

IMPROVEMENT OF LARCH (LARIX SP.) FOR BETTER
GROWTH, STEM FORM AND
WOOD QUALITY

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BIODIVERSITY OF SIBERIAN LARCHES

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Abstract

The results of inter- and intraspecific biodiversity researches of the *Larix* species in Siberia have been given. The materials about variability and polymorphism of these species on morphological, karyological and biochemical features are reported.

Biodiversité des mélèzes sibériens

Les résultats des recherches sur la biodiversité intra- et inter- spécifique des espèces de mélèzes en Sibérie sont donnés dans cet article. Cette étude présente des résultats sur la variabilité et le polymorphisme de ces espèces sur base de caractères morphologiques, karyologiques et biochimiques.

Introduction

Larch is the main forest forming species of Russia. The larch forests occupy the area of 254 mln. ha which makes about 40% of the total forested area of Russia. Growing stock is about 25.4 billion m³ which makes more than 34% of the whole Russian growing stock. Therefore the problems of systematics and generally of the larch biological diversity are of great scientific and practical importance. Unfortunately, differentiation of the *Larix* genus is vague. It is considerably explained by the fact that the main criterion of species, namely the reproductive isolation of larch, shows itself weakly, and they tend to hybridize easily under natural conditions. Up to the present time there is no consensus even on number of species. V. N. Sukachev (1924) recognized and described 14 species, V. L. Komarov (1934) reported of 25 species, N. V. Dylis (1961) mentioned 20 species, E. G. Bobrov (1972, 1978) distinguished 16 species.

Material and Methods

These studies were based mainly on two approaches: analysis of the *Larix* species population structure and study of established experimental objects (provenance trials and others). Studies were carried out in complex, by different specialists (forest plant breeding, karyology, biochemical genetics). Material from natural populations of the *Larix* were used for karyological studies. Standard techniques with own modification and methods of cytological analysis have been used. Seeds were germinated under laboratory conditions. Germinating seeds were pretreated in 0.5% colchicine solution for 6-8 hours, fixed in 3:1 ethanol:acetic acid mixture and stained with acetohematoxylin. Root tip meristem cells were used for study, and slides were prepared using the squash technique. Seeds collected in natural population also were as a material for electrophoretic analysis of the *Larix* species. Method of electrophoresis in 13-14% starch gel was used. The level of genetic variability in population was estimated using several generally accepted parameters: P - percentage of polymorphic loci, A - number of alleles per locus, He and Ho - expected and observed heterozygosity. Genetic distance coefficient D (Nei, 1972) was used as a measure of genetic differentiation.

Results and Discussion

At present four larch species naturally growing in Siberia are described: *Larix sukaczewii* Dylis (= *L. russica* (Endl.) Sabine ex Trautv.), *L. sibirica* Ledeb., *L. gmelinii* (Rupr.) Rupr., *L. cajanderi* Mayr. The half of these species (*L. sukaczewii*, *L. cajanderi*) are not universally recognized as taxons and are the subject to be discussed among the specialists. Besides, the following hybrid complexes of larch are distinguished: *L. sukaczewii* x *L. sibirica*, *L. sibirica* x *L. gmelinii* (= *L. czekanowskii* Szaf), *L. gmelinii* x *L. cajanderi*] (Abaimov et al., 1998).

The description of the main *Larix* species in Siberia should be started with the most known species - *L. sibirica*. Stands of this larch species occupy nearly 14% of the larch forest area in Russia. Their highest concentration is in the continental mountain regions of southern Siberia which are characterized by low humidity. *L. sibirica* is found in the sites with colder temperature as compared to *L. sukaczewii* sites. But in contrast with *L. gmelinii* it is less resistant to low temperatures. The boundary between *L. sibirica* and *L. gmelinii* coincides with the south-western timberline of the permafrost zone.

L. sibirica is not similar in its ecological and morphological features over its vast areal and forms some intraspecific taxons. Generalized results of our study as well as numerous literature data allow us to describe these taxons, though their rank was interpreted by different scientists variously (subspecies, ecotypes, varieties). And although all these names of taxons conceptually are similar, we use the term "variety" to unify the intraspecific systematics of *L. sibirica*.

L. sibirica has following varieties: *rossica* (the northern and north-eastern regions of the European part of Russia, west of the Urals); *obensis* (the Ob river basin, except the Altai region); *altaica* (the Altai region); *jenisseensis* (the Yenisei river basin); *sajanensis* (the Eastern Sayan); *polaris* (northern Siberia including Arctic regions); *lenensis* (the upper Lena river basin and regions of the Irkutsk Priangarie); *baicalensis* (the south-western and south-eastern Baikal coasts); *transbaicalensis* (the western Zabaikalie mountains). Some of these varieties were transformed in certain way. Particularly, var. *rossica*, and substantial part of var. *obensis* were combined by N. V. Dylis (1947) into independent *L. sukaczewii*.

L. sukaczewii still remains a debatable species though it is described in many dendrological summaries. On the one hand, there are many evidences showing that *L. sukaczewii* differs from *L. sibirica* in many morphological and biochemical features (Deryuzhkin, 1970; Iroshnikov, 1980, and other publication). On the other hand, there are serious objections against distinguishing of *L. sukaczewii* as of an independent species. In particular, the scientists of our laboratory (Myliutin et al., 1993) showed the absence of considerable genetical and karyological differences of *L. sukaczewii* from *L. sibirica*. E. G. Bobrov (1972, 1978) even concluded that *L. sibirica* and *L. sukaczewii* "can not be distinguished from each other by their morphological, geographical, genetical, coenotal and caryological features...". Surely, such a conclusion is too vigorous. There are some particular differences between *L. sukaczewii* and *L. sibirica*: morphological differences, geographical isolation, distinctions in ecology, but the problem remains debatable whether they are profound enough to consider *L. sukaczewii* as a separate independent species.

This situation is mainly due to the fact that initially *L. sukaczewii* was distinguished by N. V. Dylis (1947) mainly according to quantitative characteristics, which show a large overlap of amplitudes of variability in *L. sibirica* and *L. sukaczewii*. Later N. V. Dylis (1981) described some specific differences in qualitative characteristics as well; however, the majority of these characteristics also show large variations which makes diagnostics of species difficult. It was noted in one of our papers that such characteristics as the length of bract scales deserves special attention. These scales of *L. sukaczewii* are usually small and hardly visible, but the ones of *L. sibirica* are long and easily seen. In opinion of Canadian palaeobotanists B. A. LePage and J. F. Basinger (1991), two different groups of species were formed in the evo-

process of *Larix* genus, one of them having short bract scales and another having long

However, recently an information (Kisanuki et al., 1995) appeared that even within one form (*L. leptolepis*) these two forms are encountered, namely, one with short bract scales and another with long ones; it means that intraspecific variability is observed in this characteristic as well.

L. sukaczewii occupies certain rather limited habitats in the north-eastern regions of the European part of Russia, in the Urals and western Siberian regions bordering with the Urals. Its stands occupy only a small area, about 0,1% of larch forest area of Russia. In the «ВРЯ» of some researchers (Dylis, 1947; Iroshnikov, 1980) the zone of natural hybridization of *L. sibirica* and *L. sukaczewii* is located in the lower Ob river. However, nobody has ever observed geographical spreading of hybrids, probably because of difficulties with the diagnosis not only of these hybrids, but of their parent species themselves as well.

Proceeding to the description of *L. gmelinii*, we should remember the statement of N. V. Dylis (1961) that for the whole history of studies of this larch species its specific independence is never subject to either doubt or negation. Moreover, the studies of V. N. Sukachev (1964) and B. P. Kolesnikov (1946) showed that *L. sibirica* and *L. gmelinii* were very far from each other in *Larix* genus system and that they belonged to different species series of the genus.

It should be added that many studies, including ours, showed that *L. sibirica* and *L. gmelinii* were also specific in their ecology. As it was mentioned above, the southwestern limit of *L. gmelinii* areal greatly coincides with the permafrost border. Besides, *L. gmelinii* areal scarcely coincides with areals of other species: *Pinus pumila*, *Betula middendorffii* etc., and *L. sibirica* areal coincides with *Abies sibirica* and *Pinus sibirica* areals. Agreement of the areal as well as phytocoenotic relations of *L. sibirica* with one group of species, and those of *L. gmelinii* with the other group points out to the difference of historical conditions responsible for forming of these species.

Both *L. gmelinii* and *L. sibirica* form various types of forest stands. In the mountainous southern Siberia 172 larch forest types formed by *L. sibirica* are distinguished. Only in Eastern Zabaikalie I. I. Panarin (1965) distinguished 50 forest types formed by *L. gmelinii*. Stands of *L. gmelinii* (without *L. cajanderi*) comprise about 35% of the larch forest area in Russia. Considering intraspecific differentiation of *L. gmelinii*, we should first concentrate on *L. cajanderi*. Distinguished by H. Mayr (1906) as a species, it was not recognized as one by V. N. Sukachev and his successors (Dylis, 1961; Pozdnyakov, 1975). N. V. Dylis (1961) described it as an eastern subspecies of *L. dahurica* ssp. *cajanderi* (in parallel with the western subspecies of *L. dahurica* ssp. *dahurica*).

E. G. Bobrov (1972, 1978) restored the species rank for *L. cajanderi*. The specific status of *L. cajanderi* is supported by I. Yu. Koropachinsky, and most actively by scientists of our Institute of Forest - A. P. Abaimov (Abaimov, Koropachinsky, 1984), E. N. Muratova (1995), etc. While avoiding the discussion of this problem here, we'd like only to express our opinion that for the moment there are no strong arguments in favour of *L. cajanderi* specific status. *L. cajanderi* stands take nearly a half (48%) of larch forest area in Russia. This larch grows under severe conditions of the Siberian North-East where it meets almost no competitors — among other forest forming species.

Intraspecific differentiation of *L. gmelinii*, except the already mentioned western and eastern subspecies interpreted by N. V. Dylis, is not enough developed yet. Here we can only mention an ecotype growing under xerophytic conditions of the Zabaikalie region, which was distinguished by V. A. Povarnitsyn (1949). Certain deviations from the type were noted by different researchers; they were separated from *L. gmelinii* and ranked as independent species or local complexes. However, even if we consider *L. gmelinii* as it was understood by E. G. Bobrov (1972), namely without taxa derived from the species (for instance, *L. x amurensis* etc.) naturally it will not appear homogeneous within its vast area. Growing under different

natural conditions in such regions as Taimyr, Evenkia, West Yakutia, Zabaikalie and oиeнИ *L. gmelinii* of course must be differentiated into smaller intraspecific taxons differing in various features and properties. However, the fact of this species having been studied insufficiently (as it is of *L. cajanderi*) does not allow us presently to make its differentiation accurately enough.

As it was mentioned already, some interspecific hybrid complexes were distinguished within *Larix* genus. *L. x czekanowskii*, the hybrid complex in the contact zone of *L. sibirica* and *L. gmelinii*, is the mostly studied. The hybrid populations are usually comprised both by hybrid individuals and by representatives of one and sometimes two parent species. As a rule, morphological features of hybrid trees are combinations of the features of parent species, but sometimes they have new characteristics, which the parent species do not have. The mass populational heterosis in hybrid populations is not observed while some small part of trees (few per cent) shows distinct somatic heterosis. Under certain conditions the reproductive heterosis is observed as well.

Discussing the problems of larch variability in Siberia, it should be noted first of all that there are literature data based on studying allozyme polymorphism of *L. sibirica* and *L. sukaczewii* (Shurkhal et al., 1989; Shigapov et al., 1998) which show that *Larix* species, as a whole, have lower genetic variability compared to other genera of *Pinaceae* family. In our opinion, such a conclusion is not enough relevant since genetic variability of the most *Larix* species is studied poorly, and moreover the genetic variability of the most spread *Larix* species (*L. gmelinii*, *L. cajanderi*) is almost totally unknown. The principal parameters of genetic diversity (proportion of polymorphic loci, average number of alleles per locus, average observed and expected heterozygosities) vary in different populations of *L. sibirica* and *L. gmelinii*. They are in the range values established for *Larix* species. The studies of allozyme polymorphism did not reveal large genetic differences between *L. sibirica* and *L. sukaczewii*, while it confirmed the validity of distinguishing of *L. sibirica* varieties mentioned above.

Karyotypes of *Larix* species include 24 chromosomes ($2n=24$). Diploid complement consists of 6 pairs of symmetric (metacentric) chromosomes and 6 pairs of asymmetric (submeta- and intercentric) ones. These species differ in number of nucleolar chromosomes and nucleolus in the interphase nucleus.

Studies on karyological polymorphism in larch species of Siberia (Krukliis, 1974; Krukliis, Myliutin, 1977; Muratova, 1991, 1993, 1994, 1995) showed particular differences between *L. sibirica* and *L. gmelinii*. It allowed characterize karyotypes of *L. x czekanowskii*, *L. cajanderi* as well as other species and hybrid complexes. It was established absence of karyotypic differences between *L. sibirica* and *L. sukaczewii*.

It should be especially noted that (first occasion for *Larix* genus) the *L. gmelinii* trees with B-chromosomes were encountered in Zabaikalie region (Muratova, 1991, 1994). The length of B-chromosomes is 4,5-5,3 μ m. They are metacentric (centromeric index is 47,5%) or slightly submetacentric (centromeric index is 39,9%). The role of B-chromosomes in evolution of genus *Larix* is unknown.

Morphological variability of *L. sukaczewii*, *L. sibirica*, *L. gmelinii* is well studied, the variability of *L. cajanderi* is studied less. According to homological series in hereditary variability of N. I. Vavilov the same morphological forms are encountered in all the *Larix* species: forms in young cone color, in anther color, in bark nature etc., but the ratio of these forms in populations of different species also differs. Separate forms are met only in some species, for example, forms with different downiness degree of seed scales are only in *L. sibirica* and *L. sukaczewii*, forms with different angle of position of seed scales from cone axis are, mostly, met in *L. cajanderi* and less in *L. gmelinii*.

Summing up the review of the material on systematics (including the intraspecific one) of larch species in Siberia, the undefined nature of many distinguished taxons should be stressed once more. It is explained both by complexity of the problem and by its being studied only poorly. Recently a large research works on larch systematics and polymorphism in Rus-

has been started, involving use of methods of molecular genetics and engaging not only Russian scientists but their foreign colleagues as well. We can hope that the research works started will cast light on the debatable problem.

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