-Sancho E., Matesanz S., Meischner H., Michotey C., Milesi P., Morganti S., Myking T., Nilsen A., Notivol E., Opgenoorth L., Østreng G., Pakull B., Piotti A., Plomion C., Poinot N., Pringarbe M., Puzos L., Pyhäjärvi T., Raffin A., Ramírez-Valiente J., Rellstab C., Richter S., Robledo-Arnuncio J., Segundo S., Savolainen O., Schneck V., Schueler S., Scotti I., Semerikov V., Sønstebo J., Spanu I., Thévenet J., Tollefsrud M., Turion N., Vendramin G., Villar M., Westin J., Fady B., and Valladares F., 2021, The GenTree Leaf Collection: inter- and intraspecific leaf variation in seven forest tree species in Europe, *Global Ecology and Biogeography*, 30(3): 590-597.
<https://doi.org/10.1111/geb.13239>
- Calleja-Rodríguez A., Li Z., Hallingbäck H., Sillanpää M., Wu H., Abrahamsson S., and García-Gil M., 2019, Analysis of phenotypic- and Estimated Breeding Values (EBV) to dissect the genetic architecture of complex traits in a Scots pine three-generation pedigree design, *Journal of Theoretical Biology*, 462: 283-292.

- Cantalapiedra C., Hernández-Plaza A., Letunic I., Bork P., and Huerta-Cepas J., 2021, eggNOG-mapper v2: functional annotation, orthology assignments, and domain prediction at the metagenomic scale, *Molecular Biology and Evolution*, 38: 5825-5829.
<https://doi.org/10.1093/molbev/msab293>
 PMid:34597405 PMCID:PMC8662613
- Cappa E., Klutsch J., Sebastian-Azcona J., Ratcliffe B., Wei X., Ros L., Liu Y., Chen C., Benowicz A., Sadoway S., Mansfield S., Erbilgin N., Thomas B., and El-Kassaby Y., 2022, Integrating genomic information and productivity and climate-adaptability traits into a regional white spruce breeding program, *PLoS One*, 17(3): e0264549.
<https://doi.org/10.1371/journal.pone.0264549>
 PMid:35298481 PMCID:PMC8929621
- Carpenter S., and Conlan R., 2021, Clinical functional genomics, *Cancers*, 13(18): 4627.
<https://doi.org/10.3390/cancers13184627>
 PMid:34572854 PMCID:PMC8465855
- Cortés A., Restrepo-Montoya M., and Bedoya-Canas L., 2020, Modern strategies to assess and breed forest tree adaptation to changing climate, *Frontiers in Plant Science*, 11: 583323.
<https://doi.org/10.3389/fpls.2020.583323>
 PMid:33193532 PMCID:PMC7609427
- Depuydt T., and Vandepoele K., 2021, Multi-omics network-based functional annotation of unknown Arabidopsis genes, *The Plant Journal*, 108(4): 1193-1212.
<https://doi.org/10.1111/tpj.15507>
 PMid:34562334
- Dijk E., Jaszczyszyn Y., Naquin D., and Thermes C., 2018, The third revolution in sequencing technology, *Trends in Genetics*, 34(9): 666-681.
<https://doi.org/10.1016/j.tig.2018.05.008>
- Du Q., Lu W., Quan M., Xiao L., Song F., Li P., Zhou D., Xie J., Wang L., and Zhang D., 2018, Genome-wide association studies to improve wood properties: challenges and prospects, *Frontiers in Plant Science*, 9: 1912.
<https://doi.org/10.3389/fpls.2018.01912>
 PMid:30622554 PMCID:PMC6309013
- Fattel L., Psaroudakis D., Yanarella C., Chiteri K., Dostalík H., Joshi P., Starr D., Vu H., Wimalanathan K., and Lawrence-Dill C., 2021, Standardized genome-wide function prediction enables comparative functional genomics: a new application area for Gene Ontologies in plants, *GigaScience*, 11: giac023.
<https://doi.org/10.1093/gigascience/giac023>
 PMid:35426911 PMCID:PMC9012101
- Gagalova K., Warren R., Coombe L., Wong J., Nip K., Yuen M., Whitehill J., Celedon J., Ritland C., Taylor G., Cheng D., Plettner P., Hammond S., Mohamadi H., Zhao Y., Moore R., Mungall A., Boyle B., Laroche J., Cottrell J., MacKay J., Lamothe M., Gérardi S., Isabel N., Pavy N., Jones S., Bohlmann J., Bousquet J., and Birol I., 2022, Spruce giga-genomes: structurally similar yet distinctive with differentially expanding gene families and rapidly evolving genes, *The Plant Journal*, 111(5): 1469-1485.
<https://doi.org/10.1111/tpj.15889>
- Gao J., Liu Z., Zhao W., Tomlinson K., Xia S., Zeng Q., Wang X., and Chen J., 2020, Combined genotype and phenotype analyses reveal patterns of genomic adaptation to local environments in the subtropical oak *Quercus acutissima*, *Journal of Systematics and Evolution*, 59(3): 541-556.
<https://doi.org/10.1111/jse.12568>
- Grattapaglia D., 2022, Twelve years into genomic selection in forest trees: climbing the slope of enlightenment of marker assisted tree breeding, *Forests*, 13(10): 1554.
<https://doi.org/10.3390/f13101554>
- Grattapaglia D., Silva-Junior O., Resende R., Cappa E., Müller B., Tan B., Isik F., Ratcliffe B., and El-Kassaby Y., 2018, Quantitative genetics and genomics converge to accelerate forest tree breeding, *Frontiers in Plant Science*, 9: 1693.
<https://doi.org/10.3389/fpls.2018.01693>
 PMid:30524463 PMCID:PMC6262028
- Holliday J., Aitken S., Cooke J., Fady B., González-Martínez S., Heuertz M., Jaramillo-Correa J., Lexer C., Staton, M., Whetten R., and Plomion C., 2017, Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding, *Molecular Ecology*, 26(3): 706-717.
<https://doi.org/10.1111/mec.13963>
- Hu T., Chitnis N., Monos D., and Dinh A., 2021, Next-generation sequencing technologies: an overview, *Human Immunology*, 82(11): 801-811.
<https://doi.org/10.1016/j.humimm.2021.02.012>
- Huang Y., Chen Y., Castro-Izaguirre N., Baruffol M., Brezzi M., Lang A., Li Y., Härdt W., Oheimb G., Yang X., Liu X., Pei K., Both S., Yang B., Eichenberg D., Assmann T., Bauhus J., Behrens T., Buscot F., Chen X., Chesters D., Ding B., Durka W., Erfmeier A., Fang J., Fischer M., Guo L., Guo D., Gutknecht J., He J., He C., Hector A., Hönig L., Hu R., Klein A., Kühn P., Liang Y., Li S., Michalski S., Scherer-Lorenzen M., Schmidt K., Scholten T., Schuldt A., Shi X., Tan M., Tang Z., Trogisch S., Wang Z., Welk E., Wirth C., Wubet T., Xiang W., Yu M., Yu X., Zhang J., Zhang S., Zhang N., Zhou H., Zhu C., Zhu L., Bruehlheide H., Ma K., Niklaus P., and Schmid B., 2018, Impacts of species richness on productivity in a large-scale subtropical forest experiment, *Science*, 362: 80-83.
<https://doi.org/10.1126/science.aat6405>
 PMid:30287660

- Hug L., Baker B., Anantharaman K., Brown C., Probst A., Castelle C., Butterfield C., Hernsdorf A., Amano Y., Ise K., Suzuki Y., Dudek N., Relman D., Finstad K., Amundson R., Thomas B., and Banfield J., 2016, A new view of the tree of life, *Nature Microbiology*, 1: 16048.
<https://doi.org/10.1038/nmicrobiol.2016.48>
 PMid:27572647
- Isabel N., Holliday J., and Aitken S., 2019, Forest genomics: advancing climate adaptation, forest health, productivity, and conservation, *Evolutionary Applications*, 13: 3-10.
<https://doi.org/10.1111/eva.12902>
 PMid:31892941 PMCID:PMC6935596
- Jactel H., Gritti E., Drössler L., Forrester D., Mason W., Morin X., Pretzsch H., and Castagneyrol B., 2018, Positive biodiversity- productivity relationships in forests: climate matters, *Biology Letters*, 14: 20170747.
<https://doi.org/10.1098/rsbl.2017.0747>
 PMid:29618520 PMCID:PMC5938561
- Kelblervová R., Dvorák J., and Korecký J., 2022, Genetic diversity maximization as a strategy for resilient forest ecosystems: a case study on Norway spruce, *Forests*, 13(3): 489.
<https://doi.org/10.3390/f13030489>
- Kumar K., Cowley M., and Davis R., 2019, Next-generation sequencing and emerging technologies, *Seminars in Thrombosis and Hemostasis*, 45: 661-673.
<https://doi.org/10.1055/s-0039-1688446>
 PMid:31096307
- Levy S., and Boone B., 2018, Next-generation sequencing strategies, *Cold Spring Harbor Perspectives in Medicine*, 9: a025791.
<https://doi.org/10.1101/cshperspect.a025791>
 PMid:30323017 PMCID:PMC6601457
- Li F., Chen X., Luo H., Meiners S., and Kong C., 2022, Root-secreted (-)-loliolide modulates both belowground defense and aboveground flowering in *Arabidopsis* and tobacco (*Nicotiana benthamiana*), *Journal of Experimental Botany*, 74(3): 964-975.
<https://doi.org/10.1093/jxb/erac439>
 PMid:36342376
- Lu M., Cao M., Yang J., and Swenson N., 2023, Comparative transcriptomics reveals divergence in pathogen response gene families amongst 20 forest tree species, *G3: Genes, Genomes, Genetics*, 13(12): jkad233.
<https://doi.org/10.1093/g3journal/jkad233>
 PMid:37812763 PMCID:PMC10700026
- Ma W., Tang S., Dengzeng Z., Zhang D., Zhang T., and Ma X., 2022, Root exudates contribute to belowground ecosystem hotspots: a review, *Frontiers in Microbiology*, 13: 937940.
<https://doi.org/10.3389/fmicb.2022.937940>
 PMid:36274740 PMCID:PMC9581264
- Mahood E., Kruse L., and Moghe G., 2020, Machine learning: a powerful tool for gene function prediction in plants, *Applications in Plant Sciences*, 8(7): e11376.
<https://doi.org/10.1002/aps3.11376>
 PMid:32765975 PMCID:PMC7394712
- Meger J., Ulaszewski B., and Burczyk J., 2021, Genomic signatures of natural selection at phenology-related genes in a widely distributed tree species *Fagus sylvatica* L., *BMC Genomics*, 22: 583.
<https://doi.org/10.1186/s12864-021-07907-5>
 PMid:34332553 PMCID:PMC8325806
- Mendler K., Chen H., Parks D., Hug L., and Doxey A., 2018, AnnoTree: visualization and exploration of a functionally annotated microbial tree of life, *Nucleic Acids Research*, 47: 4442-4448.
<https://doi.org/10.1093/nar/gkz246>
 PMid:31081040 PMCID:PMC6511854
- Müller B., Filho J., Lima B., Garcia C., Missiaggia A., Aguiar A., Takahashi E., Kirst M., Gezan S., Silva-Junior O., Neves L., and Grattapaglia D., 2018, Independent and joint-GWAS for growth traits in *Eucalyptus* by assembling genome-wide data for 3373 individuals across four breeding populations, *The New Phytologist*, 221(2): 818-833.
<https://doi.org/10.1111/nph.15449>
 PMid:30252143
- Musunuru K., Arora P., Cooke J., Ferguson J., Hershberger R., Hickey K., Lee J., Lima J., Loscalzo J., Pereira N., Russell M., Shah S., Sheikh F., Wang T., and Macrae C., 2018, Interdisciplinary models for research and clinical endeavors in genomic medicine: a scientific statement from the American heart association, *Circulation: Genomic and Precision Medicine*, 11: 6.
<https://doi.org/10.1161/HCG.0000000000000046>
- Naidoo S., Slippers B., Plett J., Coles D., and Oates C., 2019, The road to resistance in forest trees, *Frontiers in Plant Science*, 10: 273.
<https://doi.org/10.3389/fpls.2019.00273>
 PMid:31001287 PMCID:PMC6455082

- Neale D., Martínez-García P., Torre A., Montanari S., and Wei X., 2017, Novel insights into tree biology and genome evolution as revealed through genomics, *Annual Review of Plant Biology*, 68: 457-483.
<https://doi.org/10.1146/annurev-arplant-042916-041049>
- Osborne O., Dobrevá M., Papadopoulos A., Moura M., Brunello A., Queiroz L., Pennington R., Lloyd J., and Savolainen V., 2022, Mapping the root systems of individual trees in a natural community using genotyping-by-sequencing, *The New Phytologist*, 238(3): 1305-1317.
<https://doi.org/10.1111/nph.18645>
- Saha S., Cooksey A., Childers A., Poelchau M., and McCarthy F., 2021, Workflows for rapid functional annotation of diverse arthropod genomes, *Insects*, 12(8): 748.
<https://doi.org/10.3390/insects12080748>
- Satam H., Joshi K., Mangrolia U., Waghoo S., Zaidi G., Rawool S., Thakare R., Banday S., Mishra A., Das G., and Malonia S., 2024, Next-generation sequencing technology: current trends and advancements, *Biology*, 13(5): 286.
<https://doi.org/10.3390/biology13050286>
PMid:38785841 PMCID:PMC11107263
- Sharma T., Devanna B., Kiran K., Singh P., Arora K., Jain P., Tiwari I., Dubey H., Saklani B., Kumari M., Singh J., Jaswal R., Kapoor R., Pawar D., Sinha S., Bisht D., Solanke A., and Mondal T., 2018, Status and prospects of next generation sequencing technologies in crop plants, *Current Issues in Molecular Biology*, 27: 1-36.
- Silva P., Silva-Junior O., Resende L., Sousa V., Aguiar A., and Grattapaglia D., 2020, A 3K Axiom SNP array from a transcriptome-wide SNP resource sheds new light on the genetic diversity and structure of the iconic subtropical conifer tree *Araucaria angustifolia* (Bert.) Kuntze, *PLoS One*, 15(8): e0230404.
<https://doi.org/10.1371/journal.pone.0230404>
PMid:32866150 PMCID:PMC7458329
- Stephan T., Burgess S., Cheng H., Danko C., Gill C., Jarvis E., Koepfli K., Koltes J., Lyons E., Ronald P., Ryder O., Schriml L., Soltis P., Vandewoude S., Zhou H., Ostrander E., and Karlsson E., 2022, Darwinian genomics and diversity in the tree of life, *Proceedings of the National Academy of Sciences of the United States of America*, 119(4): e2115644119.
<https://doi.org/10.1073/pnas.2115644119>
PMid:35042807 PMCID:PMC8795533
- Szechyńska-Hebda M., Lewandowska M., Witoń D., Fichman Y., Mittler R., and Karpiński S., 2022, Aboveground plant-to-plant electrical signaling mediates network acquired acclimation, *The Plant Cell*, 34: 3047-3065.
<https://doi.org/10.1093/plcell/koac150>
PMid:35595231 PMCID:PMC9338792
- Torres L., Andrade S., and Mazzafera P., 2021, Split-root, grafting and girdling as experimental tools to study root-to shoot-to root signaling, *Environmental and Experimental Botany*, 191: 104631.
<https://doi.org/10.1016/j.envexpbot.2021.104631>
- Wan X., Chen X., Huang Z., and Chen H., 2021, Contribution of root traits to variations in soil microbial biomass and community composition, *Plant and Soil*, 460: 483-495.
<https://doi.org/10.1007/s11104-020-04788-7>
- Wambugu P., Ndjiondjop M., and Henry R., 2018, Role of genomics in promoting the utilization of plant genetic resources in genebanks, *Briefings in Functional Genomics*, 17(3): 198-206.
<https://doi.org/10.1093/bfpg/ely014>
PMid:29688255 PMCID:PMC5967547
- Wang W., He X.F., Yan X., Ma B., Lu C., Wu J., Zheng Y., Wang W., Xue W.B., Tian X.C., Guo J.F., El-Kassaby Y., Porth I., Leng P., Hu Z., and Mao J., 2023, Chromosome-scale genome assembly and insights into the metabolome and gene regulation of leaf color transition in an important oak species, *Quercus dentata*, *The New Phytologist*, 238(5): 2016-2032.
<https://doi.org/10.1111/nph.18814>
- Webber C., 2020, Functional genomics, In: Geddes J.R., Andreasen N.C., and Goodwin G.M. (eds.), *New Oxford textbook of psychiatry*, Oxford University Press, Oxford, UK, pp.144-153.
- Wen Z., White P., Shen J., and Lambers H., 2021, Linking root exudation to belowground economic traits for resource acquisition, *The New Phytologist*, 233(4): 1620-1635.
<https://doi.org/10.1111/nph.17854>

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