


Review

Genetic Improvement of *Pinus koraiensis* in China: Current Situation and Future Prospects

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Abstract: *Pinus koraiensis* (Sieb.et Zucc) is an economically and ecologically important tree species, naturally distributed in northeastern China. Conservation efforts and genetic improvement for this species began in the 1960s and 1980s, with the establishment of several primary seed orchards based on range-wide provenance evaluations. The original breeding objective was to improve growth and wood yield, but during the recent decade, it was redefined to include other traits, such as an enhancement of wood properties, seed oil content, cone yield, and the development of elite provenance with families, clones, and varieties with good tolerance to biotic and abiotic stresses. However, improvement processes are slow due to a long breeding cycle, and the number of improved varieties is still low. In this review, we summarize the recent progress in the selective improvement of *P. koraiensis* varieties, such as elite provenance, family, and clones, using various breeding procedures. We collate information on advances in the improvement of *P. koraiensis*, based on conventional breeding and molecular marker-assisted breeding methods; identify gaps in our understanding of the tree improvement processes; and propose future research directions, which will provide new insight for subsequent genetic breeding research on *P. koraiensis*.

Keywords: *Pinus koraiensis*; cone yield; genetic gain; improved variety; breeding advances

1. Introduction

Pinus koraiensis (Sieb.et Zucc), an evergreen coniferous tree species belonging to the Pinaceae family, is an important afforestation tree species with high value for timber production in northeastern China [1,2]. Under natural conditions, it has a life span of over 1000 years and can attain a height of more than 40 m. Large-diameter timber of *P. koraiensis* is often processed for the manufacture of furniture, ships, and other materials. Its wood and seeds can also be used as industrial raw materials in food, cosmetics, medicine, and polymer material production, owing to its abundant polyphenols and resins [3,4]. Pine polyphenols also have various biomedical applications, including free radical scavenging, inhibition of lipid peroxidation, anti-inflammatory and analgesic properties, and antibacterial, antiviral, anti-cancer, anti-tumor, and anti-radiation actions. They can also play a role in lowering blood sugar, blood pressure, and blood lipids [5,6]. The nuts of *P. koraiensis* are edible and rich in fatty acids, proteins, carbohydrates, and other nutrients [7]. In addition, *P. koraiensis* is a strong pioneer species, which establishes successfully through natural succession, with significant ecological bearing in northeast China owing to its stable population structure and strong environmental adaptability.

The natural distribution range of *P. koraiensis* is mainly in northeast China, but there are few natural populations of *P. koraiensis* sporadically distributed in the Far East region of Russia, the Korean Peninsula, and Japan [8,9]. Its distribution from the Xiaoxinganling Mountains to the Changbai Mountains in northeast China includes more than half of *P. koraiensis* forests in the world (Figure 1). However, natural populations of *P. koraiensis* have declined sharply due to an increasing demand for timber. As a result, *P. koraiensis* was listed as a second-class nationally protected plant in the Chinese Red Data Book in 1999 [10] and a low-risk species in the 2013 International Union for Conservation of Nature (IUCN) red list [11]. Strategies for protection and utilization of its populations in China, genetic evaluation of natural populations, and establishment of a state-level improved genotype base were limited until the 1960s. Thereafter, major conservation efforts were implemented, followed by efforts at genetic improvement in the 1980s, with the establishment of several primary seed orchards based on range-wide provenance evaluations.

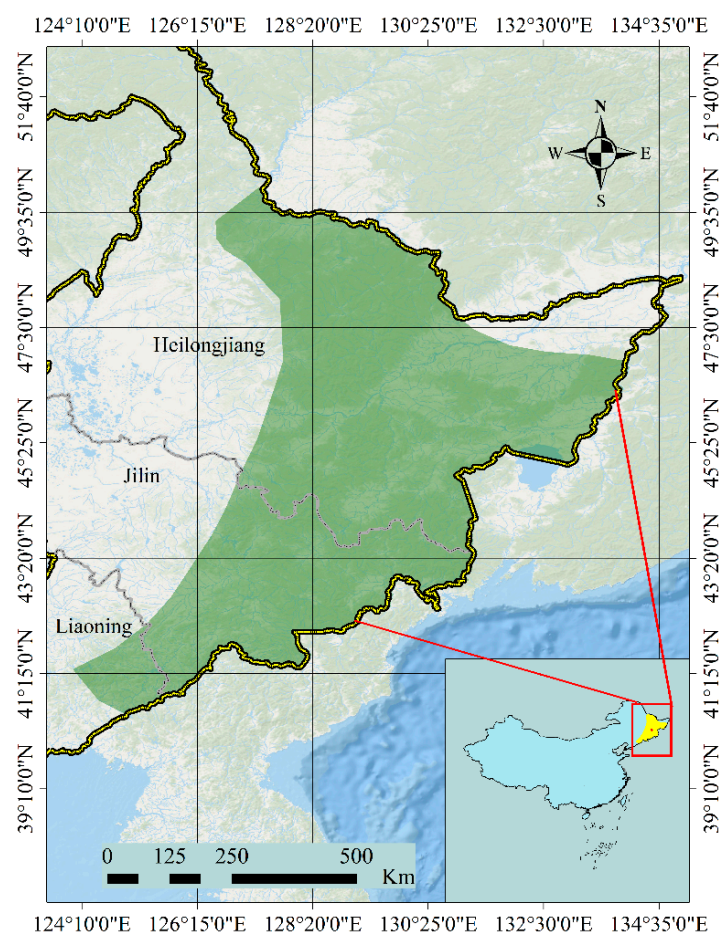


Figure 1. Distribution of *Pinus koraiensis* in China.

This review collates information on advances in the improvement of *P. koraiensis*, based on conventional breeding and molecular marker-assisted breeding methods, and to identify gaps in our understanding of tree improvement processes and propose future research directions. We also considered other related research works for improving the growth and regeneration of *P. koraiensis*, and highlight the achievements, challenges, and future directions in its breeding, with the aim to expedite the breeding cycle and achieve better genetic gain in targeted traits.

2. Research Progress on Conventional Breeding of *Pinus koraiensis*

Conventional plant breeding has been carried out for centuries, and remains in common use. Plant breeders select superior plants and cross them to create new and improved varieties, which increases their productivity and quality. The study of genetic and breeding improvement for forest trees had commenced later than for crops, and remains in the traditional breeding stage. Genetic improvement of *P. koraiensis* began in the 1980s, with the aim of improving tree yield and quality in order to increase economic and social benefits. Primary breeding objectives included the selection of genotypes with good timber quality, including fiber length, fiber width, lignin content, wood density, and stem straightness. With increasing awareness of *P. koraiensis*' value aside from timber production, breeding objectives were broadened to include improvements in cone/seed yield, carbon sequestration potential, and resistance to biotic stressors, such as disease. Consequently, several studies have been conducted to quantify variations in those traits among provenances and the selection of families and clones (Table 1). Provenance selection is an important breeding measure for forest improvement, and can provide rich breeding materials for forest genetic improvement research [12]. Because of the differences in geographical and climatic conditions, different provenances will yield natural variation in morphology, physiology, structure, and gene expression in long-term phylogenetic processes and natural selection in plants [13,14].

Table 1. Studies made on genetic improvement of *Pinus koraiensis*.

Study Level	Number	Trait	Name of Superior Provenances/Improved Varieties	References
Provenance	18	Growth, wood characteristics and carbon storage	Lushuihe, Linjiang, Dahailin	[15]
Provenance	23	wood characteristics	Caohekou, Wangqing, Dahailin	[16]
Provenance	17	Growth traits	Caohekou, Bajiazi, Changbaixian	[17]
Family	53	Growth traits and shape traits	115, 117, 138, 133, 112	[18]
Family	551	Growth, fruiting and resistance to disease	PK315, PK187, PK539, PK547, PK544, PK541, PK520, PK156, PK323, PK534, PK177, PK132, PK146, PK540, PK139, PK46, PK207, PK118, PK431, PK105, PK170, PK296, PK246, PK537, PK377, PK288, PK101, PK543	[19]
Family	68	Growth and fruit traits	50, 112, 107, 95	[20]
Clone	50	Growth traits	PK11, PK19, PK04, PK14, PK28	[21]
Clone	170	Growth and fruit traits	14, 84, 83, 138, 85, 82, 1110, 88, 123, 126, 820, 137, 81, 86, 11, 12, 810	[22]
Clone	50	Growth and wood characteristics	PK6, PK47, PK15, PK37, PK27, PK6, PK47, PK15, PK37, PK27	[23]

The natural variation of different geographical provenances is the result of interactions between plant heredity and the environment, which is of great significance to cross breeding and genetic evolution. Characterization of the natural variation in *P. koraiensis* has attracted extensive attention and a number of conventional breeding studies have been carried out on seed orchard establishment, provenance regionalization, geographical provenance testing, and selection of excellent provenances [24–26]. In a previous study, the natural distribution range of *P. koraiensis* was divided into three sub-regions based on the mountain region and latitude, including the northern sub-region (Xiaoxing'anling forest

region), middle sub-region (Wandashan, Zhangguangcailing forest region), and southern sub-region (Changbai Mountain forest region), with the provenance in the Changbai Mountains found to have the largest variation and an excellent genetic resource base [27]. On the basis of this division, a large number of provenance experiments have been carried out since the 1980s for the entire distribution of *P. koraiensis*, including Heilongjiang, Jilin, and Liaoning provinces, in China. Evaluation of the selected provenances was based on multiple breeding traits, with comprehensive selection in the same environment. For example, in the study of 24 *P. koraiensis* provenances distributed in the north-east Lushuihe Forestry Bureau area of Jilin Province, significant differences in the growth among provenances were observed, and the Lushuihe and Dahailin provenances were found to be the best [28]. For wood properties, certain radial variation patterns in wood parameters were observed among 26 provenances of 17-year-old tree individuals from the Maoershan Mountain, and the Caohekou provenance was judged to be optimal, followed by the Wangqing provenance [16,29]. This provided a theoretical basis for provenance selection of *P. koraiensis*. For carbon sequestration, Lushuihe, Linjiang, and Dahailin provenances were found to be the best of 18 in a 27-year-old Lushuihe forestry bureau area in Jilin province [15]. Overall, these provenance experiments have led to the selection of many excellent provenances plus helping to improve stand productivity and provide original materials for further selective breeding, cross breeding, ploidy breeding, and targeted improvement of genetic engineering. On this basis, a large number of primary seed orchards and 13 national-level key improved genotype bases for *P. koraiensis* were established to produce seeds with good genetic quality, which greatly increased the genetic gain in growth and provided improved genotypes (Table 2).

Table 2. Distribution of national-level *Pinus koraiensis* improved variety bases in China.

Codes	Establishment Time of Base	Location	Longitude	Latitude	Altitude (m)	Improvement Base
L1	1974	Benxi, Liaoning	124°12'33.80"	41°26'59.87"	276	Primary
L2	1968	Benxi, Liaoning	124°20'57.16"	40°10'50.76"	616	Primary
J1	1972	Wangqing, Jilin	129°45'37.57"	43°19'47.93"	320	Primary
J2	1958	Tonghua, Jilin	125°33'41.71"	41°52'57.50"	543	Primary
J3	1985	Longjin, Jilin	129°45'20.18"	42°42'11.96"	164	Primary
J4	1984	Baishan, Jilin	127°48'30.16"	42°31'36.87"	745	Primary, 2 generation
J5	1978	Linjiang, Jilin	126°50'55.32"	41°45'12.02"	324	Primary
J6	1989	Baishan, Jilin	126°49'06.24"	42°36'12.41"	606	Primary
H1	1958	Ningan, Heilongjiang	128°42'29.24"	44°10'33.05"	585	Primary
H2	1965	Hegang, Heilongjiang	130°13'59.02"	47°24'25.03"	197	Primary
H3	1978	Jiamusi, Heilongjiang	130°40'47.06"	46°25'46.80"	201	Primary
H4	1973	Yichun, Heilongjiang	130°13'61.05"	46°50'08.12"	465	Primary, 2 generation
H5	1981	Shangzhi, Heilongjiang	130°13'62.21"	44°40'21.72"	398	Primary, 1.5 generation

Selective breeding, a conventional breeding method, has the function of controlling the direction of variation, promoting the accumulation of variation, and increasing and creating important economic traits, which can eventually improve important information for tree genetic improvement [30]. Family and clonal selection is an effective means of tree genetic improvement, which is crucial for improving the yield, wood characteristics, and stress resistance of forest trees. Family selection is based on the phenotypic value of a family while clonal selection is a genetic improvement method based on asexual

reproduction techniques, which can yield greater genetic gain. There are abundant variation patterns among families, clones, and individuals, and within individuals in *P. koraiensis* natural forests [11,31]. Recently, the use of clones for directed cultivation of plantations has yielded successful outcomes for species, such as *Pinus radiata* [32], *Dalbergia sissoo* [33], *Juglans regia* [34], and *Populus deltoides* [35]. Since the 1980s, more than 20 *P. koraiensis* clonal seed orchards have been established based on provenance and tree selection, and the first clonal seed orchard was flowered and fruited. Many excellent families and clones of *P. koraiensis* have been screened for various traits, including growth, wood properties, seed yield, and others [36]. Regarding growth and fructification properties, Wang et al. [20] investigated tree height, diameter at breast height (DBH), and seed yield in 68 half-sib families in the *P. koraiensis* seed orchard in Wangqing, and selected four families with optimized traits. Jiang et al. [22] measured the height, DBH, and seed traits of 170 Korean 38-year-old pine clones in Linjiang Forest Farm in the Linjiang Forestry Bureau area of Jilin Province, and selected 17 excellent 38-year-old clones. Liang et al. [21] measured and analyzed the growth and wood traits of 50 *P. koraiensis* clones in the Kaishanyu Forest Farm of Longjing City, Jilin Province, and selected five excellent clones.

In recent years, multi-character selection and directional selection have become significant strategies for the selection and breeding of superior tree species. The selection and breeding of new varieties with fast growth, high yield, high timber quality, and strong resistance is an effective means of improving productivity and expanding the forest resources of *P. koraiensis*. However, progresses in the selection and breeding of improved varieties were slow due to limited genomic information and a longer breeding cycle. A few recent studies have been conducted to carry out cross breeding of *P. koraiensis* [37,38], but they have not reported on new excellent hybrids cultivated by cross-breeding technology. Owing to the difficulty in asexual propagation of *P. koraiensis*, such as cuttings, tissue culture, and somatic embryogenesis, the establishment of seed orchards is considered the main approach for genetic improvement and high genetic quality seed production of *P. koraiensis*. Many conventional breeding processes for *P. koraiensis*, including superior provenance and family and clonal selection, are based on seed orchards. As the main means of forest tree seed production, seed orchards can improve the genetic gain of forest trees' growth and improve the genetic quality of seeds, which is of great significance to forest tree germplasm innovation [39,40].

3. Research Progress on Molecular Breeding of *Pinus koraiensis*

Advanced molecular and genomic tools, such as molecular markers, expressed sequence tags (ESTs), microarrays, and genetic transformations, enable exploration of the genetic basis of biotic and abiotic stress tolerance, leading to the development of improved cultivars. Recent developments in DNA marker technology have helped to develop the concepts of quantitative trait loci (QTL) mapping, marker-aided selection (MAS), and genetic transformation to produce plants of superior quality. In addition, molecular markers can be used to assess genetic diversity, fingerprinting genotypes, separating hybrids from self-crossed progeny, and other uses. Thus, genetic information is important for studying the evolutionary history and genetic improvement of forest trees. However, due to the lack of whole-genome information in *P. koraiensis*, there have been few studies on its molecular genetics.

3.1. Genetic Structure and Genetic Diversity

Pinus koraiensis is an allogamous hermaphroditic tree species with high heterozygosity and a complex genetic background. In the absence of genomic information, analysis of its natural population structure and genetic diversity is required to rationally formulate a genetic conservation strategy. DNA molecular markers are now widely used in many aspects of research, including population structure, genetic diversity, and genetic relationship and fingerprint mapping. Molecular markers have been used to explore the population structure and genetic diversity of natural populations and clonal

seed orchards of *P. koraiensis*, including single primer amplification reaction (SPAR) [41,42], random amplified polymorphic DNA (RAPD) [43,44], inter-simple sequence repeat (ISSR) [45–47], chloroplast microsatellites (cpSSRs) [48], and expressed sequence tag-simple sequence repeat (EST-SSR) [49,50]. Compared with other molecular markers, simple sequence repeat (SSR) markers are characterized by simple operation, good reproducibility, rich polymorphism and co-dominance, and are effective for genetic diversity analysis. Using nine polymorphic nuclear SSRs, Tong et al. [51] evaluated the genetic diversity and population structure of seven populations of *P. koraiensis* located throughout its native distribution and found high genetic diversity in all populations, with an average expected heterozygosity of 0.610. The northern-most populations (Dailin and Fenglin) showed slightly higher diversity than the other five populations. Yu et al. [52] researched the genetic diversity of *P. koraiensis* in northeast China using SSR molecular markers developed by magnetic bead enrichment, and found that its genetic variation mainly existed within the population. Researchers also successfully developed 20 microsatellite markers for *P. koraiensis* using AFLP of sequences containing repeats [53], and used these to study the genetic diversity and population structure throughout the natural distribution area of China. Studies have shown that the genetic diversity of natural *P. koraiensis* populations in northeast China is higher, but gene flow among the populations is low, and there is a degree of genetic differentiation within populations consistent with the weak differences observed among populations of other wind-pollinated gymnosperms [54]. In addition, some studies have found that due to geographic restrictions and gene flow during the Penultimate Glacial Period, the genetic diversity of *P. koraiensis* in Zhangguangcailing Mountains and Lesser Khingan Mountains is relatively high, forming a shelter for natural *P. koraiensis* populations [46]. However, using maternally inherited mtDNA, Aizawa et al. [55] demonstrated that the continental populations exhibited no diversity in mtDNA despite the species' current extensive range and large populations.

3.2. Transcriptomics

Transcriptome sequencing is an important method of analyzing genes related to important phenotypic traits, such as seed germination, flowering and seed setting, and stress resistance, and provides significant references for research on plant functional genes, molecular marker development, and genetic improvement of germplasm resources. Due to its advantages of high throughput, high sensitivity, and low cost, transcriptome sequencing technology has been applied to many plants, including *Oryza sativa* [56], *Camellia sinensis* [57], *Pinus halepensis* [58], and *Acer miaotaiense* [59]. However, there have only been a few transcriptomic studies on the genetic improvement of *P. koraiensis*. Using transcriptome sequencing of various tissues, Zhang et al. [60] analyzed the expression of genes related to secondary metabolites in the growth and development of *P. koraiensis*, and developed a large number of EST-SSR markers. Liu et al. [61] explored the related genes of polyphenol synthesis by transcriptome sequencing technology during the development of adventitious buds, which provided a theoretical basis for further development and utilization of polyphenols.

3.3. Construction of Genetic Map

A genetic linkage map is constructed using genetic markers of polymorphisms and the exchange rate of two loci. It can be used in genetic analysis and gene mapping on many important traits and is a powerful tool for plant breeding and gene transduction. With the continuous development of sequencing technology, the construction of genetic linkage maps has been widely used in model plants. However, few of these have been developed for many non-model organisms, especially in the genome research of the Pinaceae. Chen et al. [62] constructed the first genetic linkage map of *P. koraiensis* using molecular markers, such as SRAP, SSR, ISSR, and AFLP, and conducted dynamic QTL mapping for the basal diameter and tree height using a large number of loci.

4. Other Related Research Works on *Pinus koraiensis*

Several physiological studies focusing particularly on photosynthesis have been carried out on *P. koraiensis*. Photosynthesis is an important plant physiological trait, and largely determines growth and development processes and environmental adaptability [63,64]. Key photosynthesis characteristics include the stomatal conductance, net photosynthetic rate, transpiration rate, and intercellular CO₂ concentration [65,66]. The strength of photosynthesis is closely related to genetic characteristics, and is also affected by external environmental factors, such as temperature, light, and humidity [67–70]. In *P. koraiensis*, photosynthetic characteristics were investigated in relation to nitrogen utilization [71], different light conditions [72], various stress treatments [73], CO₂ concentration changes [74], and needle age [71]. These studies provide theoretical basis for comprehensive evaluation of *P. koraiensis* clones and the selection of genotypes and economic traits. It should be noted that photosynthesis is closely related to growth and development, which in turn indirectly affects the survival rate of seedlings and fruiting of large trees [75]. Interestingly, *P. koraiensis* has a variable demand for light, wherein its light requirements increase with aging [76,77]. Sun et al. [78] reported that *P. koraiensis* seedlings acclimate to forests with relatively weak light intensity by adjusting the morphological characteristics of their needles. Changes in leaf morphology lead directly to corresponding changes in leaf area, which in turn affects the photosynthesis rate of leaves. Zhu et al. [79] found that photosynthesis in *P. koraiensis* needles of different ages plays a cumulative role during the growing season in such a way that annual needles most strongly affected photosynthesis in the early stages of growth while current year needles were the greater determinant in later growth stages. Furthermore, there is intra- and interspecific variability in photosynthesis parameters as well as among different clones of *P. koraiensis* [80,81].

5. Research Gaps and Future Research Directions

Considerable conventional breeding work has been carried out over the last three decades, including evaluation of provenance and genetic variations, selection of elite families and clones, establishment of seed orchards, and improvement of propagation techniques. However, the pace of developing improved varieties is still slow. To accelerate the genetic improvement process of *P. koraiensis* in China, future breeding programs should aim to shorten the breeding cycle, collect and evaluate germplasm resources, carry out comparative experiments, improve high reproductive efficiency, and combine molecular marker-assisted selection and multi-trait improvement.

Germplasm resources are important materials for forest breeding, particularly for studying the origin and evolution of plants and cultivating new varieties of plants. Because *P. koraiensis* has historically been mainly used for timber production in northeastern China, the main breeding objective was the genetic improvement of wood properties, including lignin content, cellulose content, and cellulose length. Large-scale exploitative harvesting of natural forests has resulted in a significant loss of resources and a lack of natural germplasm resources of *P. koraiensis*. Collection and evaluation of natural germplasm resources, along with analysis of the genetic structure and genetic diversity of natural populations among geographic distributions, are urgently needed. In addition, a large-scale comparative experiment of different provenances, families, and clones of *P. koraiensis* should be conducted to select and cultivate a number of improved varieties to improve the actual genetic gain in important economic traits. Given global climate change predictions and associated risks from pests and diseases, it is of paramount importance to evaluate new germplasm collections for potential resistance to pest and disease outbreaks.

Seed orchards are important for improving the selection of varieties as a fundamental material and also for their momentousness value in the genetic improvement of forest trees. At present, research on *P. koraiensis* seed orchards mainly focuses on growth, wood quality, and cone/seed traits as well as seed orchards' upgrading, which lays the foundation for genetic and further orchard development. However, there are still some problems in the genetic improvement of seed orchards of *P. koraiensis*. Increased collection and evaluation of additional germplasm resources from natural *P. koraiensis* populations is still required. Additionally, the seed yield in the *P. koraiensis* seed orchards is low due to

the lack of superior provenance and a long growth cycle, and since plantation quality after afforestation is poor, it is unable to meet the growing demand for seed production. Provenance experiments have not been completed, and most *P. koraiensis* seed orchards are still at the primary level. Advanced generation seed orchards have not been established for scientific development of long-term breeding strategies. Unfortunately, the work of collecting cones is dangerous and expensive in the annual production process due to the height of *P. koraiensis*; Finally, there is a lack of national-level improved varieties and low use ratio for existing improved varieties. Therefore, it is necessary to cultivate improved varieties and further upgrade the current seed orchards. In the future, the main breeding work for genetic improvement of seed orchards should include the establishment of germplasm resource banks and evaluation of germplasm resources. Studies on height growth control, including the selection of natural dwarf individuals, could overcome the difficulty in collecting cones. For cone traits, orchards could be established by collecting trees from natural forests or seed orchards to produce a large number of high-quality scions. Further, work should also be carried out on the selection and breeding of improved clones based on the cone and seed traits as well as resistance to pests and disease. Improved and advanced generation seed orchards based on natural forests or primary orchards, good provenance, families, and clones can improve the yield and quality of seed orchards. In addition, practical experiments should be developed to increase the flowering rate and seed/fruit set percentage by different treatments, such as hormones, girdling, and fertilizer application, and their combinations. Finally, an evaluation of the photosynthetic efficiency of different provenances, families, and clones should be further studied in order to obtain genetic improvement of *P. koraiensis* resources. Transcriptome research on *P. koraiensis* is slow compared with model plants, such as *Arabidopsis thaliana*, rice, and *Populus trichocarpa*, and there is a need for more comprehensive, systematic, and in-depth studies in the future.

These breeding objectives may be difficult to achieve in a reasonable time with conventional breeding due to the fragmentation of natural *P. koraiensis* populations, long reproductive cycle, high genetic heterozygosity, and unclear genetic mechanism of important traits. Molecular breeding could help circumvent this problem, and molecular breeding could play a significant role. In the past decade, molecular biology studies have been initiated in *P. koraiensis*, especially DNA molecular markers, which have contributed to characterizing genetic diversity and the construction of genetic maps. However, there are still gaps in our understanding of the molecular breeding of *P. koraiensis*. Functional genes related to some important traits have not yet been discovered, and the work for whole genome sequencing of *P. koraiensis* is incomplete. Multi-omics analyses, such as transcriptomics and metabolomics, are also lacking, and much genetic information of gene expression regulation networks has not been completely characterized. QTL mapping and genome-wide association analysis of important traits, such as cone, seed, needle, and wood properties, have not been carried out based on various molecule markers, and the relevant mechanisms governing these traits is still unclear. Finally, a genetic transformation system has not yet been established, and relevant research has not yet been carried out. Future research should focus on these issues to lay the foundation for marker-assisted breeding work on *P. koraiensis*.

Genetic improvement strategies for *P. koraiensis* should combine both conventional breeding and molecular marker-assisted breeding (Figure 2). Since previous genetic improvement works were based on seed orchard materials and focused on growth and wood quality traits, new germplasm collections from natural populations should be developed. New germplasm should be evaluated for cone/seed characteristics as the main economically important traits. Parallel to traditional breeding using provenance, family, clones, and cross breeding, genomic selection and marker-assisted selection should be applied to speed up the breeding cycle. Thus, the selected improved varieties will greatly improve the genetic gain of important economic traits, solving the demand for cones/seeds and wood and helping to achieve sustainable development in the *P. koraiensis* industry.

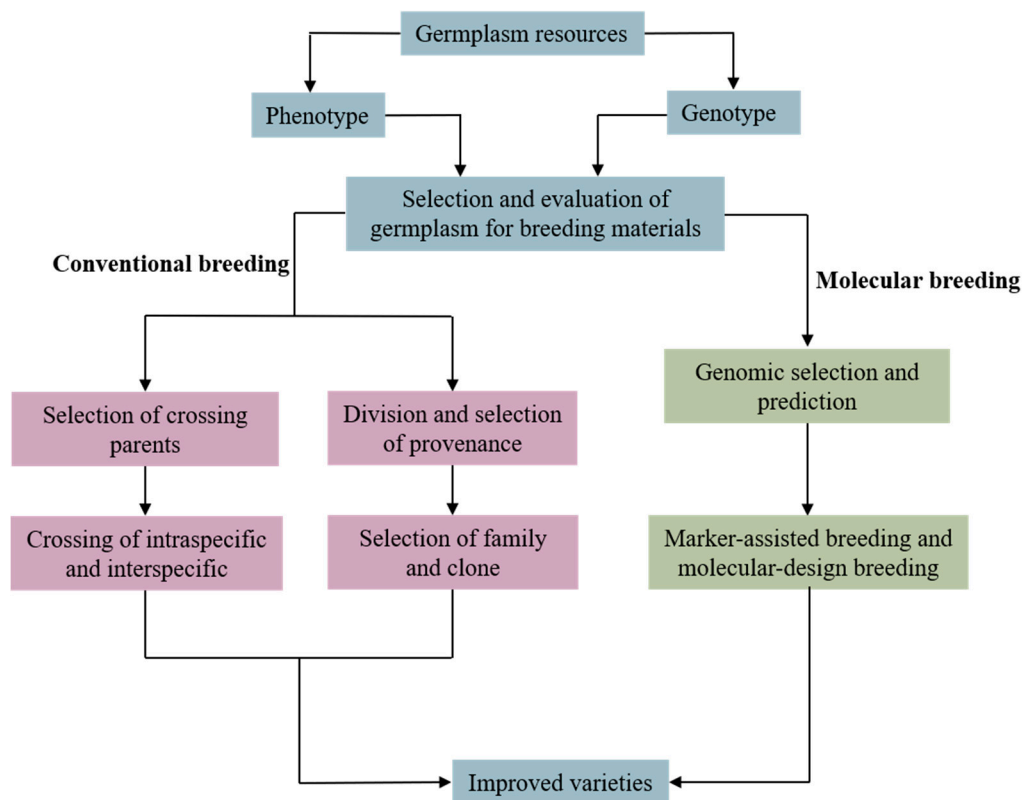


Figure 2. Genetic improvement strategies for *Pinus koraiensis*.

6. Conclusions

Natural *P. koraiensis* populations provide wood, cones/seeds, and forest by-products, and play an important ecological role in China. Considerable traditional breeding work has been carried out and several excellent families and clones were selected to improve the genetic gain in growth, wood quality, and cone/seed yields. Most of this selection work has been conducted using seed orchard materials, which were initially established based on growth traits. However, breeding progress regarding these important traits is still slow due to a long breeding cycle, and the number of improved varieties is low. To shorten the breeding cycle and improve breeding efficiency, the use of genomic selection and marker-assisted selection (MAS) will have huge potential for improving important economic traits, such as wood properties, cone/seed yield, and biomass. However, further studies are required to design molecular breeding in *P. koraiensis*, including the construction of a high-density genetic map and genome-wide association study (GWAS) based on polymorphic molecular markers, as well as whole genome sequencing. These issues need to be addressed in future research, particularly using new germplasm collections from natural populations, since previous seed orchards were established based on growth traits only.

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