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Poplar genomics: a brief 20-year retrospective and future outlook

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Abstract

Over the past two decades, poplar (*Populus*) genomics has evolved from the construction of initial single-species reference genomes to the resolution of complex genomic variation within and across species. This review traces this trajectory, highlighting how advances in sequencing and assembly technologies have enhanced genomes' quality and yielded new insights into species' evolution and the molecular basis underlying key breeding traits. Throughout this progression, first-generation Sanger sequencing produced the first tree reference genome of *Populus trichocarpa*, establishing a foundation for comparative and functional studies. Second-generation short-read sequencing subsequently lowered the costs and enabled broader sampling, although assemblies often remained fragmented in repetitive regions and areas of complex structural variation. More recently, third-generation long-read sequencing (e.g., PacBio HiFi), combined with long-range scaffolding techniques, have dramatically improved contiguity. These technologies are now approaching telomere-to-telomere (T2T) completeness, making haplotype-resolved assemblies practical for both wild and cultivated species. On this stronger genomic foundation, comparative genomics, population genomics, and pangenome analyses can more accurately detect structural variants and variation in genes' presence/absence, better associating them with adaptation, divergence, and agronomically important traits. Finally, we summarize the contributions of poplar genomics to forest tree biology and discuss future directions, including T2T and haplotype-resolved pangenomes, as well as the deeper integration of multi-omics, artificial intelligence (AI), and genome editing technologies to facilitate and accelerate future AI-driven smart breeding of poplar for diverse environments.

Keywords: Poplar (*Populus*), Genome assembly, Long-read sequencing, Comparative genomics, Telomere-to-telomere (T2T), Pangenome

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Populus: from ecological keystone tree to the genomic model system

Forest trees are long-lived perennial species that play critical roles in global carbon cycling, biodiversity maintenance, and ecosystems' stability[1,2]. However, compared with annual model plants such as *Arabidopsis thaliana* and major crops, genetic and genomic studies in trees are often constrained by their inherent biological factors. Characteristics such as long generation times, large physical size, and predominantly outcrossing mating systems hinder the elucidation of the molecular basis underlying complex traits that are economically and ecologically important[3,4]. These include secondary growth, dormancy, and responses to biotic and abiotic stimuli. Consequently, functional validation and both conventional and molecular breeding efforts have been significantly impeded in trees relative to other plant species[3,5].

Within this context, poplar (*Populus*), has emerged as a premier woody model system that integrates ecological relevance with experimental tractability. The genus *Populus* (Salicaceae) comprises approximately 30 species that are native to the Northern Hemisphere, where they are widely distributed from temperate to boreal regions[6]. As pioneer or foundation species in riparian and early-successional habitats, poplars exhibit rapid growth, pronounced developmental plasticity, and dioecy, which is a mating system that maintains high levels of genetic diversity in natural populations[7,8]. Moreover, poplars are economically and ecologically important in timber and pulp production, short-rotation bioenergy systems, and phytoremediation, linking poplar research to both traditional forestry and climate-oriented land-use strategies[9–11]. Collectively, these characteristics, together with their broad environmental adaptability, make poplars an ideal system for investigating how long-lived trees respond to heterogeneous environments and climate change as well as for advancing forestry breeding programs[8,12].

Notably, poplar is widely regarded as an ideal model tree for genomics and functional biology because of its relatively compact genome (~400–500 Mb), which greatly facilitates sequencing, assembly, and annotation of this species compared with the exceptionally large genomes of many conifers[13]. Moreover, stable *Agrobacterium*-mediated transformation systems and well-established transient expression assays (including protoplast-based systems) have made poplar highly amenable to molecular experimentation[14,15]. The development of clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated protein (Cas) technologies has further strengthened functional testing of the genes and regulatory elements involved in wood formation, development, and stress responses[16,17]. Consequently, poplar serves as a complementary comparative model to *Arabidopsis* for distinguishing conserved biological pathways from tree-specific innovations, especially those related to secondary growth, secondary metabolism, and long-term environmental responses[7,8,13].

Marking two decades since the release of the first poplar genome, this review synthesizes the progress of poplar genomics over the past 20 years. We emphasize how technological transitions have driven improvements in the quality of genome assemblies and enabled deeper inference of genomic variation and its biological

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consequences. We summarize key milestones spanning construction of the reference genome[13], population-scale genomics and pangenome resources[18–20], and multi-omics-enabled functional annotation and trait–mechanism dissection[21,22]. Together, these advances reflect both methodological progress and increasing application-oriented momentum in forest tree genomics[8,12,23]. By reviewing these milestones, we aim to provide a forward-looking perspective on the future directions of poplar genomics and its potential to address challenges common to long-lived woody plants. Ultimately, we hope this synthesis offers transferable frameworks for resource development, genomic variation analysis, and molecular breeding in other forest tree species[12,20–23].

Two decades of progress in *Populus* genome sequencing and assembly

Over the past 20 years, the *Populus* genus has become an indispensable model system for understanding the molecular biology, evolution, and environmental adaptation of woody plants. As one of the few perennial genera with broad ecological amplitude and economic significance, *Populus* displays remarkable genetic diversity and adaptive traits related to growth, phenology, and stress tolerance. The progress of *Populus* genomics closely parallels advances in sequencing technologies, from the first Sanger-based assembly to the current era of haplotype-resolved and pangenomic approaches (Fig. 1; Supplementary Table S1).

The Sanger sequencing era and the first tree genome

First-generation sequencing, commonly known as Sanger sequencing[24], is renowned for its high accuracy (approaching 99.99%). It remains the gold standard for validating relatively short sequences (< 1 kb) and served as the cornerstone of the Human Genome Project[25]. In woody plant genomics, Tuskan et al. published the genome of *Populus trichocarpa* (black cottonwood), which was the first-ever release of a tree genome[13]. Using Sanger-based whole-genome shotgun sequencing of the female clone 'Nisqually-1', the consortium assembled a 485-Mb draft genome ($2n$ = 38), anchoring ~410 Mb (94%) to the 19 chromosomes via integrated genetic and physical maps[13]. Genome annotation predicted 45,555 protein-coding genes and revealed a recent whole-genome duplication (the Salicoid event, ~65 Mya) that retained approximately 8,000 paralogous gene pairs[13].

As the third plant genome sequenced after *Arabidopsis thaliana*[26] and rice (*Oryza sativa*)[27], *P. trichocarpa* marked the dawn of the "tree genomics era". This foundational resource not only demonstrated the feasibility of assembling moderately complex, heterozygous genomes using first-generation technology but also established a critical reference framework for subsequent comparative and functional studies across the genus *Populus* and other Salicaceae species[13]. Nevertheless, the inherent limitations of Sanger sequencing, namely its low throughput, high cost, and protracted turnaround times, ultimately constrained its scalability for widespread application in other nonmodel trees[24,25].

The next-generation sequencing boom and population genomics

Next-generation sequencing (NGS) catalyzed a fundamental shift in population genetics, moving the field from low-throughput, locus-by-locus genotyping toward genome-wide inference at the population scale[28]. Given the advantages of the technology, whole-genome resequencing became feasible for many nonmodel organisms[28]. Dense variant discovery, initially dominated by single nucleotide polymorphisms (SNPs) and short insertions and deletions (indels), and increasingly encompassing structural variants (SVs), emerged as a routine foundation for population-level inference of population structure, genetic diversity, natural selection, and environmental adaptation[28,29]. These advances were particularly consequential for long-lived forest trees, where extended generation times, pronounced population structure, and complex trait architectures often limit experimental approaches[4,30]. Consequently, by enabling genome-wide data generation at a population scale, NGS advances helped establish a unified analytical toolkit spanning diversity inference, selection scans, demographic reconstruction, association mapping, and genotype–environment analyses, thereby accelerating the rise of modern tree population genomics[28,30].

Driven by these advances, *Populus* rapidly emerged as a flagship system for studies of the population genomics of forest trees. A representative study in *P. trichocarpa* integrated genome-wide scans for selection with trait association analyses, illustrating how population resequencing can identify candidate targets of selection and connect them to adaptive phenotypic variation across environmental gradients[31]. At the species level, resequencing-based analyses across multiple *Populus* species showed that genome-wide diversity and differentiation patterns are nonrandom and have been strongly shaped by heterogeneity in the recombination rateand pervasive linked selection[32]. This provided a general explanatory framework that ties recombination landscapes, effective population size, and selection together at the genomic scale[32]. Moreover, population genomic studies enabled more mechanistic interpretations of divergence landscapes. This includes evidence that "genomic islands" can arise through processes such as ancient polymorphism and divergence hitchhiking rather than necessarily requiring extensive recent gene flow[33], and that the joint effects of demography and selection can be traced across genomes to illuminate the distribution of barriers to introgression and the dynamics of deleterious variation[34].

More recently, the focus of tree population genomics has expanded beyond identifying adaptive loci toward predicting adaptive capacity under climate change. Studies have increasingly integrated genotype–environment association (GEA) analysis with climate modeling to infer climate-related genetic variation, quantify potential maladaptation, and identify populations that may be especially vulnerable under future scenarios[35,36]. At the same time, integrative designs that combine chromosome-level reference genomes, population resequencing, and multi-omics evidence (e.g., stress-responsive transcriptomics) are strengthening the link between statistical associations and biological mechanisms, thereby providing a more comprehensive framework for understanding climate responses and adaptive evolution in long-lived forest trees[37,38].

Overall, the NGS era fundamentally reshaped *Populus* genomics by extending analyses beyond single-reference genomes to population-scale investigations of genetic diversity. Large-scale resequencing studies enabled the systematic characterization of the population history, gene flow, linked selection, and variation in the recombination rate across the genus, substantially improving our understanding of its local adaptation and climate responsiveness.

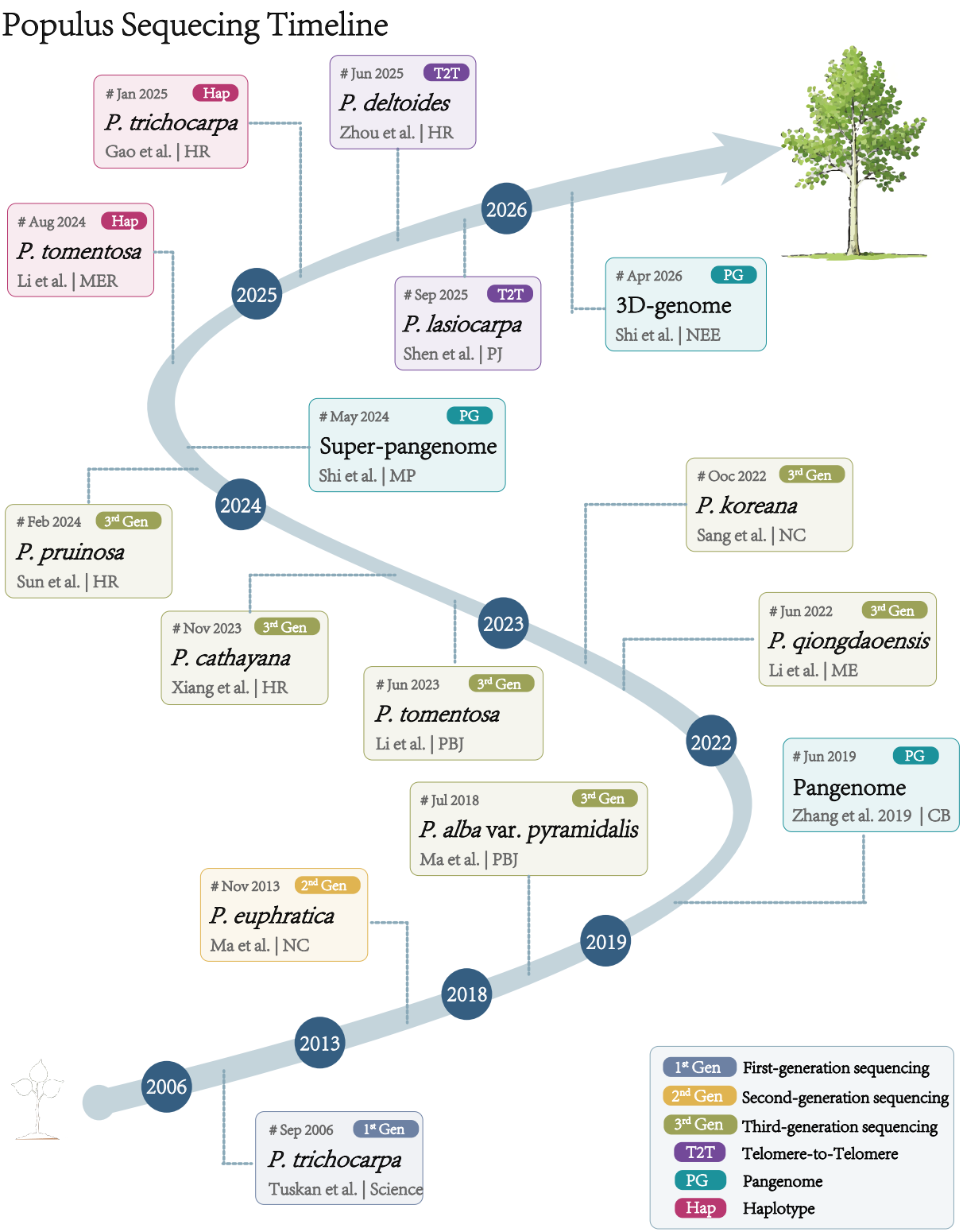

Fig. 1 Representative milestones in *Populus* genome sequencing and assembly over the past 20 years. The timeline summarizes major advances from the first *P. trichocarpa* reference genome in 2006 to recent telomere-to-telomere, haplotype-resolved, pangenome, super-pangenome, and three-dimensional (3D)-genome resources. Key representative studies are arranged chronologically along the curved timeline, with each box showing the species or genomic resource, publication date, authors, and journal abbreviation. Different colors indicate the dominant technical category of each milestone, including first-generation sequencing, second-generation sequencing, third-generation sequencing, telomere-to-telomere assembly, pangenome or super-pangenome construction, haplotype-resolved assembly, and 3D-genome resources. This timeline illustrates the transition of *Populus* genomics from single-reference genome construction toward high-continuity, population-scale, and structurally comprehensive genome resources. Journal abbreviations: NC, Nature Communications; PBJ, Plant Biotechnology Journal; CB, Communications Biology; ME, Molecular Ecology; HR, Horticulture Research; MP, Molecular Plant; MER, Molecular Ecology Resources; PJ, The Plant Journal; NEE, Nature Ecology & Evolution.

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Third-generation sequencing and applications in wild species

Third-generation sequencing technologies, also known as single-molecule sequencing, have advanced rapidly since the early 2010s. These platforms primarily include PacBio's single-molecule real-time (SMRT) sequencing and Oxford Nanopore Technologies (ONT) nanopore sequencing, both capable of generating long reads ranging from ~10 kb to the megabase scale. Compared with first-generation Sanger sequencing and second-generation NGS, the long reads generated from third-generation sequencing enable improved resolution of repetitive regions, structural variations, and epigenetic modifications such as DNA methylation[39–41].

By leveraging long-read capabilities, third-generation sequencing platforms (PacBio and Nanopore) overcame the fragmentation limitations that were inherent to second-generation assemblies, expanding research into the poplar genome to include more cultivated varieties and wild species. For instance, long-read sequencing substantially improved the continuity and overall quality of the genome of the ecologically important nonmodel poplar species, *Populus euphratica*, a desert-adapted tree species known for its capacity to adapt to extreme environments[42]. Furthermore, the integration of PacBio and Hi-C technologies enabled chromosome-level assemblies of both male and female individuals, leading to the identification of the sex determination region and *ARR17*-associated regulatory mechanisms, and clarifying the molecular basis of sexual dimorphism[43].

For species widely used in breeding, such as *Populus tomentosa*, long-read sequencing resolved major assembly challenges, producing a high-quality, haplotype-resolved genome that clarified its hybrid origin from *Populus adenopoda* and *Populus alba* var. *pyramidalis*, as well as its evolutionary characteristics[44]. Using a chromosome-level genome, Li et al. revealed associations between heterozygous alleles and wood traits in *P. tomentosa*, identifying the regulatory roles of heterozygous alleles (e.g., *PtoARF8*) in determining wood cellulose content[45]. In addition, long-read sequencing can also be used to sequence and assemble mitochondrial genomes, which are usually characterized by complex structures, enriching our understanding of how the organelle genome evolved[46].

Beyond these examples, third-generation sequencing has been widely applied to genomic studies in multiple wild *Populus* species, including *Populus deltoides*, *P. alba*, *Populus qiongdaoensis*, *Populus simonii*, and *Populus tremula*[47–56]. Additionally, the high-quality genome assemblies facilitated by long-read sequencing have further advanced population genomic studies of local environmental adaptation and adaptive evolution in species such as *Populus koreana*, *Populus cathayana*, and *Populus lasiocarpa*[35,36,38].

The introduction of third-generation sequencing technologies markedly improved the resolution of complex genomic architectures in *Populus*. Long-read sequencing substantially enhanced assemblies' continuity, completeness, and haplotype-resolved accuracy, allowing repetitive regions, structural variants, and heterozygous loci to be characterized with greatly improved precision. These advances facilitated the generation of high-quality genomes from nonmodel *Populus* species and elite breeding materials, while also strengthening efforts to link structural genomic variation to adaptive and agronomically important traits. Nevertheless, highly repetitive regions, such as telomeres and centromeres, continue to challenge even long-read assemblies, leaving many population- or lineage-specific genomic components incompletely represented.

The current frontier: telomere-to-telomere gap-free assemblies and the pangenome era

With the widespread adoption of long-read sequencing technologies such as PacBio HiFi and ONT, poplar genomics has entered the telomere-to-telomere (T2T) gap-free assembly era. The central goal of T2T assembly is to achieve complete chromosome-scale continuity, allowing the precise resolution of highly repetitive and structurally complex regions, including the centromeres and telomeres[57]. This advancement provides a robust and precise reference genome for downstream studies. By conducting comparative analyses of four nearly complete Salicaceae genomes[58], Wang et al. characterized the genetic and epigenetic landscapes of their centromeres, revealing transposable element-dominated centromere organization and rapid turnover dynamics across species[58]. In addition, a haplotype-resolved T2T assembly of *P. lasiocarpa* further elucidated retrotransposon-driven centromere evolution[59], while the gap-free genome of *P. deltoides* resolved centromeric sequences and deepened our understanding of karyotype evolution within Salicaceae[60]. Methodological innovations have also contributed to improved assembly quality. For example, the nearly gapless genome of *Populus ussuriensis*, generated using a doubled haploid line, reduced assembly complexity caused by heterozygosity and provided a practical strategy for resolving highly heterozygous poplar genomes[61]. Beyond structural genomics, T2T assemblies have substantial value for molecular breeding by enabling precise genome-wide marker localization and optimizing selection strategies, as demonstrated in hybrid populations of *P. deltoides*[62].

T2T assembly is also driving a paradigm shift in poplar genomics from collapsed single-reference genomes toward refined, haplotype-resolved assemblies. The high heterozygosity of poplar genomes frequently causes traditional assemblies to merge parental haplotypes, thereby masking true allelic and structural differences and limiting downstream genetic analyses. Haplotype-resolved assemblies overcome this limitation by explicitly distinguishing homologous chromosomes and revealing extensive inter-haplotype variation, providing a more reliable basis for trait-related genetic inference. Generating such assemblies typically requires the integration of long-read sequencing, long-range scaffolding technologies, and sometimes independent experimental validation. For instance, the haplotype-resolved genome of *P. trichocarpa* combined long-read data with advanced scaffolding strategies, markedly improving assembly accuracy and continuity[63]. In the hybrid poplar '84K', a widely used model for molecular functional studies, haplotype-resolved analysis identified more than 34,000 structural variants between haplotypes, directly influencing the expression of thousands of functional genes[64]. In the stabilized interspecific hybrid *P. tomentosa*, large-scale structural divergence between haplotypes has been proposed as a key factor underlying its broad environmental adaptability[44].

Building on these high-quality assemblies, poplar genomics is now moving beyond single-reference frameworks through the development of genus-wide and population-scale pangenomes. By synthesizing genomic data across diverse species and genotypes, pangenomes offer a comprehensive framework for investigating species' evolution, trait regulation, and molecular breeding[65,66]. Early milestones in this domain include comparative analyses of *P. trichocarpa*, *Populus nigra*, and *P. deltoides*, which highlighted extensive structural variation and underscored the role of dispensable genes in stress responses and disease resistance[67]. Subsequent genus-level resequencing efforts identified abundant SNPs and indels, revealing an enrichment of heterozygous loss-of-function variants in resistance genes and providing genomic

evidence of ancient hybridization across the genus[19]. More recently, a comprehensive super-pangenome integrating 19 poplar genomes demonstrated the pivotal role of variable genes and structural variation in ecological adaptation and species diversification[20]. Looking forward, rapid technological advancements are poised to establish pangenome graphs as the standard approach for capturing the full spectrum of high-resolution genetic variation in *Populus*—a methodological leap that will likely expand to other forest tree species in the near future.

In summary, the emergence of T2T assemblies, haplotype-resolved genomes, and pangenomic approaches has further expanded *Populus*-related genomics from improving reference assemblies to comprehensively capturing genomic diversity across the genus. Near-complete assemblies of centromeric and telomeric regions, together with large-scale analyses of haplotype divergence, structural variation, and dispensable genes, have revealed previously inaccessible aspects of the genome's evolution and trait differentiation. Concurrently, pangenomic analyses now provide a broader foundation for investigating hybridization history, ecological adaptation, and functional diversification both within and across *Populus* species.

Translating high-quality genome resources into trait architectures in *Populus*

Advances in sequencing technologies have shifted *Populus*-related genomics from a resource-oriented field to a systems-level framework for understanding the genetic basis of complex traits. This transition is particularly important, given the high heterozygosity, frequent hybridization, extensive structural variation, and dynamic sex chromosomes in *Populus* species, as these features are difficult to fully capture using single-reference genomes. Because wood formation is one of the most important traits in trees, the genes and regulatory networks involved in this process have been rapidly and comprehensively characterized. This progress has been driven by the availability of high-quality genome assemblies and gene annotations, as well as advances in other omics technologies such as epigenomics, single-cell transcriptomics, and spatial transcriptomics. Given these advances, it is now possible to reveal cellular heterogeneity in cambial tissues and uncover developmental trajectories linking stem cell maintenance, vascular differentiation, hormone signaling, and chromatin regulation[68,69]. Within this context, regulatory modules such as *PtrWOX4a–PtrVCS2*[70], *Auxin–PLT5*[71], *PagMYB31*[72], and *PtrSHR1*[73] are increasingly regarded as interconnected components within broader developmental networks coordinating wood formation and secondary growth.

In addition to wood formation, complex environmental adaptation represents another crucial set of traits in forest trees. Recent studies have emphasized multilayered regulatory systems involving transcriptional, post-transcriptional, and epigenetic regulation. For example, *SC35*-mediated alternative splicing of *bZIP49* regulates *AKT1*-dependent ion homeostasis under salt stress, whereas the *miR169z–NF-YA5–GPDHc1* module contributes to drought tolerance in poplar by reducing the accumulation of reactive oxygen species (ROS)[74,75]. Beyond acute stress, perennial adaptation in *Populus* is frequently described as involving interactions among hormonal signaling, circadian regulation, developmental age pathways, and seasonal environmental cues[76–79].

Moreover, benefiting from the high quality of genome assemblies across a broader range of *Populus* species, recent studies have expanded into previously inaccessible areas of research regarding sex chromosomes' evolution. The sex-determining regions in Salicaceae are highly repetitive and structurally dynamic and are often associated with suppressed recombination. Recent studies identified *ARR17* as a key regulator of sex determination and reported recurrent suppression of recombination, gene movement, and transitions between XY and ZW systems[55,80,81]. Beyond reproduction, sex-linked loci may also influence growth and physiological traits. For example, sex-dependent regulation of cytokinin signaling contributes to differences in drought responses between male and female individuals, highlighting pleiotropic links between reproductive and environmental adaptation governed by sex determination loci in *Populus*[82,83].

Lastly, because most complex traits are regulated by many small-effect loci, genomic selection (GS) has revolutionized the breeding of forest trees, including *Populus*, by overcoming traditional bottlenecks such as long generation times and late-expressing phenotypes. By utilizing genome-wide markers to predict genomic estimated breeding values (GEBVs) at the seedling stage, GS significantly accelerates breeding cycles and enhances the genetic gain of complex traits like wood quality, growth rate, and stress resilience[62,84–86]. In addition to traditional SNP markers, incorporating SVs, presence–absence variation, and regulatory variation could capture a greater proportion of the genetic variance underlying these traits, driven by advances in pangenomics and associated methodologies[45,62]. Thus, a broader and more comprehensive capture of genomic variation could facilitate the development of more accurate, advanced predictive breeding tools in the future, although their practical performance will continue to depend on high-quality phenotyping, multienvironment trials, and robust model validation.

Together, these findings support a more integrated view of *Populus* biology, in which regulatory modules operate across reproductive, developmental, and environmental contexts. Enabled by long-read sequencing, T2T assembly, pangenomics, and multi-omics integration, current studies are yielding increasingly comprehensive insights into wood formation, environmental adaptation, and sex chromosomes' evolution. Ultimately, *Populus* genomics has evolved from gene-centric and resource-building efforts to integrative analyses of regulatory systems across molecular, developmental, and ecological scales.

Challenges and future perspectives: from poplar genomic resources to predictive breeding

Although current advances in genome assembly, pangenomics, population genomics, and multi-omics-based functional analysis have greatly improved our understanding of the genome's evolution, adaptive variation, and complex trait regulation in *Populus*, the practical transition from resource construction and discovery of the mechanisms to their application in breeding remains incomplete. This section therefore focuses on current progress, emerging technologies, and future directions for developing a *Populus*-centered genomics-assisted breeding framework. Such a framework should connect the discovery of natural variation, functional validation, predictive modeling, genome editing, and evaluations of field-based breeding trials, while providing useful guidance for the genetic improvement of other woody species (Fig. 2).

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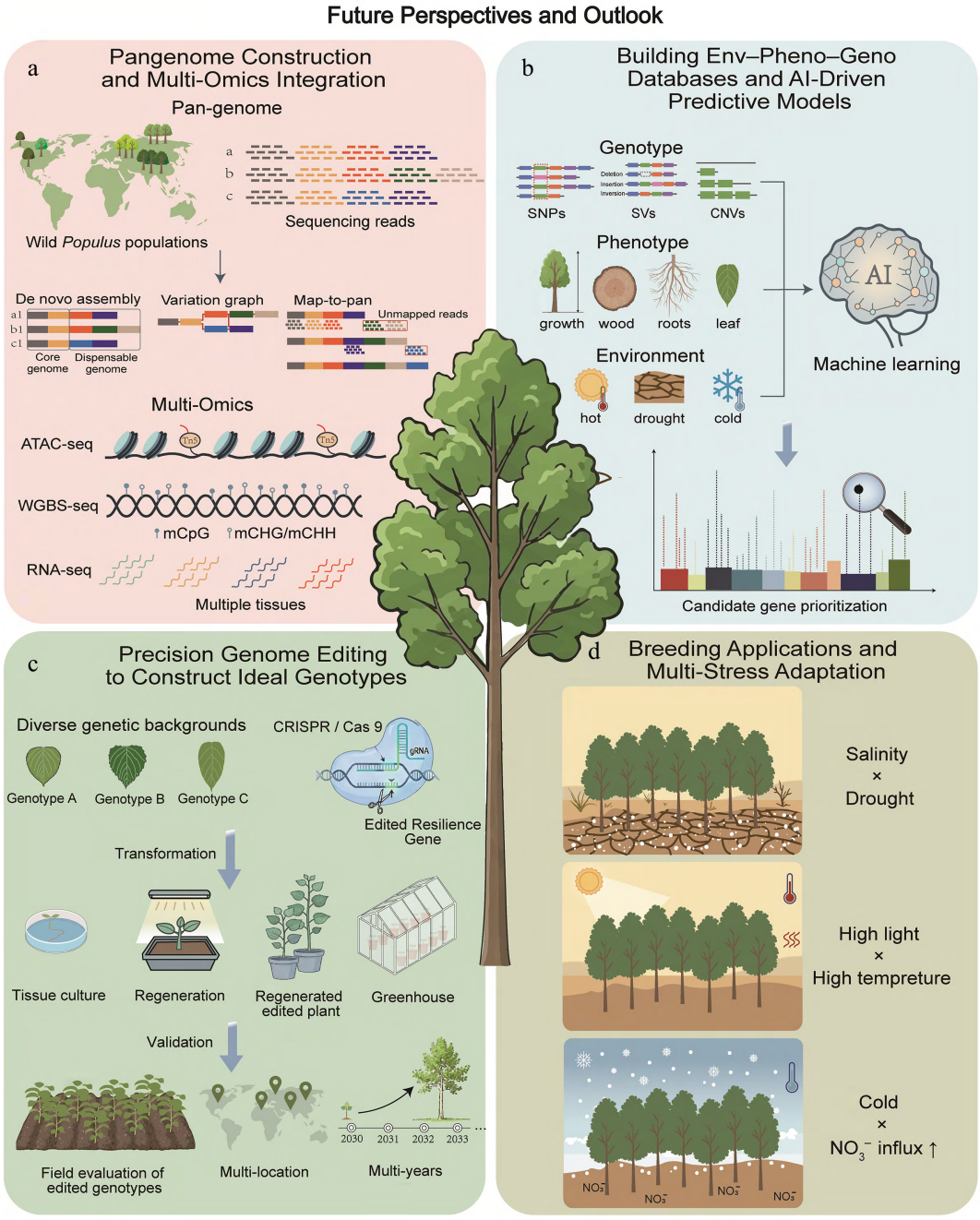

Fig. 2 Future perspectives on translating the genomic resources of *Populus* into predictive breeding applications across the following four directions. (a) Construction of population-scale pangenomes from wild *Populus* populations using *de novo* assembly, variation graphs, and map-to-pan strategies, integrated with multi-omics data across various tissues (e.g., assay for transposase-accessible chromatin using sequencing [ATAC-seq] for chromatin accessibility, whole-genome bisulfite sequencing [WGBS] for DNA methylation, and RNA sequencing [RNA-seq] for transcriptomics). (b) Development of integrated genotype–phenotype–environment databases that combine phenotypic and environmental data with genomic variations, including SNPs, SVs, and copy number variants (CNVs). Artificial intelligence and machine learning approaches will facilitate predictive modeling and prioritization of the candidate genes. (c) Precision genome editing across diverse genetic backgrounds to generate elite genotypes, followed by tissue culture, plant regeneration, greenhouse validation, and multilocation, multiyear field evaluations. (d) Translation of genomic discoveries into breeding applications to improve adaptations to combined stresses (e.g., salinity and drought, high light and high temperature, or nutrient uptake and cold tolerance).

Progress and remaining challenges in poplar genomics

Although important foundations have been established for constructing reference genomes, population resequencing, identification of adaptive loci, and discover of functional genes in *Populus* species, which have long served as a representative model system for forest trees, there are still unresolved challenges and bottlenecks in transitioning from genomic resource accumulation to functional interpretation of the mechanisms and breeding applications[31]. Most studies to date that have detected genetic variation across populations and species continue to rely on a single reference genome. However, a major limitation of this

single-reference framework is its incomplete representation of genomic diversity, especially for tree species like *Populus* that exhibit a wide geographic distribution, frequent interspecific hybridization and introgression, and generally high heterozygosity[20,87,88]. Consequently, reliance on a single reference genome and SNP-centered analytical strategies may underestimate genome-wide genetic variation and miss important components of functional and adaptive variation in *Populus*[15,20], particularly SVs, variation in the presence/absence of certain genes, and copy number variation.

Recent pangenome and super-pangenome studies that integrate multiple representative individuals and/or species offer new opportunities to capture a more complete spectrum of genomic variation. Compared with materials that have experienced long-term artificial selection and cultivation, wild poplar germplasm resources typically retain richer natural genetic variation. Over evolutionary timescales, they have accumulated favorable allelic variants associated with drought, cold, salt, and alkali tolerance; pest and disease resistance; phenological regulation; root adaptation; and growth stability[89–91] (Fig. 2a). Therefore, the systematic collection and analysis of wild *Populus* resources will help expand the variation spectrum of poplar pangenomes and graph-based pangenomes, thereby reducing the bias caused by single-reference genomes, but also provide a more realistic natural experimental background for identifying adaptive loci and mining favorable alleles[90].

However, although wild germplasm facilitates the identification of more adaptive variants, subsequent functional validation and applied translation still face multiple constraints, including low transformation efficiency, genotype dependence, outcrossing, highly heterozygous genetic backgrounds, gene redundancy, and long life cycles. Consequently, although the efficient use of wild resources will probably provide higher resolution for identifying variants closely associated with ecological adaptation, species diversification, phenological regulation, stress resistance, and growth-related traits, the transition from adaptive allele discovery to practical application will require substantial future work[17,23,91].

Emerging technologies for functional dissection of key traits in *Populus*

Beyond the development of advanced pangenomes, recent breakthroughs in single-cell and spatial transcriptomics have provided cell-type- and tissue-resolved contexts for interpreting candidate genes and regulatory variants in *Populus*[21,92–97]. Rather than relying solely on bulk tissue profiles, these approaches allow researchers to link genomic and transcriptomic variation to specific cell types, developmental stages, and spatial domains. Together with epigenomic and chromatin accessibility data, these technological development and multi-omics datasets have established a crucial foundation for connecting functional regulatory networks to developmental and environmental responses at a finer cellular scale[21,68,69,76,92,98].

Alongside advances in multi-omics, genome editing technologies are rapidly progressing and have emerged as a practical means of validating candidate adaptive loci and improving key traits in poplar. Broadly, genome editing tools include zinc finger nucleases (ZFNs) , transcription activator-like effector nucleases (TALENs), and CRISPR/Cas systems. ZFNs and TALENs are among the earliest gene editing tools, but because of their complex design, lower efficiency, and higher operational costs, their application in forest trees has been limited. In contrast, CRISPR/Cas systems are simpler to design, highly efficient, and highly scalable, making them increasingly popular for functional genomics and genetic improvement in poplar[99,100]. Furthermore, emerging technologies such as base editors, prime editing, mitoTALEN, and retron library recombineering (RLR), which enable targeted mutations, base substitutions, small indels, transcriptional regulation, and genome modifications of organelles, hold immense promise for future research[17,99–103]. Nevertheless, although genome editing provides essential tools for dissecting the molecular mechanisms underlying important traits in poplar, its widespread application remains constrained by factors such as transformation efficiency, regeneration capacity, genotype dependency, off-target effects, and editing stability. These limitations are particularly evident in wild *Populus* species, as successful editing is currently restricted to a few cultivated genotypes[17,104–107].

Future perspectives: from genomic advances to breeding applications

Despite some unresolved challenges, current technological foundations provide an optimistic outlook for translating advanced technologies into breeding applications for poplar. Leveraging the extensive genomic variation found in wild *Populus* species and germplasms, the integration of pangenome and multi-omics datasets will help establish a comprehensive understanding of natural genomic diversity (Fig. 2a). Alongside the wealth of genomic resources generated by advanced sequencing technologies, the rapid development of high-throughput phenotyping, artificial intelligence (AI), and machine learning are poised to become essential tools in modern forest tree breeding, mirroring their success in many crop species[108–111]. For example, a recent study demonstrated that machine learning approaches have been successfully integrated into multi-parameter phenotyping systems, enabling the precise assessment of drought responses by combining proximal sensing with high-throughput imaging[112]. Consequently, establishing large-scale genotype–phenotype–environment data platforms will provide a robust foundation for identifying candidate adaptive loci, prioritizing favorable allele combinations, and optimizing data-driven breeding decisions[109,110].

Looking ahead, AI models may further enable the *in silico* simulation of virtual genotypes under multiple stress scenarios (such as drought, salinity, and extreme temperatures), thereby helping to identify superior genomic configurations (Fig. 2b). This capability could provide precise guidance for targeted genome editing and molecular breeding strategies in poplar. Accordingly, future genome editing strategies in poplar are expected to transition from single-gene knockout toward more precise and programmable genome engineering. Multiplex CRISPR/Cas9 editing targeting tandem arrays can generate a range of mutation types, including structural variants like translocations and inversions, highlighting the potential to engineer genome structures under controlled conditions[113,114]. Although the targeted manipulation of large genomic fragments is not yet routine in *Populus*, recent advances in plant genome engineering suggest that this approach will become feasible in the near future (Fig. 2c). Therefore, integrating AI-assisted target prioritization with next-generation genome editing platforms could accelerate the functional validation of adaptive variants and inform future breeding strategies[108,109,113,114].

Ultimately, integrating these advanced technologies aims to facilitate poplar breeding by translating genomic discoveries into the development of elite, stress-resilient cultivars (Fig. 2d). The combination of adaptive genomic resources, predictive models, and biotechnological innovations should provide a comprehensive and efficient foundation to support the creation of poplar varieties that are capable of adapting to diverse and complex environments, including drought-prone regions, saline and alkaline soils,

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high-temperature zones, and high-altitude habitats[17,31,62,91,115,116]. For this reason, future poplar breeding should not rely on any single technology. Instead, it must operate through an iterative framework that links the exploration of wild germplasm, pangenome construction, multi-omics data integration, AI-driven prediction, precision genome editing, and field validation. Within this framework, pangenomes and wild germplasm resources provide the foundational genetic variation; multi-omics analyses help prioritize candidate genes and regulatory networks; AI models support trait prediction and the design of allele combinations; genome editing enables the functional testing of selected targets; and field trials provide the definitive evaluation of breeding value. However, it should be noted that these perspectives remain largely conceptual, and their practical implementation and real-world efficacy will require extensive further research and considerable time[116–118]. As *Populus* serves as a model system for forest trees, we believe that advancements in this field will also propel research and breeding efforts in nonmodel tree species of high ecological and economic value, such as *Eucommia ulmoides*, oak (*Quercus* spp.), pine (*Pinus* spp.), and spruce (*Picea* spp.).

Ethical statements

During the preparation of this work, the authors used ChatGPT (version: 5.0) for language refinement. The authors reviewed and edited all content produced with the assistance of this tool, verified its accuracy, and take full responsibility for the integrity and originality of the final manuscript. This work represents the authors' own intellectual contribution, and no AI tool is credited as an author.

Author contributions

The authors confirm their contributions to the paper as follows: conceived the review: Wang J; conducted the literature search and collected the data: Chen S, Wei Y, Zhou X; prepared the figures: Chen S; wrote the manuscript: Chen S, Wei Y, Wang J. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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Conflict of interest

The authors declare that they have no conflict of interest.

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References

[1] Harris NL, Gibbs DA, Baccini A, Birdsey RA, de Bruin S, et al. 2021. Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change* 11:234–240

[2] Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993

[3] Wullschleger SD, Jansson S, Taylor G. 2002. Genomics and forest biology: *Populus* emerges as the perennial favorite. *The Plant Cell* 14:2651–2655

[4] Neale DB, Kremer A. 2011. Forest tree genomics: growing resources and applications. *Nature Reviews Genetics* 12:111–122

[5] Isik F. 2014. Genomic selection in forest tree breeding: the concept and an outlook to the future. *New Forests* 45:379–401

[6] Stobrawa K. 2014. Poplars (*Populus* spp.): ecological role, applications and scientific perspectives in the 21st century. *Baltic Forestry* 20:204–213

[7] Cronk QCB. 2005. Plant eco-devo: the potential of poplar as a model organism. *New Phytologist* 166:39–48

[8] Jansson S, Douglas CJ. 2007. *Populus*: a model system for plant biology. *Annual Review of Plant Biology* 58:435–458

[9] Zalesny RS, Headlee WL, Gopalakrishnan G, Bauer EO, Hall RB, et al. 2019. Ecosystem services of poplar at long - term phytoremediation sites in the Midwest and Southeast, United States. *Wiley Interdisciplinary Reviews: Energy and Environment* 8:e349

[10] Ruttens A, Boulet J, Weyens N, Smeets K, Adriaensen K, et al. 2011. Short rotation coppice culture of willows and poplars as energy crops on metal contaminated agricultural soils. *International Journal of Phytoremediation* 13:194–207

[11] Fuertes A, Oliveira N, Cañellas I, Sixto H, Rodríguez-Soalleiro R, et al. 2023. Assessing the potential of poplar short rotation plantations to contribute to a low-carbon bioeconomy under water-limited conditions. *Journal of Environmental Management* 347:119062

[12] Plomion C, Bastien C, Bogeat-Triboulot MB, Bouffier L, Déjardin A, et al. 2016. Forest tree genomics: 10 achievements from the past 10 years and future prospects. *Annals of Forest Science* 73:77–103

[13] Tuskan GA, DiFazio S, Jansson S, Bohlmann J, Grigoriev I, et al. 2006. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). *Science* 313:1596–1604

[14] Fillatti JJ, Sellmer J, McCown B, Haissig B, Comai L. 1987. *Agrobacterium* mediated transformation and regeneration of *Populus*. *Molecular and General Genetics MGG* 206:192–199

[15] Guo J, Morrell-Falvey JL, Labbé JL, Muchero W, Kalluri UC, et al. 2012. Highly efficient isolation of *Populus* mesophyll protoplasts and its application in transient expression assays. *PLoS One* 7:e44908

[16] Fan D, Liu T, Li C, Jiao B, Li S, et al. 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in *Populus* in the first generation. *Scientific Reports* 5:12217

[17] Yao T, Yuan G, Lu H, Liu Y, Zhang J, et al. 2023. CRISPR/Cas9-based gene activation and base editing in *Populus*. *Horticulture Research* 10:uhad085

[18] Lin YC, Wang J, Delhomme N, Schiffthaler B, Sundström G, et al. 2018. Functional and evolutionary genomic inferences in *Populus* through genome and population sequencing of American and European aspen. *Proceedings of the National Academy of Sciences of the United States of America* 115:E10970–E10978

[19] Zhang B, Zhu W, Diao S, Wu X, Lu J, et al. 2019. The poplar pangenome provides insights into the evolutionary history of the genus. *Communications Biology* 2:215

[20] Shi T, Zhang X, Hou Y, Jia C, Dan X, et al. 2024. The super-pangenome of *Populus* unveils genomic facets for its adaptation and diversification in widespread forest trees. *Molecular Plant* 17:725–746

[21] Yu X, Liu Z, Sun X. 2023. Single-cell and spatial multi-omics in the plant sciences: technical advances, applications, and perspectives. *Plant Communications* 4:100508

[22] Raza A, Li Y, Prakash CS, Hu Z. 2025. Panomics to manage combined abiotic stresses in plants. *Trends in Plant Science* 30:1079–1084

[23] Ming M, Liu Q, Zhang J, Zhao A, Yi M, et al. 2025. Revolutionizing poplar biotechnology: genetic transformation and CRISPR/Cas9 strategies. *Industrial Crops and Products* 233:121350

[24] Sanger F, Nicklen S, Coulson AR. 1977. DNA sequencing with chain-terminating inhibitors. *Proceedings of the National Academy of Sciences of the United States of America* 74:5463−5467

[25] International Human Genome Sequencing Consortium. 2001. Initial sequencing and analysis of the human genome. *Nature* 409:860−921

[26] The Arabidopsis Genome Initiative. 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature* 408:796−815

[27] Goff SA, Ricke D, Lan TH, Presting G, Wang R, et al. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). *Science* 296:92−100

[28] Ellegren H. 2014. Genome sequencing and population genomics in non-model organisms. *Trends in Ecology & Evolution* 29:51−63

[29] Harris L, McDonagh EM, Zhang X, Fawcett K, Foreman A, et al. 2025. Genome-wide association testing beyond SNPs. *Nature Reviews Genetics* 26:156−170

[30] Wang J, Ding J, Tan B, Robinson KM, Michelson IH, et al. 2018. A major locus controls local adaptation and adaptive life history variation in a perennial plant. *Genome Biology* 19:72

[31] Evans LM, Slavov GT, Rodgers-Melnick E, Martin J, Ranjan P, et al. 2014. Population genomics of *Populus trichocarpa* identifies signatures of selection and adaptive trait associations. *Nature Genetics* 46:1089−1096

[32] Wang J, Street NR, Scofield DG, Ingvarsson PK. 2016. Natural selection and recombination rate variation shape nucleotide polymorphism across the genomes of three related *Populus* species. *Genetics* 202:1185−1200

[33] Ma T, Wang K, Hu Q, Xi Z, Wan D, et al. 2018. Ancient polymorphisms and divergence hitchhiking contribute to genomic islands of divergence within a poplar species complex. *Proceedings of the National Academy of Sciences of the United States of America* 115:E236−E243

[34] Liu S, Zhang L, Sang Y, Lai Q, Zhang X, et al. 2022. Demographic history and natural selection shape patterns of deleterious mutation load and barriers to introgression across *Populus* genome. *Molecular Biology and Evolution* 39:msac008

[35] Sang Y, Long Z, Dan X, Feng J, Shi T, et al. 2022. Genomic insights into local adaptation and future climate-induced vulnerability of a keystone forest tree in East Asia. *Nature Communications* 13:6541

[36] Xiang X, Zhou X, Zi H, Wei H, Cao D, et al. 2024. *Populus cathayana* genome and population resequencing provide insights into its evolution and adaptation. *Horticulture Research* 11:uhad255

[37] Sun J, Xu J, Qiu C, Zhai J, Zhang S, et al. 2024. The chromosome-scale genome and population genomics reveal the adaptative evolution of *Populus pruinosa* to desertification environment. *Horticulture Research* 11:uhae034

[38] Long Z, Sang Y, Feng J, Zhang X, Shi T, et al. 2025. Evolutionary genomics unravels the responses and adaptation to climate change in a key alpine forest tree species. *Molecular Biology and Evolution* 42:msaf116

[39] Wang Y, Zhao Y, Bollas A, Wang Y, Au KF. 2021. Nanopore sequencing technology, bioinformatics and applications. *Nature Biotechnology* 39:1348−1365

[40] Sigurpalsdottir BD, Stefansson OA, Holley G, Beyter D, Zink F, et al. 2024. A comparison of methods for detecting DNA methylation from long-read sequencing of human genomes. *Genome Biology* 25:69

[41] Lee H, Gurtowski J, Yoo S, Nattestad M, Marcus S, et al. 2016. Third-generation sequencing and the future of genomics. *bioRxiv* 1−20

[42] Zhang Z, Chen Y, Zhang J, Ma X, Li Y, et al. 2020. Improved genome assembly provides new insights into genome evolution in a desert poplar (*Populus euphratica*). *Molecular Ecology Resources* 20:781−794

[43] Zhang S, Wu Z, Ma D, Zhai J, Han X, et al. 2022. Chromosome-scale assemblies of the male and female *Populus euphratica* genomes reveal the molecular basis of sex determination and sexual dimorphism. *Communications Biology* 5:1186

[44] An X, Gao K, Chen Z, Li J, Yang X, et al. 2022. High quality haplotype - resolved genome assemblies of *Populus tomentosa* Carr., a stabilized interspecific hybrid species widespread in Asia. *Molecular Ecology Resources* 22:786−802

[45] Li P, Xiao L, Du Q, Quan M, Song Y, et al. 2023. Genomic insights into selection for heterozygous alleles and woody traits in *Populus tomentosa*. *Plant Biotechnology Journal* 21:2002−2018

[46] Gao K, Guo T, An X. 2025. Comprehensive analysis of the multi-rings mitochondrial genome of *Populus tomentosa*. *BMC Genomics* 26:23

[47] Melnikova NV, Pushkova EN, Dvorianinova EM, Beniaminov AD, Novakovskiy RO, et al. 2021. Genome assembly and sex-determining region of male and female *Populus* × *sibirica*. *Frontiers in Plant Science* 12:625416

[48] Chen S, Yu Y, Wang X, Wang S, Zhang T, et al. 2023. Chromosome-level genome assembly of a triploid poplar *Populus alba* '*Berolinensis*'. *Molecular Ecology Resources* 23:1092−1107

[49] Liu YJ, Wang XR, Zeng QY. 2019. *De novo* assembly of white poplar genome and genetic diversity of white poplar population in Irtysh River basin in China. *Science China Life Sciences* 62:609−618

[50] Sarfraz I, Zuccolo A, Celii M, Francini A, Wing RA, et al. 2025. High-quality PacBio genome assembly of *Populus alba* L. 'Villafranca'. *bioRxiv* Preprint: 661909

[51] Liu S, Wang Z, Shi T, Dan X, Zhang Y, et al. 2023. Chromosomal-level genome assembly of *Populus adenopoda*. *bioRxiv* Preprint: 548479

[52] Ma J, Wan D, Duan B, Bai X, Bai Q, et al. 2019. Genome sequence and genetic transformation of a widely distributed and cultivated *poplar*. *Plant Biotechnology Journal* 17:451−460

[53] Robinson KM, Schiffthaler B, Liu H, Rydman SM, Rendón-Anaya M, et al. 2024. An improved chromosome-scale genome assembly and population genetics resource for *Populus tremula*. *Physiologia Plantarum* 176:e14511

[54] Bae EK, Kang MJ, Lee SJ, Park EJ, Kim KT. 2023. Chromosome-level genome assembly of the Asian aspen *Populus davidiana* Dode. *Scientific Data* 10:431

[55] Li Y, Wang D, Wang W, Yang W, Gao J, et al. 2023. A chromosome-level *Populus qiongdaoensis* genome assembly provides insights into tropical adaptation and a cryptic turnover of sex determination. *Molecular Ecology* 32:1366−1380

[56] Wu H, Yao D, Chen Y, Yang W, Zhao W, et al. 2020. *De novo* genome assembly of *Populus simonii* further supports that *Populus simonii* and *Populus trichocarpa* belong to different sections. *G3: Genes, Genomes, Genetics* 10:455−466

[57] Chen S, Wang X, Wei Y, Guo Q, Ren Z, et al. 2026. The complete genome sequence of a poplar, *Populus davidiana*. *Horticulture Research* 2026:uhag208

[58] Wang Y, Zhao L, Wang D, Chen K, Luo T, et al. 2025. Four near-complete genome assemblies reveal the landscape and evolution of centromeres in *Salicaceae*. *Genome Biology* 26:111

[59] Shen T, Ning Y, Wang Y, Song Z, Xi M, et al. 2025. Haplotype-resolved telomere-to-telomere genome assembly of *Populus lasiocarpa* unveils retrotransposon-driven centromere evolution. *The Plant Journal* 123:e70504

[60] Bi C, Sun N, Hou Z, Dai X, Wu H, et al. 2025. A gap-free reference genome of *Populus deltoides* provides insights into karyotype evolution of *Salicaceae*. *BMC Biology* 23:201

[61] Liu W, Liu C, Chen S, Wang M, Wang X, et al. 2024. A nearly gapless, highly contiguous reference genome for a doubled haploid line of *Populus ussuriensis*, enabling advanced genomic studies. *Forestry Research* 4:e019

[62] Zhou X, Zhang L, Zhang M, Wei H, Bai Y, et al. 2025. Genomic selection for growth and wood properties in multi-generation hybrid populations of *Populus deltoides*. *Horticulture Research* 12:uhaf165

[63] Gao W, Wang S, Jiang T, Hu H, Gao R, et al. 2025. Chromosome-scale and haplotype-resolved genome assembly of *Populus trichocarpa*. *Horticulture Research* 12:uhaf012

[64] Shi TL, Jia KH, Bao YT, Nie S, Tian XC, et al. 2024. High-quality genome assembly enables prediction of allele-specific gene expression in hybrid poplar. *Plant Physiology* 195:652−670

https://doi.org/10.48130/fra-0026-0008

[65] Schreiber M, Jayakodi M, Stein N, Mascher M. 2024. Plant pangenomes for crop improvement, biodiversity and evolution. *Nature Reviews Genetics* 25:563−577

[66] Jayakodi M, Shim H, Mascher M. 2025. What are we learning from plant pangenomes? *Annual Review of Plant Biology* 76:663−686

[67] Pinosio S, Giacomello S, Faivre-Rampant P, Taylor G, Jorge V, et al. 2016. Characterization of the poplar pan-genome by genome-wide identification of structural variation. *Molecular Biology and Evolution* 33:2706−2719

[68] Li R, Wang Z, Wang JW, Li L. 2023. Combining single-cell RNA sequencing with spatial transcriptome analysis reveals dynamic molecular maps of cambium differentiation in the primary and secondary growth of trees. *Plant Communications* 4:100665

[69] Tung CC, Kuo SC, Yang CL, Yu JH, Huang CE, et al. 2023. Single-cell transcriptomics unveils xylem cell development and evolution. *Genome Biology* 24:3

[70] Dai X, Zhai R, Lin J, Wang Z, Meng D, et al. 2023. Cell-type-specific PtrWOX4a and PtrVCS2 form a regulatory nexus with a histone modification system for stem cambium development in *Populus trichocarpa*. *Nature Plants* 9:96−111

[71] Liu S, Fu X, Wang Y, Du X, Luo L, et al. 2025. The auxin–PLETHORA 5 module regulates wood fibre development in *Populus tomentosa*. *Nature Plants* 11:580−594

[72] Zhang Y, Chen S, Xu L, Chu S, Yan X, et al. 2024. Transcription factor *PagMYB31* positively regulates cambium activity and negatively regulates xylem development in poplar. *The Plant Cell* 36:1806−1828

[73] Zhao J, Chen Y, Dai X, Su L, Zhai R, et al. 2026. *PtrSHR1* coordinates vascular cambium proliferation and xylem lignin biosynthesis to regulate wood formation in *Populus trichocarpa*. *The Plant Cell* 38:koag091

[74] Li Q, Meng S, Zhou Y, Pi H, Yun Q, et al. 2025. The miR169z-NF-YA5-GPDHc1 module improves drought tolerance by increasing NAD^+ levels to inhibit ROS production in *Populus*. *New Phytologist* 248:1822−1840

[75] Liu X, Bao Y, Zhang MY, Zhang H, Niu MX, et al. 2025. SC35-mediated *bZIP49* splicing regulates K^+ channel AKT1 for salt stress adaptation in poplar. *Nature Communications* 16:7266

[76] Li Y, Xu X, Wang K, Hu Z, Deng L, et al. 2026. Epigenetic reprogramming drives the annual growth–dormancy cycle in *Populus*. *The Plant Cell* 38:koag018

[77] Li L, Huang R, Jin Z, Zhang D, Zhang M, et al. 2025. Natural variants of *AGL80.5* and *FPA. 3* contribute to bud break timing in poplar by controlling auxin biosynthesis. *Science Advances* 11:eadz6824

[78] Liao X, Su Y, Klintenäs M, Li Y, Sane S, et al. 2023. Age-dependent seasonal growth cessation in *Populus*. *Proceedings of the National Academy of Sciences of the United States of America* 120:e2311226120

[79] Wang J, Liao X, Wu Z, Sane S, Han S, et al. 2025. Genetic control of seasonal meristem arrest in trees. *Proceedings of the National Academy of Sciences of the United States of America* 122:e2505641122

[80] Müller NA, Kersten B, Leite Montalvão AP, Mähler N, Bernhardsson C, et al. 2020. A single gene underlies the dynamic evolution of poplar sex determination. *Nature Plants* 6:630−637

[81] Xue L, Wu H, Chen Y, Li X, Hou J, et al. 2020. Evidences for a role of two Y-specific genes in sex determination in *Populus deltoides*. *Nature Communications* 11:5893

[82] Lu J, Yang Y, Yin T. 2025. Poplar sex-determining gene directly affects tree growth through regulating cytokinin signalling pathway. *Plant Biotechnology Journal* 23:5680−5693

[83] Lu J, Yang Y, Yin T. 2025. Expression of poplar sex-determining gene affects plant drought tolerance and the underlying molecular mechanism. *Horticulture Research* 12:uhaf066

[84] Alves FC, Balmant KM, Resende MFR Jr, Kirst M, de Los Campos G. 2020. Accelerating forest tree breeding by integrating genomic selection and greenhouse phenotyping. *The Plant Genome* 13:e20048

[85] Porth I, Klapšte J, Skyba O, Hannemann J, McKown AD, et al. 2013. Genome-wide association mapping for wood characteristics in *Populus* identifies an array of candidate single nucleotide polymorphisms. *New Phytologist* 200:710−726

[86] Chhetri HB, Furches A, Macaya-Sanz D, Walker AR, Kainer D, et al. 2020. Genome-wide association study of wood anatomical and morphological traits in *Populus trichocarpa*. *Frontiers in Plant Science* 11:545748

[87] Macaya-Sanz D, Heuertz M, Lindtke D, Vendramin GG, Lexer C, et al. 2016. Causes and consequences of large clonal assemblies in a poplar hybrid zone. *Molecular Ecology* 25:5330−5344

[88] Hord AM, Fischer DG, Schweitzer JA, LeRoy CJ, Whitham TG, et al. 2025. Hybrid introgression as a mechanism of rapid evolution and resilience to climate change in a riparian tree species. *Communications Biology* 8:1173

[89] Ma T, Wang J, Zhou G, Yue Z, Hu Q, et al. 2013. Genomic insights into salt adaptation in a desert poplar. *Nature Communications* 4:2797

[90] Holliday JA, Aitken SN, Cooke JEK, Fady B, González-Martínez SC, et al. 2017. Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding. *Molecular Ecology* 26:706−717

[91] Cortés AJ, Restrepo-Montoya M, Bedoya-Canas LE. 2020. Modern strategies to assess and breed forest tree adaptation to changing climate. *Frontiers in Plant Science* 11:583323

[92] Chen Y, Tong S, Jiang Y, Ai F, Feng Y, et al. 2021. Transcriptional landscape of highly lignified poplar stems at single-cell resolution. *Genome Biology* 22:319

[93] Schmidt HW, Conde D, Pereira WJ, Triozzi PM, Balmant KM, et al. 2025. Deep tissue profiling of *Populus* stem at single nucleus level reveals uncharacterized cell types and cell-specific gene regulatory networks. *Genome Biology* 26:258

[94] Wei M, Hsieh JWA, Dang JF, Tong B, Li H, et al. 2026. Integrating scRNA-seq and snRNA-seq with spatial transcriptomics to unlock the xylem puzzle. *Genome Biology* 27:109

[95] Li Y, Kong L, Guo X, Chen Y, Shao W, et al. 2026. A single-nucleus and spatial transcriptomic atlas of poplar leaves reveals the regulation of leaf polarity and cuticle deposition. *Journal of Genetics and Genomics* 015

[96] Li H, Dai X, Huang X, Xu M, Wang Q, et al. 2021. Single-cell RNA sequencing reveals a high-resolution cell atlas of xylem in *Populus*. *Journal of Integrative Plant Biology* 63:1906−1921

[97] Xie J, Li M, Zeng J, Li X, Zhang D. 2022. Single-cell RNA sequencing profiles of stem-differentiating xylem in poplar. *Plant Biotechnology Journal* 20:417−419

[98] Shi T, Long T, Wu J, Zeng X, Zhu Y, et al. 2026. Dynamic reorganization of three-dimensional genome architecture during *Populus* diversification. *Nature Ecology & Evolution* 10:1168−1183

[99] Gaj T, Gersbach CA, Barbas CF. 2013. ZFN, TALEN, and CRISPR/Cas-based methods for genome engineering. *Trends in Biotechnology* 31:397−405

[100] Bruegmann T, Fendel A, Zahn V, Fladung M. 2024. Genome editing in forest trees. In *A Roadmap for Plant Genome Editing*, eds. Ricroch A, Eriksson D, Miladinović D, Sweet J, Van Laere K, et al. Cham: Springer Nature Switzerland. pp. 347−372 doi: 10.1007/978-3-031-46150-7_20

[101] Kaur N, Pati PK. 2024. Retron library recombineering: next powerful tool for genome editing after CRISPR/cas. *ACS Synthetic Biology* 13:1019−1025

[102] Arimura SI, Nakazato I. 2024. Genome editing of plant mitochondrial and chloroplast genomes. *Plant and Cell Physiology* 65:477−483

[103] Zong Y, Liu Y, Xue C, Li B, Li X, et al. 2022. An engineered prime editor with enhanced editing efficiency in plants. *Nature Biotechnology* 40:1394−1402

[104] Pak S, Li C. 2022. Progress and challenges in applying CRISPR/Cas techniques to the genome editing of trees. *Forestry Research* 2:6

[105] Ma C, Duan C, Jiang Y, Nagle M, Peremyslova E, et al. 2022. Factors affecting *in vitro* regeneration in the model tree *Populus trichocarpa*: II. Heritability estimates, correlations among explant types, and genetic interactions with treatments among wild genotypes. *In Vitro Cellular & Developmental Biology - Plant* 58:853−864

[106] Hoengenaert L, Anders C, Van Doorsselaere J, Vanholme R, Boerjan W. 2025. Transgene-free genome editing in poplar. *New Phytologist* 247:224−232

[107] Zhang J, Tang X, Sun M, Liu C, Yu H. 2026. A genotype-independent transformation and gene-editing system for *Populus*. *Plant Biotechnology Journal* 24:520−522
[108] Farooq MA, Gao S, Hassan MA, Huang Z, Rasheed A, et al. 2024. Artificial intelligence in plant breeding. *Trends in Genetics* 40:891−908
[109] Yan J, Wang X. 2023. Machine learning bridges omics sciences and plant breeding. *Trends in Plant Science* 28:199−210
[110] Wang H, Cimen E, Singh N, Buckler E. 2020. Deep learning for plant genomics and crop improvement. *Current Opinion in Plant Biology* 54:34−41
[111] Wang H, Chen M, Wei X, Xia R, Pei D, et al. 2024. Computational tools for plant genomics and breeding. *Science China Life Sciences* 67:1579−1590
[112] Fan X, Zhang H, Zhou L, Bian L, Jin X, et al. 2024. Evaluating drought stress response of poplar seedlings using a proximal sensing platform via multi-parameter phenotyping and two-stage machine learning. *Computers and Electronics in Agriculture* 225:109261
[113] Gilbertson L, Puchta H, Slotkin RK. 2025. The future of genome editing in plants. *Nature Plants* 11:680−685
[114] Chen YH, Sharma S, Bewg WP, Xue LJ, Gizelbach CR, et al. 2023. Multiplex editing of the *Nucleoredoxin1* tandem array in poplar: from small indels to translocations and complex inversions. *The CRISPR Journal* 6:339−349
[115] Gong Z, Yang S. 2026. *NRT1*. 1B: a dual receptor integrating ABA and nitrate signals for plant adaptation to compound stresses. *Science China Life Sciences* 69:705−706
[116] Feng J, Dan X, Cui Y, Gong Y, Peng M, et al. 2024. Integrating evolutionary genomics of forest trees to inform future tree breeding amid rapid climate change. *Plant Communications* 5:101044
[117] Xu Y, Zhang X, Li H, Zheng H, Zhang J, et al. 2022. Smart breeding driven by big data, artificial intelligence, and integrated genomic-enviromic prediction. *Molecular Plant* 15:1664−1695
[118] Syeda A. 2025. Harnessing multi-omics and genome-editing technologies for climate-resilient agriculture: bridging AI-driven insights with sustainable crop improvement. *Plant Molecular Biology* 115:120