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Review

Insights into the Biotechnology and Genetics of Sugi (*Cryptomeria japonica*, Japanese Cedar), a Model Conifer Tree

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Abstract

The Japanese cedar (*Cryptomeria japonica*), also known as sugi, is one of the most important trees in Japanese forests. It covers 44% of artificial forests, spanning approximately 4.5 million ha. It is cultivated in East Asia, the Azores archipelago, and some islands in the Indian Ocean. It is also grown worldwide as an ornamental tree in parks and gardens. The cultivation and use of sugi in Japan dates back centuries, and clonal forestry through cuttings has been practiced since the early 15th century. Its broad adaptability, genetic diversity, rapid growth, easy propagation, and precocious flowering—enabling early generational crosses—combined with their advanced genomic resources and efficient biotechnological tools, make sugi an outstanding conifer model. This review aims to provide an overview of the biotechnology and genetics of sugi for researchers and stakeholders.

Keywords: diversity; genetic transformation; genomics; in vitro propagation; photosynthesis; pollen-free plants; somatic embryogenesis

1. Introduction

Sugi (*Cryptomeria japonica*, Japanese cedar) is Japan's most important forestry species, covering 44% of all artificial forests and approximately 4.5 million ha [1]. Its use as timber spans over 3000 years, while artificial plantations, including clonal forestry by cuttings, have been practiced for more than 500 years [2,3]. Beyond Japan, it has been introduced to parts of China [4], the Azores archipelago [5], and islands of the Indian Ocean [6].

Sugi is well suited as a model conifer owing to its wide adaptability, fast growth, vegetative propagation capacity by cutting, grafting, and tissue culture, and the existence of genetically diverse local varieties. In addition, experimental manipulation is also feasible: applying gibberellic acid can induce flowering in juvenile plants [7], enabling artificial crosses at unusually early stages for a conifer and shortening the generation time.

Furthermore, a somatic embryogenesis protocol has been firmly established [8]. *Agrobacterium*-mediated transformation [9] and CRISPR/Cas9 genome editing [10] have been achieved using embryogenic tissues. Nishiguchi et al. [11] recently produced male-sterile lines through genome editing, demonstrating the feasibility of functional genomics and targeted breeding in this species. Moreover, a chromosome-level genome assembly provides a robust platform for molecular genetics [12]. These resources have enabled the identification of male-sterile loci and the development of breeding markers for pollen-free trees, thereby addressing a significant public health concern in Japan. Recent advances in comparative analyses of long terminal repeat (LTR) retrotransposons across conifer

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genomes have further revealed unique evolutionary dynamics in sugi, underscoring its value for evolutionary studies [12].

Together, these biological traits and the integrated advanced genomic resources and biotechnological techniques establish sugi as an exceptional conifer model for both basic and applied research. Additionally, it will serve as a comparative model and genomic reference for other conifers.

2. History, Distribution, and Status of Cultivation

The genus *Cryptomeria* has a limited global distribution and consists of a single species, *C. japonica* (L.f.) D. Don (Japanese cedar, sugi; Cupressaceae) [13]. Sugi occurs naturally in cool temperate regions of Japan, mainly from the Aomori Prefecture southward through Honshu, Shikoku, and Yaku Island [14]. A variant *C. japonica* (L.f.) D. Don var. *sinensis* Siebold (also known as *C. fortunei* Hooibrenk ex Otto et Dietr.) is found in southern China, although its classification and origin remain controversial [15,16]. Fossil evidence indicates ancient origins of the *Cryptomeria* genus in East Asia since the Eocene and in Europe since the Miocene, where several species have been identified [17,18]. Fossils resembling extant *Cryptomeria* species have been found throughout Japan since the Miocene [18]. Fossil pollen records indicate widespread distribution during the Pliocene [19], followed by a contraction. During the last glacial period (~15,000 years ago), sugi populations were restricted to several refugia, such as the Izu Peninsula, Wakasa Bay, and the Oki and Yaku islands, before expanding with postglacial warming [20,21]. The current distribution of sugi is believed to have been formed approximately 4000 years ago [21].

Sugi has long been valued in Japan for its softness and workability. A 6 m long log boat made of sugi, excavated from the Torihama shell mound in Fukui Prefecture, dates to the early Jomon period (approximately 6000 years ago), along with a large amount of planks made of cedar wood [22]. By the Yayoi period (300 B.C.E. to 300 C.E.), cedar was widely used for houses, household utensils, and paddy field partitions [23,24]. The continuous logging of natural forests has left almost no pristine old-growth sugi forests in Japan. Beyond timber, sugi remains embedded in daily Japanese life—seen, touched, smelled, and even tasted.

Sugi plantations also have an ancient history. The Man'yō-shū, Japan's oldest surviving poetry collection (compiled during the Nara period, A.D. 710–794), contains a verse describing "branches of sugi planted by ancient people" (Man'yō-shū vol. 10, No. 1814; liberal translation by authors), suggesting over 1200 years of silvicultural practice [25]. Historical records indicate that the sugi tree was first planted in Kitayama (Kyoto Prefecture, central Honshu) as early as the 15th century [3]. Following World War II, afforestation policies greatly expanded sugi plantations through active planting, making it the most widely planted tree species in Japan. Today, sugi forests cover 4.5 million ha, representing approximately 44% of artificial plantations and 18% of the total forest area [1]. Outside Japan, sugi has also been planted in China, the Korean Peninsula, Taiwan, Reunion Island, and the Azores archipelago [4–6]. Numerous ornamental lines differing in leaf shape and tree form are also distributed globally, making sugi a species of worldwide presence [26]. Modern sugi breeding began with elite tree selection projects in the 1950s, followed by mass selection for desirable traits [27]. More recently, in response to the rising prevalence of sugi pollinosis in Japan [28], breeding programs aim to develop varieties combining superior growth and wood quality with reduced or absent pollen production.

3. Conventional Propagation Methods

Currently, Japan produces approximately 30 million sugi seedlings annually for reforestation [1], with roughly half derived from seeds collected at seed orchards. These orchards

contain multiple clones with desired growth and wood traits, and cross-pollination among them is expected to yield viable seeds. Miniature seed orchards, in which trees are maintained at heights of 1–2 m, have become standard [29]. To address sugi pollinosis, orchards using cultivars with reduced pollen production ("specified mother trees") and closed orchards breeding specific strains to produce male-sterile trees have been established [30,31]. The resulting seeds are grown into container seedlings for reforestation.

Another major method of seedling production is through cuttings, as sugi is readily propagated using this method [32–34]. Tens of millions of seedlings are produced annually using this method. In Kyushu, cuttings dominate seedling supply, and clonal forestry is actively promoted. Cuttings have a long history in this region [2,3], and numerous varieties with strong rooting capacity have been selected. Propagation gardens have also been established for shoot collection.

To meet the growing demand for seedlings, particularly for replanting as a countermeasure against sugi pollinosis, new production systems are required in addition to conventional methods.

4. Biotechnological Approaches

4.1. Tissue Culture

Since the 1970s, studies on tissue culture of sugi using various explants have been reported. Ishikawa [35] described adventitious bud and root formation from hypocotyl explants, whereas Sato [36] achieved plant regeneration by inducing multiple shoots from cotyledons, hypocotyls, and young buds. Callus formation was investigated using cultured cambial explants [37], shoot tips [38], premature embryos [39], and male flower scales or immature seeds [40].

Subsequent studies reported successful in vitro regeneration through axillary bud formation from shoot explants of selected adult trees [41–43]. Similarly, Hine-Gómez & Valverde-Cerdas [44] established in vitro shoots from 20-year-old trees. Ishii et al. [45] also achieved long-term in vitro shoot culture and storage for more than two years at 25 °C in 300 mL flasks containing medium supplemented with 5 g/L activated charcoal. More recently, Rojas-Vargas et al. [46] comprehensively examined micropropagation factors, including explant type, basal media, light treatments, and plant growth regulators, using material from trees older than 30 years. Furthermore, Maruyama T.E. (unpublished) achieved flowering in some somatic plants cultivated in vitro. This suggests that, in addition to the demonstrated ability to flower ex vitro through stimulation with gibberellic acid, it may also be possible to manipulate flowering under aseptic conditions (Figure 1).

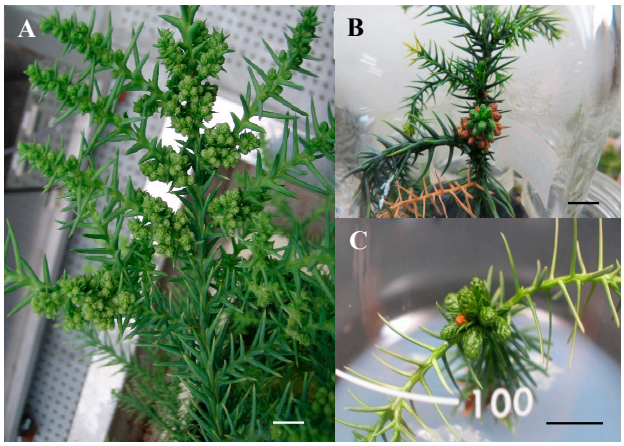


Figure 1. Flowering in sugi (*Cryptomeria japonica*, Japanese cedar). (**A**) Ex vitro flowering induction after gibberellin application; (**B**,**C**) In vitro flowering of plants growing in bio-flasks. Bars: 10 mm.

4.2. Somatic Embryogenesis

Somatic embryogenesis (SE) is a powerful technique for propagating selected trees and for cell biology and genetic engineering research. It also enables long-term ex situ conservation of genetic resources through cryopreservation. SE and plantlet regeneration in gymnosperms were first reported in Norway spruce (*Picea abies* L. Karst.) [47–49] and later extended to many other conifers [50–52].

For sugi, Ogita et al. [53] as well as Taniguchi and Kondo [54] initiated embryogenic cultures, followed by Maruyama et al. [55], who first achieved somatic plant regeneration. Since then, efforts to optimize SE protocols have included induction of embryogenic cells [56–59], production of mature embryos [60–63], plant conversion [64,65], and in vitro growth of somatic plants [66]. Hosoi et al. [67] further demonstrated plant regeneration via somatic embryos derived from protoplasts isolated from embryogenic cells. An improved stepwise protocol covering culture initiation, maintenance, proliferation, embryo production, germination and conversion, ex vitro acclimatization, and containerized seedling development was later published (for details about the components of the culture media and the procedures for each step, see Maruyama et al. [8]). This method enables the production of more than 500 high-quality somatic embryos per plate via genotype selection, with yields exceeding 1000 embryos per gram of fresh weight. Recently, Maruyama et al. [68] reported advances in somatic embryo production and storage, demonstrating that sugi somatic embryos can be stored at 25 °C, 15 °C, or 5 °C for 6, 12, or 24 months, respectively, without significantly reducing germination capacity (Figure 2).

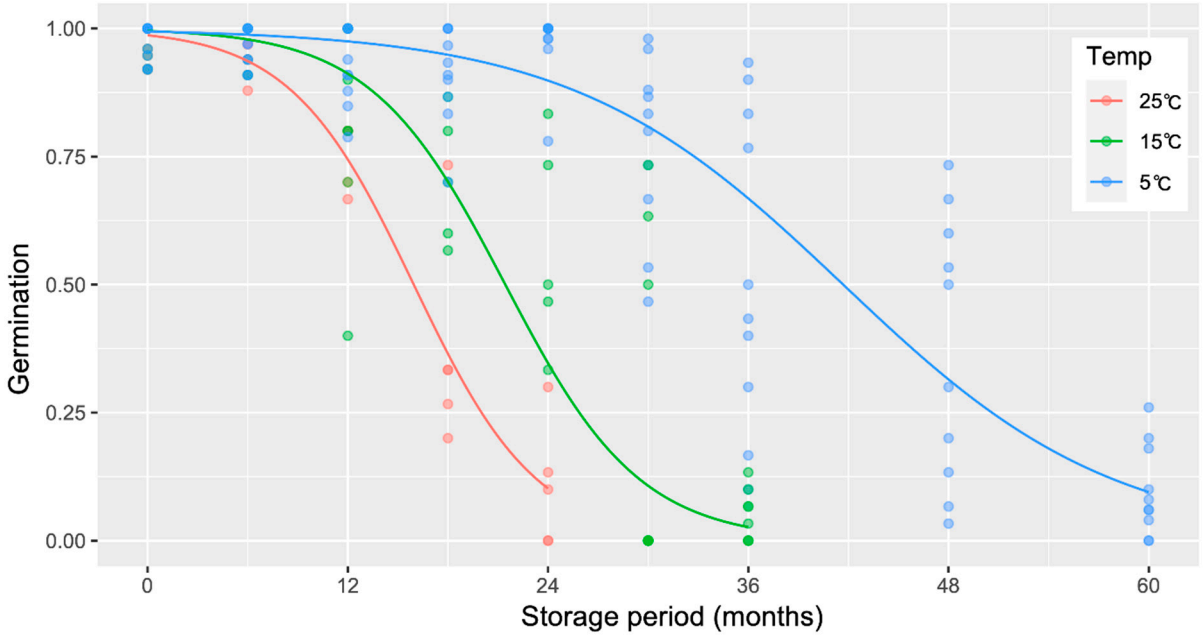


Figure 2. Germination response of sugi (*Cryptomeria japonica*, Japanese cedar) somatic embryos after different storage periods at 25 °C, 15 °C, and 5 °C. Figure adapted from Maruyama et al. (2025) [68], published by *Forests* as the original publisher.

4.3. Cryopreservation of Embryogenic Cells

Because prolonged subculture often leads to the loss of embryogenic potential, embryogenic cells are typically stored at ultra-low temperatures (−150 °C to −196 °C). Following the cryopreservation protocol developed for *Picea abies* by Kartha et al. [69], modified protocols have been established as integral components of SE programs for various conifer species [70].

For sugi embryogenic cells, Niino et al. [71] reported cryopreservation protocols using the vitrification solution PVS2 [72] or modified solutions containing 10% DMSO or a mixture of 20% glycerol and 15% sucrose. Survival rates varied across embryogenic lines and protocols, with an overall average of approximately 50%. Later, Taniguchi et al. [58] introduced a simplified, efficient protocol adapted from Sakai et al. [72] and Ogawa et al. [73]. This method employed a cryoprotectant solution of 2 M glycerol, 0.4 M sucrose, and 1 g/L proline, with precooling at −30 °C for six hours in expanded polystyrene tube containers before immersion in liquid nitrogen. Using this approach, 27 of 28 cell lines (96.4%) were successfully cryopreserved.

4.4. Propagation of Pollen-Free Plants

Sugi forests, while commercially important, release large amounts of pollen each spring, causing allergic reactions in approximately 40% of residents [28]. Sugi pollinosis represents a serious socioeconomic and public health issue in Japan, with recent estimates placing daily economic losses from absenteeism alone at over 230 billion Japanese yen [74]. The use of male-sterile or pollen-free plants (PFPs) in reforestation offers a promising strategy to mitigate this problem.

Sugi PFPs are typically produced by artificially crossing a male-sterile tree (*ms1*/*ms1*) with a heterozygous *MS1* carrier (*Ms1*/*ms1*) [75]. The resulting seedlings are screened for sterility after male flower induction via the gibberellin application, which promotes flowering in sugi [7,76]. However, because approximately half of the seedlings segregate as nonsterile, the efficiency is very low, and many seedlings are discarded [65]. Tissue culture as a tool for clonal propagation could significantly accelerate sugi PFP breeding.

Although in vitro propagation of sugi has been studied since the 1970s (Section 4.1), reports on the organogenesis of male-sterile sugi are limited. Tsubomura & Taniguchi [77] reported micropropagation of the male-sterile clone ‘Soushun’, and Ishii et al. [78] achieved in vitro culture of twelve male-sterile genotypes and three male-sterile hybrids by crossing individuals carrying the sterile gene as a heterozygous allele. Although axillary bud induction was possible, the number of shoots produced per explant was low, limiting large-scale propagation. Therefore, developing efficient methods for mass PFP propagation remains a priority.

Genomic advances in sequencing and assembly have recently enabled more efficient selection. Following the publication of the sugi draft genome [79] and subsequent chromosome-level assembly in sugi [12], genes associated with male sterility were identified [80,81], and molecular markers were developed [82,83]. These breakthroughs allowed the initiation of marker-assisted selection combined with SE for efficient PFP production [65]. Based on this, an improved stepwise SE protocol [8] and a practical manual for PFP propagation with 100% discrimination efficiency in a short period [84] were released (Figure 3). These tools are now applied in producing somatic seedlings for reforestation and genome-edited plants for biological studies. Additionally, genetic engineering is now a viable method of producing sugi PFPs (for more details, see Section 4.5).

4.5. Genetic Transformation

Genetic transformation is a valuable approach for elucidating unknown functional genes and modifying physiological and biochemical properties. The first transformation of woody plants was achieved using *Agrobacterium* (now classified as *Rhizobium*), a genus of plant-pathogenic bacteria [85,86]. *Agrobacterium*-mediated transformation has also been applied to gymnosperms such as *Pinus lambertiana* [87], *Larix decidua* [88], and *Picea abies* [89], among others [90,91].

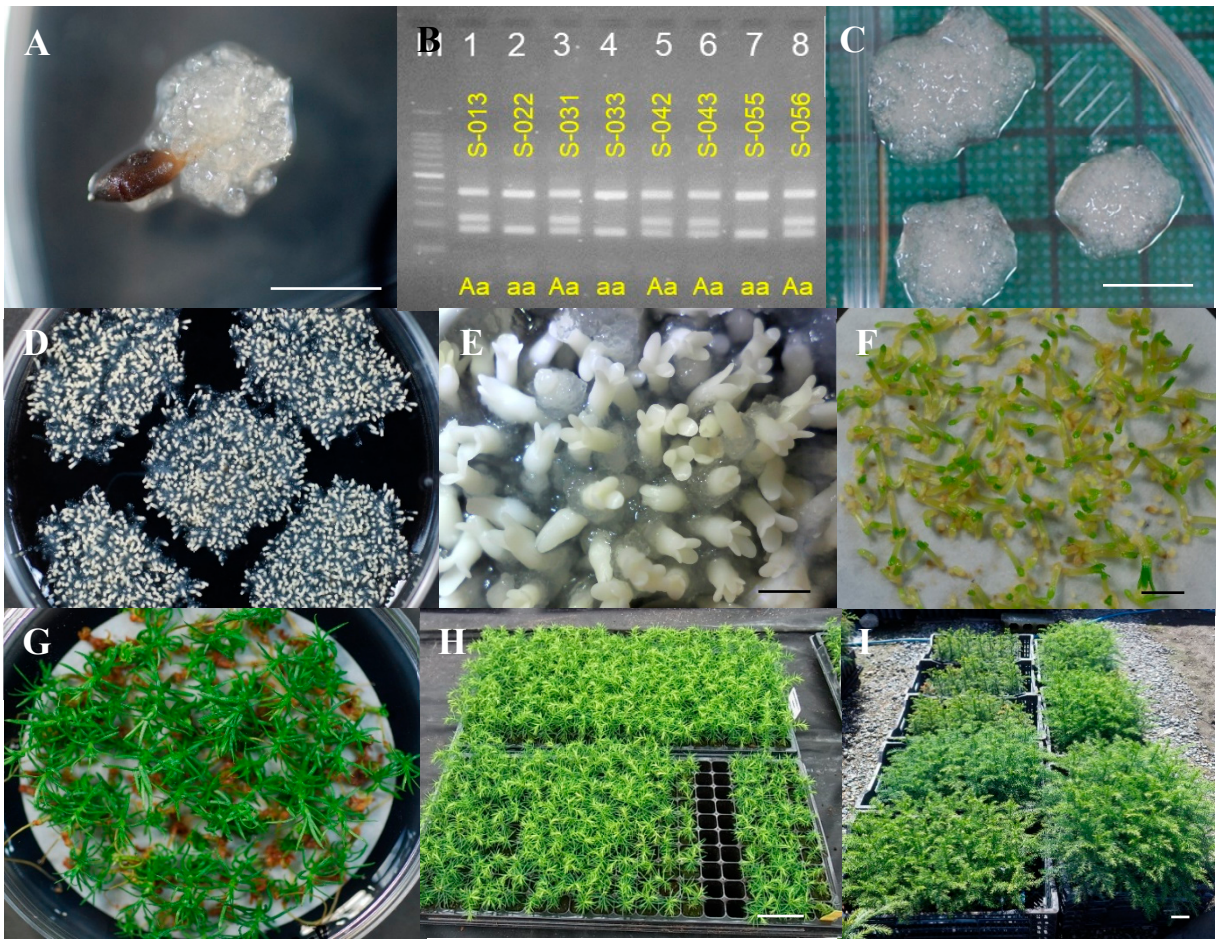


Figure 3. Propagation of sugi (*Cryptomeria japonica*, Japanese cedar) PFPs via SE. (**A**) SE initiation from an immature megagametophyte explant; Bar: 10 mm. (**B**) Discrimination of male-sterile cell lines by genetic marker. (**C**) Proliferation of male-sterile embryogenic cell line; Bar: 10 mm. (**D**) Somatic embryo maturation. The diameter of plate is 90 mm. (**E**) A close-up view of matured somatic embryos; Bar: 10 mm. (**F**) Somatic embryo germination; Bar: 10 mm. (**G**) Somatic embryo conversion. The diameter of plate is 90 mm. (**H**) Acclimatized PFPs growing into plant plugs; Bar: 50 mm. (**I**) Containerized PFPs; Bar: 50 mm. Figures reproduced from Maruyama et al. (2022) [8], originally published by *Frontiers in Plant Sciences*.

In sugi, the initial transformation was attempted using a microparticle delivery system. Small gold particles coated with plasmid DNAs carrying an exogenous reporter gene were shot into zygotic embryos [55]. Exogenous reporter genes, such as β-glucuronidase and luciferase [92] as well as green fluorescent protein (GFP) [93], were transiently expressed in zygotic embryos, but no stable transgenic trees were obtained. To establish stable transformation, *A. tumefaciens* (*Rhizobium radiobacter*)-mediated transformation was applied to embryogenic cells. GFP-expressed sugi trees were successfully regenerated from somatic embryos derived from *A. tumefaciens*-infected embryogenic cells [94]. The method was later optimized to achieve higher recombination efficiency [95].

A detailed transformation protocol for sugi was subsequently reported [9]. Embryogenic cells derived from immature seeds were infected with *A. tumefaciens* harboring a binary vector and then co-cultivated on filter paper soaked in a liquid medium. Following co-cultivation, cells were washed and cultivated on a medium containing the antimicrobial agent meropenem and selective antibiotics, such as kanamycin or hygromycin. Viable calli are transferred to an embryogenesis medium to form somatic embryos that germinate and regenerate into transgenic sugi trees.

Genome editing tools, including zinc-finger nucleases, transcription activator-like effector nucleases, and CRISPR/Cas9, have emerged as powerful methods for targeted gene modification in animals, microorganisms, and herbaceous and woody plants [96]. In 2021, CRISPR/Cas9 was first applied to sugi [10]. In the first experiment, GFP-expressing sugi embryogenic cells were edited at the GFP locus, resulting in nucleotide insertions or deletions that quenched *GFP* expression in somatic embryos. In the second experiment, the CRISPR/Cas9 system targeted the magnesium chelatase subunit I (*CjChlI*) gene, producing regenerated transgenic sugi trees with chlorosis due to impaired chlorophyll synthesis.

Given the strong allergic impact of sugi pollen in Japan, efforts have also focused on developing pollen-free sugi trees using transgenic technology. The ectopic expression of barnase (a ribonuclease) and barstar (a barnase inhibitor) induces male sterility in transgenic sugi trees [97]. The *Arabidopsis thaliana* acyl-CoA synthetase 5 (ACOS5) protein is essential for sporopollenin synthesis in the pollen wall [98]. The sugi homolog (*CjACOS5*) was targeted using the CRISPR/Cas9 system [11]. Consequently, DNA deletions or insertions were detected in allelic *CjACOS5* genes. Transgenic trees with a biallelic *CjACOS5* mutation produced pollen-free male strobili. More recently, Cas9 codon optimization has improved genome editing efficiency in sugi [99].

Overall, genetic transformation and genome editing technologies in sugi have advanced substantially. These technologies are critical for functional gene analysis and new traits improvement, with future applications expected to mitigate pollen allergy syndrome and enhance growth, wood quality, stress tolerance, and forest management.

5. Photorespiratory Metabolism

Recent research has shown that photosynthesis-related metabolic processes in conifers, such as sugi, differ significantly from those in angiosperms with the C_3 photosynthetic pathway [100–102]. A major distinction lies in photorespiration, which is initiated by the oxygenation reaction of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the enzyme responsible for CO_2 fixation. Photorespiration generates CO_2 and ammonia (NH_3) through a series of reactions tightly linked to carbon and nitrogen metabolism. In angiosperms, chloroplast-localized glutamine synthetase (GS2) plays a central role in assimilating NH_3 released during photorespiration, as demonstrated in reverse genetic studies of barley and *Arabidopsis* mutants [103,104]. In contrast, GS2 is absent from conifer leaves and is thought to be replaced by cytosolic glutamine synthetase (GS1). This was first reported in *Pinus* species (Pinaceae) in the early 1990s [105,106] and was later confirmed in sugi (Cupressaceae) and other conifers through database searches and Western blot analyses [107,108].

Another key difference involves catalase (CAT), the enzyme that detoxifies hydrogen peroxide (H_2O_2), a reactive oxygen species generated during photorespiration. CAT is peroxisomal in angiosperms, with a carboxyl-terminal sequence that directs its transport into these organelles. This sequence diverges in conifers, implying altered subcellular localization [109]. In sugi, approximately 13% of total leaf CAT activity is localized in peroxisomes, suggesting that most of the enzymes are located elsewhere in the cell [109]. This low peroxisomal CAT activity may allow H_2O_2 to decarboxylate photorespiratory intermediates, increasing CO_2 release. Although this could increase carbon loss during photorespiratory metabolism, much of the CO_2 is likely recaptured by chloroplasts, thereby mitigating the effect.

Transcriptomic analyses of sugi revealed structural differences in photorespiratory enzymes compared with *Arabidopsis* homologs [110]. Notably, glycerate kinase (GLYK) in sugi showed the lowest sequence identity (49%) and similarity (84%) with its *Arabidopsis*

counterpart [102], suggesting distinct enzymatic properties and evolutionary divergence in conifer GLYK photorespiratory metabolism.

Recently discovered differences in the subcellular localization and amino acid structure of photorespiratory enzymes in sugi emphasize the distinct metabolism of conifers, potentially linked to their carbon–nitrogen usage strategies, ecological niches, and evolutionary history.

6. Genetic Studies

6.1. Genome Sequencing and Assembly

Conifer genomes are exceptionally large and rich in repetitive sequences [111], making assembly both challenging and costly. Early attempts to decode conifer genomes were hindered by high heterozygosity and the lack of sufficiently accurate long-read sequencing technologies. To reduce heterozygosity and facilitate assembly, a third-generational self-progeny of sugi (line Kunisaki-3, I-4-2, S3-3) was developed, achieving an estimated homozygosity rate of 0.96—among the highest reported in this species [12]. This strategy overcame major obstacles of outbred conifer genomes, including ambiguous haplotypes and excessive fragmentation, and enabled the construction of a high-contiguity sugi reference genome.

High-molecular-weight DNA was sequenced from the inbred line using PacBio HiFi (29× coverage) and Illumina short reads (26×) with Omni-C (Hi-C) library preparation. The de novo assembly with hifiasm produced 2651 contigs totaling 9.1 Gb (N50: 12.0 Mbp). The Hi-C scaffolding yielded eleven chromosome-scale sequences covering 97.6% of the genome. Structural accuracy was validated against a 7781-marker genetic linkage map, and assembly completeness was supported by high scores (Mercury: 94.95%, BUSCO: 91.4%).

6.2. Gene Expression and Functional Genomics

Research on the sugi transcriptome has progressed through successive technological phases, each contributing to gene expression data and functional insights. The first stage involved expressed sequence tag (EST) collection [112], with sequences obtained from the inner bark [113] and pollen grains [114]. These findings provided the earliest sequence-level information on sugi gene expression. A major advance followed with the construction of a full-length enriched cDNA library [115], which supported gene annotation and the development of specific markers [116]. This EST resource also enabled the development of microarrays for expression profiling [117–123]. Although these microarray platforms interrogated only the genes represented on the array, they include developmental stages, tissues, and various field conditions that have not yet been re-analyzed by RNA-Seq. By remapping the array probes onto the current SUGI_1 gene models, these legacy datasets can be re-used to complement RNA-Seq studies that are underrepresented in recent transcriptome data.

The adoption of RNA-Seq marked a turning point, enabling high-resolution transcriptome profiling across diverse tissues, developmental stages, and stress conditions [110,124–126]. Small RNA sequencing further broadened transcriptomic research, uncovering post-transcriptional regulation by micro RNAs (miRNAs) and small interfering RNAs (siRNAs) [127]. To integrate and standardize these datasets, the curated expression database SugiExDB was established [128], compiling both public and newly generated RNA-Seq data. This platform provides searchable expression profiles across tissues and conditions, serving as a valuable resource for gene discovery, functional annotation, and breeding applications in sugi. Transcriptome studies of reproductive traits have emphasized male sterility, leading to the identification of candidate genes at the *MS1* and *MS4* loci [81,129,130].

6.3. Genetic Diversity

Genetic studies of sugi have advanced in parallel with molecular marker development. Early investigations used isozyme and allozyme markers to reveal patterns of genetic variation across natural populations, providing foundational insights into population genetic diversity [131–133]. These markers were followed by microsatellite (simple sequence repeat, SSR) markers, which improved the resolution and analytical power due to their codominant inheritance and high polymorphism [116,134–136]. Later, high-throughput sequencing facilitated the discovery of extensive single-nucleotide polymorphism (SNP) datasets through approaches such as RAD-seq and transcriptome mining [82,129,137]. SNP markers now underpin genetic diversity, linkage mapping, and genome-wide association studies (GWAS).

At the within-population scale, microsatellites revealed clonal structures, particularly in old-growth stands, indicating that vegetative propagation contributes to the persistence of stands in snowy regions [138–140]. In seed orchards, marker-based paternity analyses revealed directional and occasional long-distance pollen flow [141,142]. At the species level, three varieties have been identified: Omotesugi (*C. japonica* var. *japonica*) and Urasugi (*C. japonica* var. *radicans*), distinguished by genetic markers. Urasugi, found in heavy-snow regions along the Sea of Japan, exhibits adaptive traits, including soft, pendulous branchlets and flexible foliage [143]. Two additional lineages have been discovered in cryptic northern refugia [144]. Moriguchi et al. [145] used targeted amplicon sequencing of 120 nuclear genes across 94 individuals representing four lineages to estimate divergence times (~0.85 Mya for the Yakushima split; ~0.32 Mya for the mainland lineages). Tsumura et al. [146] performed a genome-wide SNP analysis across natural populations, identifying loci potentially under climate-related selection. These results suggest that sugi have a genetic basis for local adaptation, which is relevant to forest management under climate change. Recent work by Uchiyama et al. [147] projected future genetic shifts using landscape genomic models.

Beyond the Japanese variety, the Chinese variety (var. *sinensis*) has drawn attention due to its ambiguous taxonomic and evolutionary position [15]. Cai et al. [16] examined seven ancient *C. japonica* var. *sinensis* populations using ddRAD-seq, reporting lower genetic diversity (H_O = 0.143) and higher differentiation (F_{ST} = 0.120) than in Japanese sugi. Li et al. [148] analyzed 14 nSSR markers and needle morphology, identifying three distinct geographic clusters and phenotypic divergence beyond neutral expectations, pointing to local adaptation in southern China.

6.4. QTL Analysis and GWAS

Early QTL studies identified loci linked to growth traits and male strobili production [149], providing initial genetic insights into quantitative trait variation in sugi. Tani et al. [150] developed a consensus linkage map of two pedigrees, strengthening the foundation for QTL mapping. Subsequent studies identified QTLs for male strobili production [151] and used GWAS to detect SNPs associated with wood properties and male strobili traits [152]. Hiraoka et al. [153] analyzed genome-wide SNP datasets in unrelated plus trees, identifying associations with growth, wood quality, and male fecundity, while also demonstrating the feasibility of genomic prediction in breeding populations. Multi-environment QTL analyses of growth, wood density, and heartwood color revealed significant genotype–environment interactions [154–156]. Simulation models evaluating genomic selection further provided a framework for integrating molecular data into conifer breeding strategies [157].

6.5. Radiation Breeding

Before the advent of molecular tools, sugi was used in pioneering radiation breeding experiments. Beginning in the mid-20th century, Kihachiro Ohba and collaborators irradiated seeds, seedlings, and cuttings with gamma rays, inducing somatic mutations [158–162]. These efforts yielded morphological and physiological mutants, including chlorophyll-deficient, waxless, and dwarf phenotypes. Cytological and physiological studies later detailed chromosomal abnormalities, variation in pollen fertility, and enhanced rooting ability in gamma-induced mutant lines [163]. More recently, Ueno et al. [164] assessed the genetic effects of chronic low-dose radiation following the Fukushima Daiichi nuclear power plant accident. Using parent–offspring RAD-seq analysis, they measured de novo mutation (DNM) rates in sugi trees exposed to up to 6.86 μGy h^{-1} and found no significant increase in DNM frequency, suggesting limited mutagenic effects of low-dose radiation on sugi.

6.6. Comparative Genomics and Phylogenetic Insights

Comparative genomics has provided key insights into conifer genome evolution. One of the earliest contributions was the construction of a chloroplast restriction map in sugi [165], followed by the publication of its complete chloroplast genome, which revealed structural divergence from other gymnosperms, particularly in inverted repeat content and gene order [166].

At the nuclear genome level, comparisons of sugi sequences with those of other conifers and model plants have revealed shared features, including large genome sizes, low gene density, and extensive repetitive element content. Kado et al. [167] sequenced seven nuclear loci and demonstrated species-wide polymorphism patterns. Subsequently, Kusumi et al. [168] revealed remarkably low synonymous substitution rates (~0.59×10^{-9} per site per year), underscoring the slow molecular evolutionary pace of sugi compared with angiosperms. Tamura et al. [169] analyzed random BAC clone sequences and identified an abundance of LTR retrotransposons, mainly from the Gypsy and Copia superfamilies. A chromosome-level genome assembly later provided a detailed comparative landscape across *C. japonica*, *Pinus tabuliformis*, and *Sequoia sempervirens*, showing that although all conifer genomes are universally repeat-rich, lineage-specific variation exists. Notably, sugi harbors a relatively high proportion of ancient, diverged LTR insertions compared with Pinaceae species [12].

At the chromosomal level, extensive rearrangements during conifer evolution were revealed by comparisons with Pinaceae [170], suggesting a major role for structural changes in diversification. More recently, comparative linkage mapping across *C. japonica*, *Chamaecyparis obtusa*, and *Thujopsis dolabrata* revealed both conserved synteny and lineage-specific rearrangements, providing new insights into the chromosomal evolution within the Cupressaceae family [171].

7. Future Perspectives

Remarkable progress has been achieved in the biotechnology, genomics, and functional biology of sugi. However, several areas remain open for future refinement. Although the current chromosome-level genome assembly is highly contiguous, it is not yet telomere-to-telomere (T2T). Gaps, particularly within repetitive and heterochromatic regions, may obscure structural variants or unannotated gene families. Moreover, the mitochondrial genome remains poorly characterized, and its integration into organellar genomics is essential for a more complete view of cellular and evolutionary dynamics [172,173].

In the post-genomic era, epigenomic regulation has emerged as a key area influencing gene expression, developmental plasticity, and stress responses [174–177]. Yet, comprehen-

sive studies of DNA methylation, histone modifications, and chromatin accessibility in sugi are lacking. Because SE and vegetative propagation are central to breeding programs, elucidating the epigenetic signatures of totipotent or embryogenic tissues will be especially valuable. It is also essential to develop efficient molecular markers to select cell lines with the greatest potential to produce high-quality embryos. In addition, an efficient methodology must be developed to induce embryogenic cells from the vegetative material of the selected adult trees. To our knowledge, no efficient, reproducible protocol has yet been published for inducing embryogenic cells from the vegetative material of adult conifer trees. Similarly, no positive results have yet been achieved in inducing embryogenic cells from the vegetative material of adult sugi trees and other Japanese conifers. Only sporadic and unrepeatable success has been achieved in inducing embryogenic cells and plantlets from shoot-disk explants of young sugi somatic plants (Figure 4) (Maruyama T.E., unpublished). These efforts could lead to improved reprogramming protocols and clonal propagation efficiency, thereby accelerating the improvement of conifer trees [8]. Advances in genetic engineering, including transformation and genome editing, are also expected to improve breeding strategies and deepen the understanding of conifer developmental and physiological processes, such as organogenesis, embryogenesis, and photorespiration metabolism.

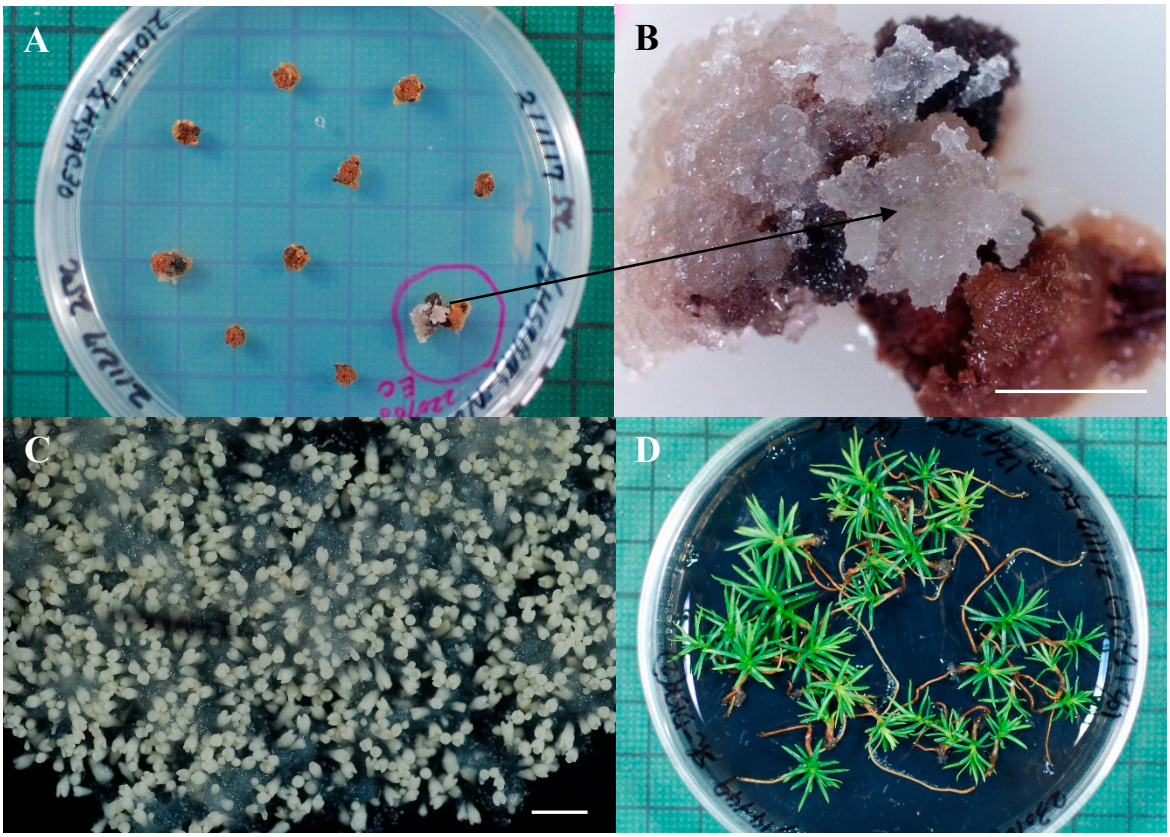


Figure 4. Somatic embryogenesis and plant regeneration from shoot-disk explants of young somatic plant of sugi (*Cryptomeria japonica*, Japanese cedar). (**A**) Embryogenic cell induction. The diameter of plate is 90 mm. (**B**) A close-up view of induced embryogenic cells; Bar: 5 mm. (**C**) Somatic embryo maturation; Bar: 10 mm. (**D**) Plant regeneration. The diameter of plate is 90 mm.

Another promising direction is re-examining inbreeding depression and deleterious allele accumulation using modern genomic tools. Previously, Ohba and colleagues conducted selfing experiments to generate homozygous mutants for genetic analysis [178–180]. These lines provide an opportunity to reexamine the genetic basis of inbreeding depression through whole-genome resequencing, mutation detection, and functional annotation. Rein-

terpreting these classical studies in a genomic framework could clarify the role of recessive lethals in fitness and breeding design.

Future advances in sugi research will rely on improving genomic resources, integrating multi-omics datasets (including epigenomics), and reevaluating classical genetics using modern tools. These efforts will accelerate tree breeding and conservation and reinforce sugi's position as a model tree for conifer genomics and forest biotechnology.

8. Conclusions

Sugi (*Cryptomeria japonica*, Japanese cedar) combines the tractability of a model species with the ecological and economic importance of a dominant forestry tree. Its exceptional traits—including wide adaptability, diversity, rapid growth, vegetative propagation capacity, and early flowering—enable efficient generational crossing. The integration of advanced genomic resources with modern biotechnological methods further establishes sugi as a premier model system for both fundamental research and applied breeding. Although using the sugi as a model system in plant research is just beginning worldwide, we believe it will accelerate our understanding of biological mechanisms in conifers. It will also serve as a platform for developing practical techniques to promote productivity and resilience in the face of global climate change.

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