Genomics studies for trait improvement in four important tree species: Current status and future prospects

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Abstract

Trees hold the lifeline of the earth's biodiversity and serve as a commercial entity delivering broad applications to humankind. In addition to being used as wood and timber, trees are a source of secondary metabolites, medicinal compounds, and other derivatives with high commercial value. Thus, the scope for improvement of these traits and quality traits (insect/pest resistance, wood quality, etc.) has always been demanding; however, limited progress has been made compared to other crop species. Trait improvement has always been challenging in trees owing to several practical difficulties, but genomics has enabled the precise identification of genetic determinants of these traits and provided tools and approaches to tweak them for enhancing the traits of interest. Next-generation sequencing (NGS) has expedited genomics and transcriptomics research by facilitating the sequencing of genomes and transcriptomes, identifying genes, profiling the regulation of their expression, and constructing gene regulatory networks. Also, NGS has enabled the development of large-scale genome-wide molecular markers for high-throughput genotyping applications, which are useful in breeding for desirable traits. As it allows improved understanding of the gene function and its network at different developmental stages of trees with reference to an environmental stimulus can further help the breeder to enhance the knowledge on spanning genotype and phenotype. Thus, the potential of genomics in expediting trait improvement has been well realized; however, its application in tree species, particularly in commercially important ones including *Tectona grandis*, *Azadirachta indica*, *Casuarina* spp., and *Salix* spp, requires further research. Given this, the present review enumerates the progress made in genomics research on these four species and provides the roadmap for their trait improvement toward enhancing productivity and ecosystem services.

Keywords: *Trees, genomics, transcriptomics, next-generation sequencing, trait improvement, genome sequencing*

Introduction

Forest ecosystems are considered an integral part of human life, constituting about 82 % of the continental biomass and harboring more than 50 % of the terrestrial biodiversity (Mooney and Saugier, 2001). While natural forests are not sufficient to meet our present demands, such as wood and bioenergy, without compromising the environmental conservation efforts, Trees Outside Forests (TOF) serve as an important resource to meet these needs (FAO 2020). Considering the vast diversity among trees in terms of morpho-physiological, wood anatomy, and secondary metabolites, it is well apprehended that each tree plays a vital role in sustainable agriculture (Groover and Cronk, 2017). Hence, encouraging farmers to take up plantations on their lands will benefit them on multiple fronts (Foresta et al. 2013), provided the farmers are given the right and improved variety for farming. Improving the beneficial traits in tree breeding suffers several shortfalls, including long generation time, high heterogeneity, difficulties in parental selection of preferred trees, and uncertainty in results which demands continuous experimentation. As mid-way

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replacement and/or reorienting or redesigning a conventional tree breeding programme is impossible, the demand for accuracy and precision in trait improvement is high in tree breeding. Recently, genomics has enabled the precise identification of genetic determinants underlying key traits in crop plants and facilitated their manipulation to develop improved varieties through genomics-assisted and transgene-based approaches. However, the application of genomics in studying complex traits in tree species has not been much realized (Alves et al. 2020). In *Eucalyptus grandis*, Lebedev et al. (2020) and Mphahlele et al. (2020) have reported that the breeding cycle can be hastened without compromising the breeding value for improving cellulose percentage and other wood traits. From the literature, it is evident that tree genomics is now gaining momentum in genetic improvement programs, developing diagnostic tools for restoration, and managing genetic resources.

Tree genomics research progress in the early 2000 had slow growth due to a lack of reference sequences to annotate tree genomes, insufficient genomic resources, and particularly substantial financial investment (Neale and Kremer, 2011). However, in the last two decades, the development of low-cost *omics* technologies changed the research dimension in this field (Gamal El-Dien et al., 2015). Particularly, next-generation sequencing technologies aid in dissecting the complex traits more precisely, such as biotic and abiotic stress tolerance, and growth parameters (Metzker, 2010; Badenes et al. 2016). Genomic tools like Genotyping by Sequencing (GBS) (Elshire et al. 2011; Poland & Rife 2012), high-throughput genotyping (Dillon et al. 2012), deep sequencing of transcriptomes for various functional traits (Galeano et al., 2015; Krishnan et al., 2016; Yasodha et al., 2018). The advancement in computational biology and bioinformatics tools, along with high throughput sequencing platforms, allows researchers to enable long-read based sequencing, assemblage, and annotation of genomes of many non-model woody species. Whole-genome sequencing evolved rapidly and progressed our understanding of trees, their structure, evolution and developmental functions, and particularly, their adaptation features (Tuskon et al., 2018; Kress et al., 2022). However, scope exists to deploy the genomics tools and approaches in identifying and characterizing the QTLs (Quantitative Trait Loci), genes and alleles underlying key traits and utilizing them in the best possible way to improve the traits-of-interest in tree species. In this context, the present review enumerates the status of tree breeding post-genomics era and compares the progress made in the genomics of four important tree species viz. *Tectona grandis, Azadirachta indica, Casuarina* spp., and *Salix* spp. Further, the review provides a roadmap for optimizing the genomics pipeline to effectively deploy the genomics tool for expediting the research in important tree species to enhance their commercial value.

Next-generation sequencing of tree genomes and transcriptomes

Advances in sequencing and sequence analysis platforms enabled decoding important tree species' genomes. However, the larger genome size and polyploidy have been the prime drawbacks that have invited collaborative efforts to sequence the genomes (Neale and Kremer, 2011). The genome of *Populus trichocarpa* was published in 2006, and being the first sequencing effort in trees, it opened the avenues for sequencing other tree genomes (Figure 1). With decreasing price of Next Generation Sequencing (NGS) and third-generation sequencing approaches, several genomes are sequenced and made available in the public domain (Table 1). For instance, the Treegenes database (https://treegenesdb.org) has the genome, transcriptome, marker, and phenotypic data of 2141 species representing 228 genera and 16 orders. The database has the complete genome sequence information of 38 important temperate and tropical trees like *Populus deltoides*, *Juglans regia*, *Eucalyptus grandis*, *Jatropha curcas*, *Hevea brasiliensis*, *Olea europae*, *Picea abies*, *Carica papaya, Gnetum montanum,* etc. PLAZA (https://bioinformatics.psb.ugent.be/plaza/) is another important source for comparative genomics studies, comprising centralized genome data for all the dicotyledonous and monocotyledonous plants generated through various sequencing initiatives, including horticultural and forestry trees. In addition, there are other tree genomic databases like TropGeneDB, TropiTree, PGP Repository, Plantgenie, etc. (Wegrzyn et al., 2020), which are striving to enhance the data generated by the researchers to store, submit and analyze forest tree data improving forest health and productivity.

The availability of genome sequencing data facilitates identifying genes, alleles, and QTLs underlying key traits through functional genomics and/or GWAS-based approaches. Candidate genes and gene families can be characterized using *in silico* tools such as HMM profiling, domain architecture analysis, expression profiling in publicly available RNA-seq data, homology modeling, etc. These analyses allow pinpointing the candidate genes, which can further be functionally characterized to elucidate their role in a particular trait. An alternate approach involves genotyping-by-sequencing, wherein the population has to be phenotyped for the given trait, and their genomes have to be sequenced to identify SNPs. The phenotyping and the genotyping data are then statistically associated with identifying the high-confidence SNPs linked to traits, and the underlying QTLs, genes and alleles can further be identified for functional characterization. Presently, genomic selection (GS) has also been seen as a promising tool in trait improvement; these approaches have been exploited in tree species like *Eucalyptus*, *Populus*, *Picea abies*, *Pinus*, *Hevea brasiliensis*, and *Castanea dentata* (Grattapaglia et al., 2018; Grattapaglia 2017; Grattapaglia 2014; Chhetri et al., 2020; Stanton et al., 2010; Pégard et al., 2020; Lebedev et al., 2020; Souza et al., 2019; Westbrook et al., 2020). In *Macadamia* sp., nut yield has been improved using GWAS and GS approaches without compromising breeding value (O'Connor, Hayes & Topp 2018). In *Coffea arabica*, genome-wide SNP analysis offered an efficient parental selection to obtain improved varieties (Sousa et al., 2017). Several traits such as wood properties, biomass, flowering, fruiting traits, and disease resistance are governed by multiple genes or QTLs exhibiting the quantitative distribution of phenotypes that can be identified using genomics tools

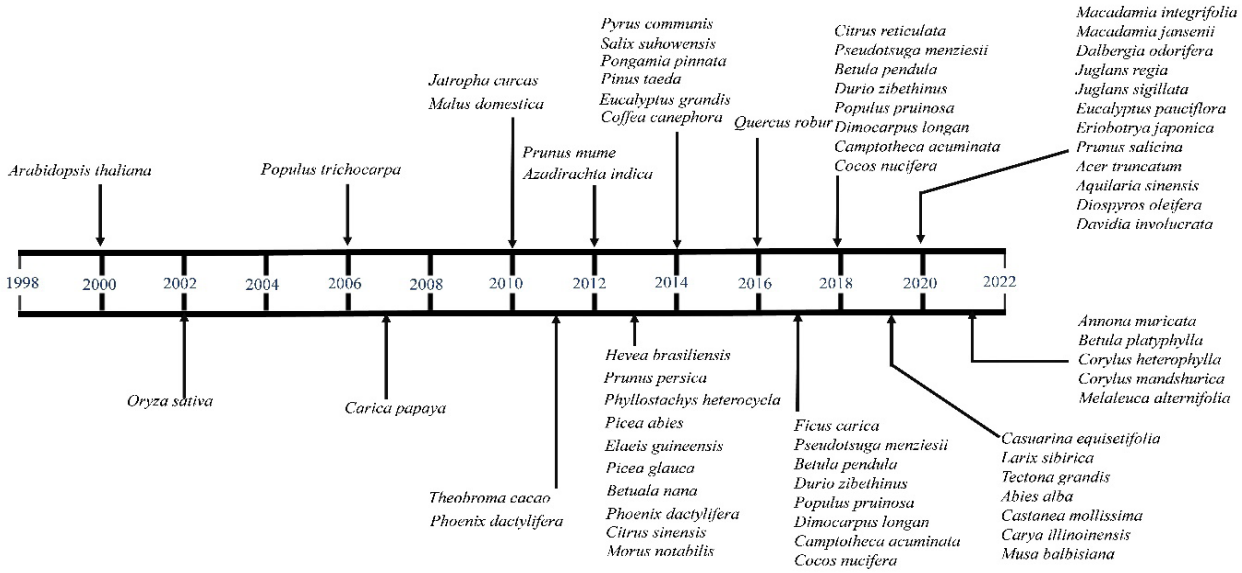


Figure 1
Timescale of plant genomics research with special focus to major tree genomics research from 2006 onwards

(Savolainen, Pyhäjärvi & Knürr 2007; Khan & Korban 2012). In *Eucalyptus nitens*, 36 QTLs were identified for pulp yield (Thumma et al. 2010). QTL association has been dissected in Populus species for growth parameters (Rae et al., 2008; Rae et al., 2007), wood properties (Zhang & Yin 2016), biotic and abiotic stress (Zhang, Yin & Xia 2008), viz. pathogenic fungi (Tagu et al., 2005), and osmotic potential (Tschaplinski et al. 2006) respectively (Table 2).

Similarly, RNA-seq enabled the decoding of transcriptomes of tree species for gene expression studies. Also, RNA-seq served as an alternate tool to identify the genes in species for which genome sequence information is not available. *De novo* assembly of transcriptome sequences did not require any reference genome. Therefore, it facilitated identifying novel genes expressed at a particular stage or time-point (of sampling) (Krishnan et al., 2012; Yasodha et al. 2018). Comparing the transcriptomes of different cultivars within the same species also enabled the identification of SNPs, which can further be used as potential markers for trait association. Also, scanning the RNA-seq reads for microsatellite motifs results in identifying SSR markers helpful in genotyping purposes. These markers are also valuable for studying genetic diversity and relationships, population structure, linkage disequilibrium, etc. Further, transcriptome analysis helps in sex identification among dioecious trees by differential sex-specific gene expressions (Ha et al. 2019). Thus, transcriptome also serves as a potential tool for the genetic improvement of tree species. Transcriptome and metabolite analysis in neem can increase the bioactive compound synthesis (triterpenoids) used in biopesticide production (Bhambhani et al., 2017). Translating this at ground level can directly affect the pulp recovery in paper industries (Mphahlele et al., 2020). Similarly, transcriptomic approaches in floral biology help reduce the profuse flowering nature of certain species (e.g., *Leucaena*), which results in abundant seed distribution as a nuisance on many cultivable farmlands. Under these circumstances, one can identify microRNAs or small RNA mediated regulatory modules that modulate the expression of flowering regulated genes at the post-transcriptional level (Waheed and Zeng, 2020), which would, in turn, aid in controlling the copious nature of the flowering trait. These studies accentuate the importance of NGS in dissecting the genetic determinants of complex traits by sequencing the genomes and transcriptomes of important tree species. The recent advancements in sequencing platforms resulted in low-cost, high-throughput approaches that can effectually be used in tree genomics.

Development of genomic resources for the improvement of four important tree species

Teak

Tectona grandis L. (Lamiaceae) is one of the major timber trees cultivated in the Indian sub-continent and other countries due to its economic significance. The improvement of teak depends on conserving the natural population with knowledge of the genetic structure and genomic patterns (Yasodha et al., 2018). The *Tectona grandis* draft genome was recently assembled using Illumina HiSeq 2000 platform and Oxford Nanopore Technologies (ONT) with reference to SSR discovery and phylogenetic relationship (Yasodha et al., 2018). The draft genome consisted of 317Mb in 2,993 scaffolds with contig N50 of 356 kb and 36,172 protein-coding genes (Table 1). Further, identification of the candidate genes for floral formation, metabolite production, and wood properties (lignification) in teak was also widely assessed through transcriptomic approaches (Diningrat et al., 2015; Galeano et al., 2015). Subsequently, a highly contiguous, chromosomal-scale genome assembly was

Table 1
Genome sequencing efforts of the selected important tree species

Tree	NGS platform used for whole-genome sequencing	Genome size (Mb)	Contigs	Scaffolds	Genes	ESTs/ SRs	SNPs	Reference
Populus trichocarpa	Short gun sanger sequencing	434	1446	1446	44976	19989	28M	(Tuskan et al. 2006)
Tectona grandis	Illumina Hiseq2000 and Oxford nanopore MinION	317	3500	3004	36172	182712 (SSRs)	-	(Yasodha et al. 2018)
Azadirachta indica	Illumina TruSeq and IonTorrent Personal Genome Machine	364	9714	9714	30236	552 for terpenoid biosynthesis	-	(Krishnan et al. 2012)
Eucalyptus grandis	Short gun sanger sequencing	691	4952	4943	36376	19996	2.39M for terpene synthesis	(Myburg et al. 2014)
Casuarina equisetifolia	PacBio RSII Single Molecule Real Time (SMRT) sequencer and Illumina HiSeq 2000	300	6611 (>100bp)	2936 (>100bp)	31818			(Ye et al. 2019) conifer-like angiosperm with resistance to typhoon and stress tolerance, is mainly cultivated in the coastal areas of Australasia. *C. equisetifolia*, making it a valuable model to study secondary growth associated genes and stress-tolerance traits. However, the genome sequence is unavailable and therefore wood-associated growth rate and stress resistance at the molecular level is largely unexplored. We therefore constructed a high-quality draft genome sequence of *C. equisetifolia* by a combination of Illumina second-generation sequencing reads and Pacific Biosciences single-molecule real-time (SMRT)
Salix sp.	Roche 454 and Illumina Hiseq 2000	450-485	-	-	26599	-	-	(Dai et al. 2014)

Table 2
Functional genomics efforts for important traits in major tree species

Tree	Growth paramaters	Wood parameters	Biotic stress	Abiotic stress	Secondary metabolites
Populus	Root, stem and leaves during annual growth rate and cycle (Quesada et al. 2008; Grönlund, Bhalerao & Karlsson 2009; Park, Keathley & Han 2008), height and DBH (Chen et al. 2021)	Xylem and cambial meristem strength (Lafarguette et al. 2004; Andersson-Gunneras et al. 2006; Goué et al. 2008; Wang et al. 2009), wood quality traits (Chen et al. 2021) and cell wall thickening (Zhao et al. 2014)	Tolerance/resistance to plant pathogens (Ralph et al. 2006; Miranda et al. 2007; Frost et al. 2008; Sjödin et al. 2009; Boyle et al. 2010); Muchero et al. 2018)	Response to water deficit (Bogeat-Triboulot et al. 2007; Brosché et al. 2005; Kreuzwieser et al. 2009); adaptation for abiotic stress (Wang et al. 2018), adaptive morphological and physiological traits (Chhetri et al. 2019; Chen et al. 2021)	Tannins and salicylate-based glycosides (Constabel & L. Lindroth 2010)
Eucalyptus	Wood growth and wood Properties (Cappa et al. 2013; Resende et al. 2012; Dasgupta et al. 2021)	Xylem, wood-forming Tissues (Barros, van Staden & Lezar 2009; Qui et al. 2008; Ranik, Creux & Myburg 2006; Solomon, Berger & Myburg 2010)	Resistance Genes for pest and diseases (Barbosa-da-Silva et al. 2005; Duplessis et al. 2005)	Cold tolerance (Keller et al. 2009)	Terpenes biosynthesis (Zhao et al. 2019)
Tectona grandis	Floral formation and metabolite production (Galeano et al. 2015; Diningrat et al. 2015)	Lignification (Galeano et al. 2015; Diningrat et al. 2015)	Pest and disease resistance (Norwati et al. 2011; El-Fattah Adnan Dababat & Alexander Sikora 2007)	Drought stress (Galeano et al. 2019; Tripathi et al. 2017)	Terpene biosynthesis (Zhao et al. 2019)
Azadirachta indica					Terpenoid biosynthesis (Krishnan et al. 2012) Azadirachtin biosynthesis (Wang & Huo 2020)
Casuarina spp.	Secondary growth (Ye et al. 2019)	Cellulose, hemicellulose, and lignin biosynthesis; Chlorophyll synthesis; cell wall biosynthesis; secondary growth (Ye et al. 2019)	Disease resistance (Modhumita et al. 2017)	Cold stress tolerance (Li et al. 2017) Salt stress tolerance (Fan et al. 2017; Graca et al. 2019)	Secondary metabolite biosynthesis (Li et al. 2017)
Salix spp.	Genetic architecture of growth traits (Zhang et al. 2017); Genome wide association of growth, phenology and plasticity traits (Hallingbäck et al. 2019)			Functional analysis of growth QTLs under salt stress (Zhang et al. 2017)	

developed using Pacific Biosciences (PacBio) long reads coupled with high-throughput chromatin conformation capture (Zhao et al., 2019). The annotation provides 31,168 genes encoding 46,826 gene models and identified 14 clusters of tandem-duplicated terpene synthases (TPSs) genes for plant defense and pollinator attraction. Likewise, teak functional genomics for drought tolerance provides information on the molecular mechanisms by *TgTPS1* and *TgDREB1* are the prominent candidate genes identified for severe water stress tolerance (Galeano et al., 2019). The genomic research progress in teak will expedite the identification of novel genes to various trait-specific functions, including i) clonal selection of superior growth phenotypes, ii) genetic diversity assessment of natural populations, iii) genetic resource conservation, iv) molecular basis of terpene biosynthesis, and v) evaluating adaptive traits responses to biotic and abiotic factors in teak.

Neem

Azadirachta indica A. Juss (Meliaceae) is a multipurpose tree species (MPT) with more than 150 bioactive compounds (Kumar and Pathak, 2018; Sarah et al., 2019). The value addition possibility has necessitated understanding the biology and molecular mechanism behind its bioactive compound synthesis (terpenoid). The draft genome of *A. indica* using short paired-end reads from Illumina Genome Analyzer IIx (GAIIx) with SOAP *de novo* (Table 1) estimated genome size (v1.0) of 364 Mb (Krishnan et al., 2012). Neem is the first tree in Meliaceae to be sequenced and the 38th plant species which was fully sequenced (Michael and Jackson, 2013). This annotation has 385 scaffolds (>N50) mapped to *Citrus sinensis* and 435 scaffolds (>N50) of *Citrus clementina* out of a total of 534 scaffolds (N50) (Krishnan et al., 2012). Further, the updated genome assembly (v2.0) comprised a 3 and 3.5 fold increase in N50 and N75, respectively; with 2.6 fold decrease in the total number of scaffolds over the previous assembly (Krishnan et al., 2016). Besides, the phylogenetic analysis suggested that *A. indica* was closely associated with *Citrus* species (Krishnan et al., 2012). However, to limonids bioactive compounds, it is reported to share an evolutionary association with *Owenia* and *Melia* species (Tan and Luo, 2011). Recently, a hybrid assembly was carried out by combining Illumina and Roche 454 reads using a clustering approach of short reads and long reads, which provided an improved genome assembly having >90 % completeness based on the eukaryotic core gene-mapping approach (CEGMA) as reported by Kuravadi and Gowda (2019). The organelle genome assembly reported that 60 scaffolds with a size of 112,958 bp and 266,430 bp of the genome in 348 scaffolds of chloroplast and mitochondria, respectively (Kuravadi et al., 2015). Based on the transcriptome study in neem, 30,236 unigenes are identified along with 112 and 552 transcripts involved in terpenoid biosynthesis and signal transduction, respectively (Wang et al., 2016). In neem, 22 differentially expressed genes (DEGs) were identified as candidates involved in azadirachtin A pathway and it could be useful in improved understanding of neem genome (Wang and Huo, 2020). Also, (Du et al., 2021) suggested that chromosome 13 may play an important role in the specific terpene biosynthesis in neem. Additionally, the genes central to steroid and triterpenoid family (TPS21, lytB, ispH, ispE, GGPS, +neomenthol dehydrogenase, FDPS, FDFT1 and SQLE) was abundant in neem than Arabidopsis, rice, citrus, and grapes (Krishnan et al., 2012). Further, the development of more genomic resources in neem viz. transcripts, SSRs, SNPs, and Indels will aid in genetic improvement programmes (Wang et al., 2020; Du et al., 2021)..

Casuarina sp.

Casuarina (Casuarinaceae) is native to Australia, Southeast Asia, and the Pacific Islands (Wheeler et al., 2011). It is mainly cultivated in coastal areas for windbreak and shelterbelts because of its ability to withstand cyclones, salinity, and water stress (Hu et al., 2016). These species have been widely studied for ecosystem services, secondary metabolites (tannins), soil nitrogen fixation, and abiotic stress resistance (Ogunwande et al., 2011). Unlocking its system biology and functional trait associations are paramount for better understanding its functional traits genetic architecture and further improvement. The draft genome of *Casuarina equisetifolia* was released using Pacific Biosciences Single-Molecule Real-Time (SMRT) sequencing, and Illumina sequencing yielded about 300 Mb with 1.06 Mb of the scaffold (N50). One-third of its genome has repetitive elements (Ye et al., 2019). The genome annotation yielded 29,827 protein-coding genes and 1983 non-coding genes with 33 % transposable elements (TE). Also, the construct of the genome-wide map of DNA modification using SMRT 17 % of 6mA modification genes; 15 % of 4mC modification genes, and alternative splicing events identified. Simultaneously, the first chloroplast genome of *Casuarina glauca* was estimated to be about 155,669 bp length with a sizeable quadripartite structure, also the phylogenetic relationship of *Casuarina glauca* is closely related to the Betulaceae (Qian and Wang, 2019). It could offers improved understanding of *C. glauca* and for future studies on the evolution of the Casuarinaceae. The reference transcriptome dataset of *Casuarina equisetifolia* using *de novo* assembly to characterize the transcriptomic responses to cold stress, in which a total of unigenes 4639 was identified as early cold response genes, including 2331 cold up-regulated and 2308 down-regulated genes (Hai et al., 2017). This is the first large-scale transcriptome annotation of *Casurania equisetifolia* to elucidate the cold response mechanisms. Other functional genomics achievements include identifying cellulose, hemicellulose, and lignin-related genes related to secondary growth, chlorophyll synthesis, cell wall biosynthesis, and secondary cell wall synthesis in different *Casuarina* species reported by Ye et al. (2019). The molecular defence in *Casuarina equisetifolia* by the novel transcript CeHMA, which was up-regulated under biotic and abiotic stress conditions, broadened the knowledge of the response of woody perennials during pathogen cell wall elicitation (Modhumita and Karpaga, 2017). These genomics studies can enhance genomic resources to elucidate the functional understanding of Casuarina trees further and will be useful in genetic improvement. The expression of WRKY29-like and expansin-like B1 was used to

validate the suitability of the reference genes identified for *Casuarina equisetifolia*. The findings could allow researchers to investigate the mechanism of salt response and gene expression in *Casuarina equisetifolia* (Fan et al., 2017). Also, it is reported that *Casuarina glauca*, salt tolerance is linked to a modest influence on the photosynthetic machinery (one of the earliest and most significant stress targets) as well as an increase in antioxidant status, which further helps to maintain cellular homeostasis (Graça et al., 2019).

Salix sp.

Willows (Salicaceae) represent one of the most taxonomically complex genera of flowering plants, mainly used for bioenergy, biofuels, and bio-products (Hanley and Karp, 2014). The whole-genome project in Salix, including the development of reference genome assemblies, was initiated at Joint Genome Institute. The female *Salix purpurea* genome was assembled in 2014 using Illumia pair-end and Mate pair library sequencing (https://phytozome.jgi.doe.gov). Further, another Salix species *S. suchowensis* genome was sequenced using a hybrid technology that combined 454 technologies and Illumia Hiseq 2000 reads (Dai et al., 2014). Also, the genomic divergence was detected among shrub willow *S. suchowensis* and *Populus trichocarpa* after common genome duplication using a combined approach of Roche 454 and Illumina Hiseq 2000 technologies. It was reported that the distinct features between these species as follows: i) *S. suchowensis* (450 Mb) has a slightly smaller genome than *P. trichocarpa* (485 Mb), ii) The nucleotide substitution rate was significantly higher in *S. suchowensis* than *P. trichocarpa*, iii) Populus species retained more gene copies than Salix following gene duplication further suggested that willow lost more genes than poplar after common genome duplication (Dai et al., 2014). Further, a basket willow draft genome by long and short-read single-molecule sequencing approaches provides information on genomic consequences of recombination suppression as well as sex chromosome formation and its regulation in sex determination (Almeida et al., 2019). Also, the genome-wide association of *S. viminalis* provided helpful information about the marker-trait association with respect to growth, phenology, and plasticity could be highly useful in future Salix breeding programs (Hallingbäck et al., 2019). In addition, identifying growth QTLs expressed under salt stress provides crucial information for marker-assisted breeding of salt tolerant Salix variants and establishes the foundation for using *S. matsudana* in coastal afforestation (Zhang et al. 2017).

Future Perspectives

Genetic and genomic resources are imperative for any trait improvement programme, where genetic resources form the base and genomic resources facilitate the effectual use of genetic resources for improving the traits of interest (Figure 2). Thus, germplasms of tree species need to be conserved and documented for their use in genomics studies. Germplasm repositories for tree species should be updated for the said purpose, and accessibility should be provided to the global research community. When an excellent germplasm resource is available, researchers can deploy high-throughput phenomics to analyze the traits of interest. From a genomics perspective, sequencing genomes would be costly, and it requires choosing the right platforms depending on the genome size and ploidy. Hybrid sequencing using two or more platforms has gained importance for generating high-quality sequence reads. Chromosome level resolution for the genomes can be achieved using long-read sequencing pipelines such as PacBioand and Nanopore. Such sequence data provides information on the coding and non-coding regions of the genome. In the coding part, the information about genes and their upstream regulatory elements serves as a valuable resource for functional genomics research. Characterizing candidate genes will provide insights into their precise roles in regulating particular traits of interest. Low-throughput sequencing of germplasm collection using Illumina or similar technology helps develop genome-wide, large-scale molecular markers such as SNPs and InDels. These markers are helpful for high-throughput genotyping applications, such as genetic diversity and relationship analysis, population structure prediction, etc. Also, SNPs were shown beneficial in genome-wide association studies to identify the marker-trait associations (MTAs), which can then be used to develop allele-specific markers for marker-assisted selection. Also, the genes underlying the MTAs shall be functionally characterized using genomics tools. Structural genomics plays a vital role in studying the non-coding elements of the genome, including transposable elements, repeat elements, etc. Microsatellite markers spanning the coding and non-coding regions of the genome have always been a choice for geneticists to study closely related species' diversity and relationships. Recently, pan-genomics has gained attention among the crop species, wherein the whole stock of different individuals present in the same species are sequenced. Such approaches will accelerate genomics-assisted breeding for improved varieties that must be tested in tree species.

In addition to genome sequencing, transcriptome sequencing provides additional information about the expressed genes and can be used to develop gene-based SSRs (genic SSR) for genotyping purposes. Small RNA sequencing has recently gained much attention as it provides insights into the microRNAs (miRNAs) and other RNAs that have a regulatory role. Long non-coding RNAs (lncRNAs) have been shown to regulate the expression of specific traits. However, such studies are scarce in tree species, and scope exists to deploy RNA-seq approaches to delineate the genes and other genomic components underlying important traits. When such precise information is available, next-generation genome editing tools such as CRISPR/Cas system are possible in tree improvement programmes. CRISPR could be a versatile tool for base editing, probing mutation patterns, exogenous gene introduction, gene regulation studies, cell imaging, etc. Thus, the 5Gs (Genome, germplasm, gene function, genomic breeding and genome editing) of crop improvement successfully demonstrated in crop species (Varshney et al. 2020) should be applied to tree genomics also, where Genome sequencing facilitates gene/trait discovery, Germplasm enables its effective characterization for mining expedient genetic information, Genes provide functional

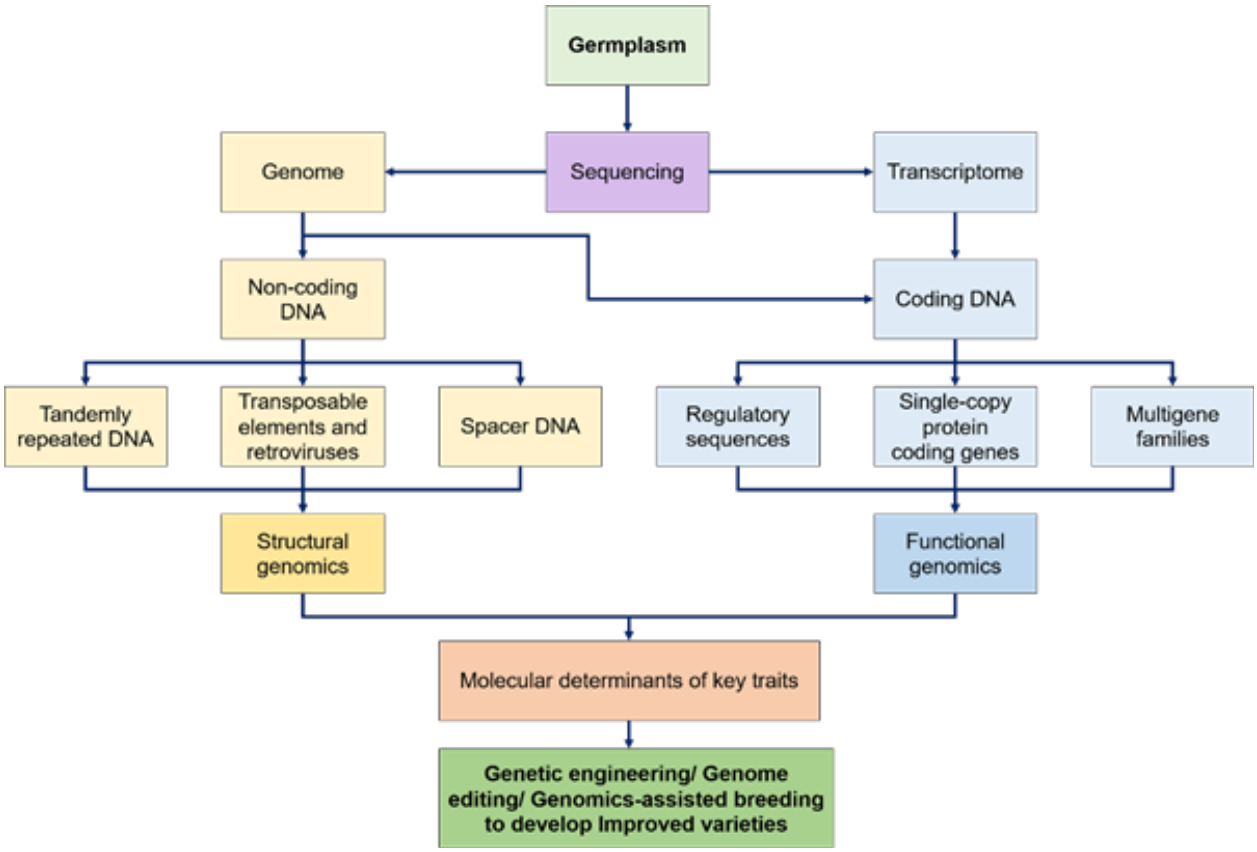


Figure 2
Application of sequencing approaches to decode the coding and non-coding elements of the genome for their effectual use in trait improvement

insights into the traits, and Genetic engineering enables the transfer of genes or modulation of their expression to achieve the desired phenotype. Gene editing plays a role in creating novel lines with appropriate phenotypes.

Conclusion

Tree genomics has a major role in the near future in understanding tree system biology and developing policy actions to conserve nature and managed forest genetic resources. In this context, tree genomic research is driven by the need to assist genetic improvement programmes and create diagnostic tools for the conservation, restoration, and management of natural tree populations. In this circumstance, developing a complete genome sequence of various trees could help in the functional analysis of genome components to use as an efficient tool for tree breeding. Therefore, a need for genomic information on native and under-utilized trees has to be pursued. This effort definitely will aid in documenting and unlocking the enormous diversity of tree species and helps in understanding their evolutionary pattern. Many trees may have limited industrial value. However, these species can be significant in terms of social-cultural beliefs and ecological service. Therefore, the funding agencies should emphasize research based on these grounds to support future needs. With the advent of third-generation technologies, it is possible to generate high-quality long-read reference genomes in less time and cost. Recently, the improved genome assembly called 'hybrid assembly' would enhance the accuracies used for most complete high-quality assemblies. In no time, more emphasis must be given to tree genome research like microbial and crop genomics. Financial investments should be made to maintain tree genomics resource databases such as Treegenes and Hardwood genomics projects (https://hardwoodgenomics.org/). Since data availability for the research community is paramount to initiate tree genomics-related research. Finally, tree genomics research must be inter-disciplinary, where tree geneticists should work more closely with foresters, physiologists, and bioinformaticians to foster tree genomics research.

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