

Population and Evolutionary Genetic Studies of Five-Needle Pines in Russia

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Three species of stone pines are native to Russia: Siberian stone pine (*Pinus sibirica*), dwarf Siberian pine (*P. pumila*), and Korean pine (*Pinus koraiensis*). Genetic differentiation by allozyme loci placed *P. sibirica* in one clade with European stone pine (*P. cembra*), whereas the Far Eastern species *P. pumila* and *P. koraiensis* represent another lineage more closely associated with the Asiatic white pines that have winged seeds: *P. armandii*, *P. parviflora*, and *P. wallichiana*. Molecular data on the large divergence of *sibirica*–*cembra* and *pumila*–*koraiensis* clades are supported by analysis of needle anatomy. The taxonomic position of the North American stone pine (*P. albicaulis*) is intermediate between the Asiatic stone pines and the North American white pines *P. flexilis*, *P. monticola*, and others.

In the central parts of their ranges, stone pine gene pools are subjected to integrating factors: extensive gene flow and balancing selection in similar environmental conditions. Populations at the margins of their range experience differentiating forces: genetic drift, disruptive selection, and gene exchange with related species. When analyzing natural populations and clonal archives of *P. sibirica* ecotypes, we observed significant correlations between frequencies of particular alleles at allozyme loci and geographic coordinates as well as climatic conditions. Analyses of multilocus genotypes showed good correspondence with recognized forest seed zoning, in many cases refining borders of seed zones, regions, and subregions. The sympatry zone between *P. sibirica* and

P. pumila is characterized by interspecific gene exchange through hybridization with bidirectional gene introgression of nuclear and mitochondrial markers. More genetically similar *P. pumila* and *P. koraiensis* do not form a hybrid zone. Formation of stone pine lineages and species putatively included multiple events of reticulate evolution. Analysis of allozyme and simple sequence repeat loci has proven that multi-trunk forms in *P. sibirica* and clumps in *P. pumila* are different genotypes (but often related as half-sibs) and therefore represent the result of germination of several seeds from the caches of nutcrackers (*Nucifraga* spp.). A substantial level of heterozygote deficiency was recorded in several *P. pumila* stands that were characterized by a low ratio of plant height to the square of a clump. This indicates inbreeding, reflecting a high proportion of selfing and consanguineous mating due to the high probability of sedimentation of the pollen cloud within a clump of genetically related individuals.

In response to global climate change, it is evident that treelines for major stone pine species are shifting to the north on the plain and upslope in subalpine mountain belts. Descriptions of local populations and inventories of genetic resources of stone pines are urgently needed to ensure conservation of among- and within-species genetic diversity. Formation of genetic collections and seed banks should be based on knowledge of the genetic structure of populations at different types of markers (nuclear, cpDNA, mtDNA) and candidate genes responsible for adaptation and economically important traits.

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