REVIEW

Technological Advances in Commercial Forestry

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Abstract Biotechnological tools such as clonal propagation, haploid production, protoplast fusion, marker-assisted selection, and quantitative trait loci mapping are the age-old approaches in commercial forestry. Biotechnology has shown immense guarantee for the subsequent generation of plant breeders to alleviate the rising demand for food, fiber, and wood. The probable social and environmental impacts of the release of transgenic trees become a progressively more debatable issue and call more considerations. The present review is an attempt to summarize how advances in molecular biology i.e., comparative genomics and genome assembly approaches identify numerous polymorphic molecular markers like microsatellite, simple sequence repeats, single-nucleotide polymorphism (SNP), random amplified polymorphic DNA etc. and revolutionize the science of forest tree biotechnology during the last decade. The advent of next-generation sequencing technology identified many microsatellite loci in forest trees. Microsatellite markers play an important role in population genetics, conservation ecology, and phylogenetic analysis. SNP markers provide novel opportunities for the discovery

of regulatory elements in the genome and eventually accelerate forest tree breeding.

Introduction

Forest and forest products are more important in the progression of forest and forest-associated industries. The decrease in forest and forest products compels industrialists not to rely on natural forests [1]. Global forest cover decreased between 1990 and 2015 from 4128.3 to 3999.1 million ha (Table 1), and pressure is mounting on the existing forests due to environmental deterioration, increase in the demand for wood, deforestation, global warming, shortage of water, and associated threats [2]. Traditional methods which are used for tree improvement are not able to fulfill the present-day demand of industry and reforestation programs. Increase in xylem fiber lengths, lignin content of wood, timber quality improvement becomes more possible due to the advancement of biotechnological tools and techniques. Genetic engineering has a tremendous capability to enhance global wood production in various ways [3]. Recent biotechnological tools and techniques are able to manipulate photosynthetic efficiency, CO_2 absorption ability, biomass production, improvement in wood and timber quality, resistance to abiotic stresses and many more [4].

Micropropagation and Genetic transformation are the two important tools used in the development of better tree species, as most of the tree species lack vegetative means of propagation [5]. Micropropagation is considered as the best method used in the development of conifers and

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Table 1 Changes in total forest area of the world during last decade (Source: Payn et al. [6])

Forest area (million ha)/year	1990	2000	2005	2010	2015
Boreal	1219.3	1219.8	1218.9	1224.9	1224.5
Temperate	618.0	640.9	659.2	673.4	684.5
Subtropics	325.4	324.8	323.9	319.6	320.1
Tropics	1965.5	1870.1	1830.8	1797.8	1770.2
Total	4128.3	4055.6	4032.7	4015.7	3999.1

Table 2 Tissue culture of various forest tree species

Species	Explant	Response	References
Bambusa arundinacea	Seeds	C, SE*	[7]
Bambusa vulgaris	Nodes	MS*	NCL (unpublished)*
Dendrocalamus strictus	Seedling	Flowering	University of Delhi (Unpublished
Conifers	–	Somatic Embryogenesis	[8]
Poplar	–	Organogenesis	[4]
Eucalyptus	–	Organogenesis	[4]

*C callus, SE somatic embryo, MS multiple shoot, NCL National Chemical Laboratory, Pune.

determinate growth of angiosperms [9]. Somatic embryogenesis is an effective and reproducible technique used in the production of somatic plants of many economically important pine species [10]. Various types of forest trees developed by tissue culture with various methods and explants are summarized in Table 2.

Technological Advancement

Revolutionary technologies of molecular markers such as gene pyramiding, QTL identification, marker-assisted selection, and transgenic crop development, in amalgamation with usual morphology-based selection, delineate the present-generation plant breeding exercises. Molecular markers identify many genetically distinct cultivars which act as an important source of germplasm for various crop improvement programs [11]. With the advent of high-throughput sequencing technologies, many single-nucleotide polymorphism (SNP) markers have been developed for a variety of plant species. Marker assisted gene pyramiding enable the development of many plant species resistant to biotic [12, 13] and abiotic stressors by pulling together a series of genes from diverse parents into a particular genotype. In addition, multiplexed shotgun genotyping [14], restriction-site-associated DNA sequencing (RAD-seq) [15], and genotyping-by-sequencing (GBS) [16] have unlocked innovative promises in plant breeding studies.

Limitations and Prospects of Forest Tree Breeding

Forest tree breeding differs primarily from yearly crops due to breeding cycles, delayed flowering, and long vegetative phases. It is pricey, and it is not easy to cross trees due to huge bodily size and expensive progeny tests to set up, manage, and compute. Large expanses of lands are needed to test desirable progeny. Seed lot cannot be replaced for tree plantation due to huge economic loss; trees requiring several years to produce seed, unsatisfactory juvenile mature correlation ship, lack of basic genetic information about genes controlling various characteristics among forest tree species are the main problems associated with forest tree breeding programs. The generation period is fairly large among forest trees which leads to atypical problems in forest tree breeding. There are reports that genotype by environmental interaction ($G \times E$) affects growth and wood properties in various economically important tree species of genuses *Eucalyptus*, *Picea*, *Pinus*, *Populus,* etc. The consideration of GxE has been vital for devising breeding and deployment policies in forest trees [17].

Tree breeders mug ever-increasing loads for food, water, and energy; climate change and its insinuation for genetic exploitation; globalization leading to the interconnectedness of markets; budding technology in molecular biology; changing ownership prototype of forestland, and the genuine prospect of entirely new forest commodities and bazaar in the future [18]. Clonal forestry is gaining attention due to the production of quality planting stock,

upholding of genetic consistency, production of disease-free plant and early flower induction [19]. The harvesting cycle of several tree species such as *Eucalyptus, Salix*ar, and *Acacia* has been shortened using various tree breeding and tree improvement programs.

Genomics-Based Breeding for Growth

Modern biotechnology-based tools have been used in forest tree breeding for attaining elevated yield of timber and wood to fulfill the huge claim of the wood market across the world. The advancement and use of new genetic tools could sharply lessen the time essential to raise the trees and help to spot trees with definite characters (Fig. 1). Genomic selection (GS) was a milestone discovery based on high-throughput sequencing technology offering an innovative tool for understanding quantitative trait variation in forest trees. GS is basically working on the principle of identifying and selecting several agronomically important traits by taking the help of a large number of markers distributed throughout the genome; this information is used to determine the breeding values [20]. It is reported that GS reduced the breeding cycle in tropical eucalyptus by 50% eliminating the progeny trial and the primary clonal trial; as a result, the length of the breeding cycle reduced by 9 years. The GS based seedlings can be easily verified through vegetative propagation and clonal trial before commercial exploitation. Genome-wide association studies and genomic selection in tree populations have accelerated breeding tools useful in the assortment of desired genes for genetic engineering [21].

Harnessing Next-Generation Sequencing (NGS) Technologies for Tree Breeding

NGS technologies fetch popularity in next-generation tree breeding programs to assess species divergence in natural populations and gain substantial momentum and attention
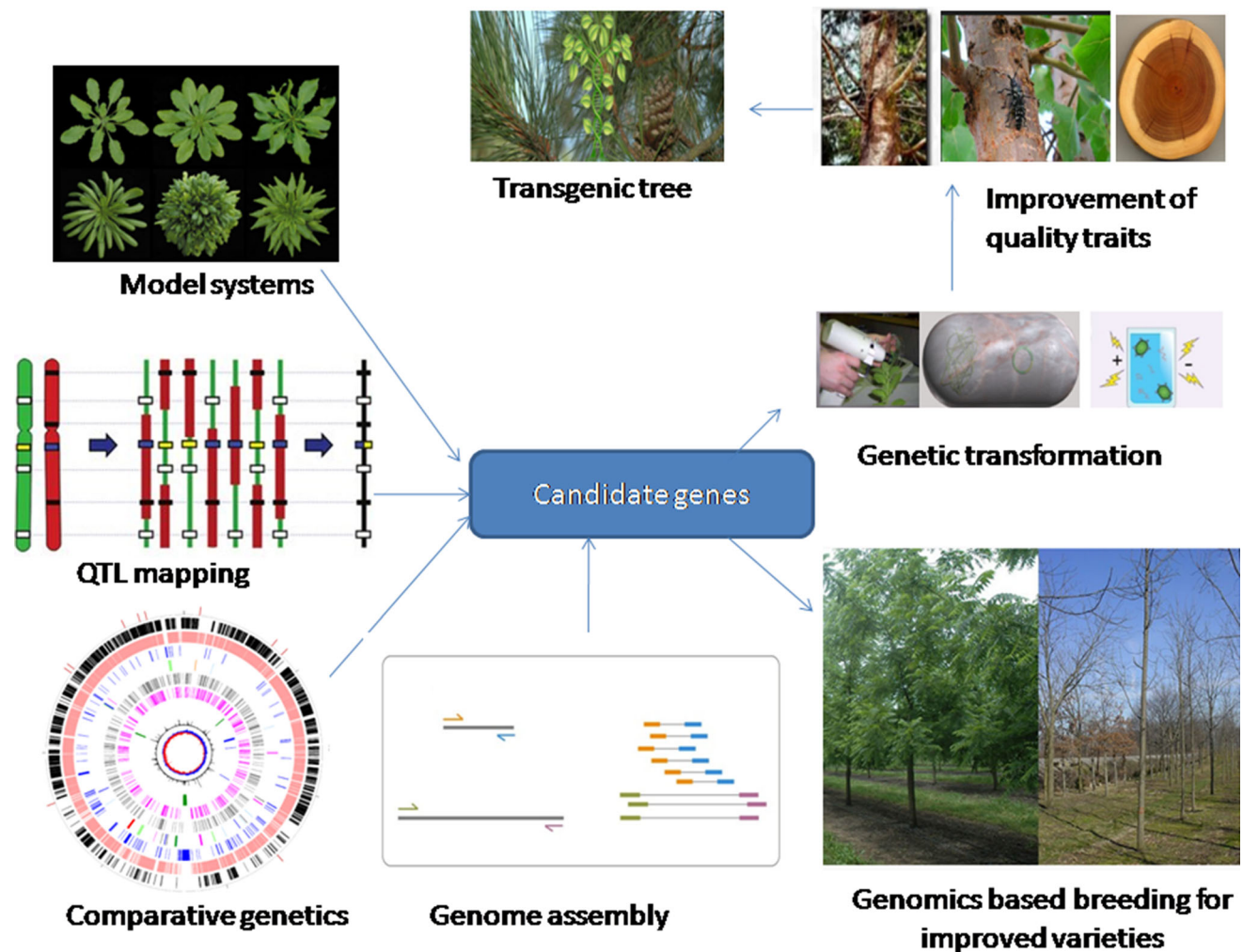

Fig. 1 Modern biotechnology tools in forest tree breeding

Table 3 Available reference genome sequences of few forest tree species

Forest tree species	Common names	Family	Genome size	References
Populus trichocarpa	Black cottonwood	Salicaceae	450 Mb	[24]
Eucalyptus grandis BRASUZ1	Flooded gum	Myrtaceae	640 Mb	[25]
Quercus ruber	Pedunculate oak	Fagaceae	1.5 Gbp	[26]
Pinus taeda	Loblolly pine	Pinaceae	20.1 Gbp	[27, 28]
Picea glauca	White spruce	Pinaceae	20 Gbp	[29]
Pseudotsuga menziesii var. menziesii (Mirb.)	Douglas fir/ Oregon pine	Pinaceae	16 Gbp	[30]

among the scientific community, tree breeders, and policymakers [22]. With the speedy expansion of sequencing technologies, population/ minor species differentiation can be observed among tree species at the molecular level by looking into nucleotide divergence between contrasting populations. Genome-scanning approaches through NGS technology identify the coding regions responsible for the maintenance of phenotypic species differentiation [23]. Various NGS platforms such as Roche 454, Illumina HiSeq 2000, Ion Torrent, Helicos HeliScope, Complete Genomics, Nanopore, the Pacific Biosciences, and others provide new tools to overcome most of the problems encountered by tree breeders. The reference genome sequences of many tree species are available, and few are summarized in the following Table 3.

Genetic Transformation of Forest Trees

Forests cover about 30% of the earth's soil surface ranging from cold temperate to hot tropical regions, and various tree species participate in foundation tasks in their environments. Modernization of breeding techniques, i.e., genetic transformation by Agrobacterium-mediated gene delivery, biolistic method, protoplast transformation, and genomic selection for identification of the desired trait, dramatically increased industrial forestry as well as remodel production and traffic of forest products.

Genetically engineered (GE) trees potentially formulate the breeding values noticeably and reduce the life cycle, resulting in increasing yield and plummeting of the exploitation load on natural forests [31]. Many wood formation traits have been identified by the advanced molecular biology approaches and are used to modify wood properties [32]. Multi-omics techniques along with systems biology approach have been applied successfully in many forest trees to produce a large amount of custom-designed biomass and biochemicals during the last decade [33, 34].

Current status of Tree Genetic Engineering

In general, industrial forestry expected to increase the quantity and quality of wood produced for the ultimate specific uses. This can be achieved by biochemical alteration of the wood character and trunk composition, biotic and abiotic stress tolerance, root formation, and flowering control. There are very few commercially grown GE forest tree species [32] in comparison with GE annual crops such as insect-resistant poplars in China, high-yielding tropical *Eucalyptus* with engineered frost tolerance in the USA [35]. Many reports have been cited on field trials of GE trees with improved plantation productivity, pest resistance, and wood processing. Many research papers have been published during the last 5 years on overexpression of drought sensing, signal transduction, and drought-responsive transcription factors in forest trees [36].

Improvement in Productivity Traits

Several reviews, research papers, editorials, books are published to update the readers regarding the genetic manipulation of various gene expressions in forest trees to improve the agronomical traits [37, 38]. Table 4 cites [39–43] a few examples of traits improved by genetic transformation techniques.

Development of Carbon Dioxide-Neutral Production Systems

Forests are the best carbon sinks, and the trees play an important role in mitigating climate change by absorbing a large amount of carbon dioxide from the atmosphere. Various tree species such as *Pinus densiflora, Quercus serrata,* and *Larix leptolepis* have been investigated during the last decade for CO_2 absorption potential [44]. Many biotechnology companies developed genetically modified

Table 4 Various traits improved in forest trees by genetic transformation

Gene	Promoter/modification	Transformed species	Trait	Improvement compared to control	References
Antisense 4-coumarate–CoA ligase (4CL) and sense conifer aldehyde 5-hydroxylase (CAld5H)	Xylem-specific promoter (Pt4CL1P)	Aspen (*Populus tremuloides*)	Reduced lignin	52% less lignin, a 64% higher S/G ratio, and 30% more cellulose	[39]
Arabidopsis CBF2 (C-repeat binding factor) cDNA	*Arabidopsis* cold-inducible promoter rd29A	EH1 genotype of *E. grandis x E. urophylla* Eucalyptus (AGEH427)	Freeze tolerance	Grew better at a site with a minimum temperature of 16.8 °F	[40]
LEA gene from *Tamarix androssowii* (named TaLEA)	CaMV 35S promoter	Xiaohei poplar (*Populus simonii* × *P. nigra*)	Salt and drought tolerance	Increase in height growth rate and decrease in number of wilted leaves under the salt and drought stresses	[41]
Gossypium hirsutum sucrose synthase (*SuSy*) gene	CaMV 35S promoter	Hybrid poplar (*Populus alba* × *grandidentata*)	Elevated cellulose	Thicker xylem secondary cell wall and consequently improved wood density	[42]
Isoprene synthase (ISPS)	Suppressed by RNA interference (RNAi)	Grey poplar (*Populus* × *canescens*)	Absence of isoprene emission	6.9% enhanced net growth	[43]

"super-carbon-absorbing" trees to develop trees more efficiently for absorbing carbon. The Empress Splendor tree, *Paulownia tomentosa*, greatest budding hardwood tree in the world (Guinness Book of World Records) already promoted in Canada carbon offset program. This tree has large, gigantic, widely spaced leaves that take up 10–20 times more carbon dioxide than a regular tree and yields lightweight and water-resistance hardwood within 7–10 years. Fast-growing trees not only generate the economy through the sale of timber but also are the key factors of the carbon sequestration market.

Enhancement of Stress Resistance

Genetic improvement of forest trees for tolerance to biotic and abiotic stresses including insect and herbicide resistance, salinity, drought and freeze resistance was attempted. China commercialized genetically modified (GM) poplar trees in 2003 with *cry1a* from *Bacillus thuringiensis* and proteinase inhibitor from *Sagittaria sagittifolia* to control the beetle. Transgenic *Eucalyptus urophylla* was developed and showed 35% improved resistance against the bacterial wilt disease caused by *Pseudomonas solanacearum*. Arborgen Inc. developed one GM *Eucalyptus* tree which contains a C-repeat binding protein from *Arabidopsis thaliana* under the control of a cold-inducible promoter that can withstand extremely low temperature. This GM *Eucalyptus* can grow up to 52.4 feet at 16.8°F, a contrast to the control trees which grew only 0.3 feet.

Perception of GM Forest Trees

Biotechnology improved many traits of forest trees such as lignin content, insect resistance, biomass growth, and many abiotic and biotic stress tolerance properties. Regardless of these prospective rewards, commercial GM forest tree plantations are not presently grown anywhere in the world, except China [45]. Socioeconomic consideration and public opinion of various genes inserted into GM trees, viz. freezing resistance gene from deep-sea fishes to Norway spruce, are one of the major concerns for the commercialization of GM forest trees including technological limitations, specifically gene stability-related issues.

Barriers to the Adaptation of GM Trees

The commercial release of GM trees crosses the line for satisfaction on the social, economic, and environmental ground. The ecological risk is associated with the transgene introgression into related wild relatives, horizontal gene flow of transgenes to unrelated organisms, impacts on critical ecosystem processes like nutrient cycling, decomposition, etc. which are the focal points of concern. The probable social and environmental impacts of the release of transgenic trees become a progressively more debatable issue that calls for more considerations.

Biosafety of GM Trees

Genetic engineering and plant transformation technologies created a large number of genetically modified trees with novel characteristics during the last decade but public acceptance is in a critical dilemma regarding their commercialization. Transgene contamination is the main concern, as a result of which genetically modified forest trees are only confined to greenhouses or field experiments. Many private companies such as Plant Genetic Systems N.v., Belgium; Bayer Cropscience SA-NV, Belgium; FuturaGene, Brazil; and Monsanto Europe conducted so many field trials for GM trees. The commercialization of GM trees is mainly based on environmental risk assessment, and many countries framed step-by-step approach for the categorization of GM trees field trials, i.e., European Union (EU); the internment of GM trees slowly decreased, and the range of the trial gradually increased in a stepwise mode.

Transgenic Roots to Increase Biomass in Forestry

The root architecture such as root length and lateral root density is the key determinant of plant water uptake efficiency. The reduced rooting ability of various *Eucalyptus* commercial clones is a rate-determining factor for clonal propagation. Improving the rooting ability of *Eucalyptus* clones by genetic transformation through *Agrobacterium rhizogenes* is well studied. Biomass augmentation can be attained through the growth of leaves, roots, and stem in transgenic trees. Root architecture can also affect drought resistance; e.g., *Arabidopsis HOMEODOMAIN GLAB-ROUS 11* (*HDG11*) gene expression enhanced drought tolerance in transgenic trees by improved root architecture with deeper and more lateral roots [46], poplar activation tagged lines with increased root growth developed under high osmotic conditions [47], and poplar FDL (flowering locus proteins) RNAi lines showed high root biomass under drought condition and became drought resistant [48]

Conclusion

Molecular markers specifically single-nucleotide polymorphisms (SNPs) and their association with complex traits in trees provide new hope for tree improvement and commercial forestry. Advancement of techniques leads to a large task where thousands of candidate genes are screened and annotated by the approaches of functional genomics. Genomic-based breeding and its advancement mainly play a pivot role to improve forest health. Genomic selection in forest trees generates a very interesting and optimistic result in terms of commercial forestry and forest tree improvements. To achieve the goals of the genomic selection strategy, a well-planned system, an efficient database, computational and quantitative tools for the management of large datasets are needed. The surplus of modern NGS-based studies led to the availability of reference genomes; genome assemblies that will combine with data from an extensive history of breeding provide new openings for exploitation of genomic and phenotypic data and concurrently will augment the command of the classical breeding.

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