

ADAPTIVE DISPARITY OF DISSYMMETRICAL FORMS OF PINUS SILVESTRIS L.
AND PICEA ABIES L. KARST. IN THE NORTH-WEST OF RUSSIAN SFSR

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Population selection and genetics of woody plants lack now knowledge of easily identifiable and informative characters of trees which could facilitate insight into regularities of changes in the intrapopulational structure of the species in response to internal (genetic) and external (environmental) factors. Of particular theoretical and practical interest in this respect is dissymmetry of plants which is essential for studies of the natural differentiation of the species and highly important for understanding evolution processes in natural populations (Urmantsev, 1974; Khokhrin, 1984; Nikulin, 1987).

Variability and natural selection have long been established to be the moving force of evolution of species. Intraspecific selection, in its turn, is based on adaptive disparity of individuals, which is determined by numerous factors whose joint influence affects the frequency of occurrence and the growth of different genotypes in a population.

All the characters that affect directly or indirectly the survivability or the competitiveness are generally agreed to be selective. Among such characters of the common pine (*Pinus silvestris* L.) and the European fir (*Picea abies* L. Karst.) is the phyllotaxis dissymmetry of the epicormic shoot.

The pine and the fir are the principal and most valuable timber species in the forests of North-Western Russia (Leningrad, Novgorod and Pskov Districts). With respect to the direction of the leaf arrangement spiral on the epicormic shoot, two forms are distinguished, viz. the laetotropic (L) and dextrotropic (D) forms.

Investigations of the intraspecific dissymmetric variability of the pine and the fir were carried out for many years both in natural populations and in plantation cenoses of this region, making it possible to establish a biological and ecological disparity of the L and D forms of these species (Golikov, 1981, 1985;

Golikov, Kartsev, 1987).

At present there is much straightforward evidence obtained from natural populations which indicates with certainty that the L forms of the species in question occur more frequently (by 5 to 26%) and grow better (by 8 to 21% in diameter and height) on dry and fresh soils, while the D forms, on the contrary, are more frequent (by 7 to 26%) on moist and wet soils. The analysis of the dissymmetric forms in terms of selection categories and habitat conditions shows that sample and growing-stock trees make up the bulk (67 to 84%) of the L forms on drained soils. These categories are considerably less frequent among the D forms (58 to 65%). The frequency of occurrence and the growth of the L and D forms were reported to depend noticeably on the forest type in pine forests of Karelia as well (Bakshaeva, 1975).

It was established by studies of the cone crop capability of the dissymmetrical pine and fir forms that on moist soils the D forms yield 13.8 to 18.2% more seeds than the L forms; seed yields of the L forms proved to be 12.9 to 16.8 higher on dry and fresh soils. These differences are statistically certain ($F_{act.} > F_{0.01}$). All this proves a reproductive disparity of the dissymmetric forms under different ecological conditions.

In order to estimate the adaptability and the growth of the L and D forms under different ecological conditions, studies were made of 5 to 8 year old test crops descending from different populations. The growth data for these plantations follow a pattern similar to that revealed for natural populations, thereby confirming that there is a substantial adaptability disparity between the L and D forms and that each of the forms needs specific environmental conditions for its fast growth and high yield.

The frequency of occurrence of the forms in question in the progeny of individual trees and populations was studied on one-year plants grown under identical conditions. It was found that the habitat conditions of the mother trees and populations affect considerably the numerical proportions of these forms in the first generation. The progeny of a majority of trees and populations growing on dry and fresh soils show a predominance of the L form, while seeds of humid habitat trees give mostly the D forms. The occurrence difference for the two forms ranges from

3 to 18%, with a high degree of certainty ($\chi^2_1 > \chi^2_{0.01}$). The reason appears to be related to the genetic mechanism, in accordance with the hypothesis by Khokhrin (1977) on numerically non-equivalent primary (zygote level) ratio of the L and D forms. Therefore the frequency of occurrence of these forms is governed not by natural selection alone; of significant importance are also genetic factors. Thus a low adaptive value of this or that dissymmetric form, coupled to a negative correlation of the seed-yielding capacity and the growth rate, results in a lower frequency of occurrence of the form in new generations thereby disturbing the genetic equilibrium of the population.

An essential growth-affecting factor for the forms under study is the stand density. The experimental finding for 10 year crops with stand densities varying from 1 to 11 thousand per hectare indicate that at lower densities of crop, under identical soil conditions, the L form trees show a better growth. The largest reliable difference between the forms in favour of the left-hand one is recorded at sparse plantations (1 to 2 thou. ha), the differences in the diameter and the height being 13-16% and 5-12%, respectively. In the high-density (11 thou. ha) crops the D forms demonstrated a better growth of 15% in the diameter and 8% in the height. The comparatively rigid intraspecific competition of the L and D forms develops with the planting density, showing the D forms to be more competitive under more severe conditions. Judging by the fact of a higher frequency of occurrence of the D form pines under the forest canopy (Khokhrin, 1984), the different response of the two forms to the crop density appears to be related primarily to the illumination level. The light competition, influenced by tree shape parameters and stand density and apparently aggravated by the root competition, affects substantially the growth rates of the L and D forms of the fir.

The fir forms respond differently to herbicides (propaesisin and glyphosate), the D forms in 5-10 year crops and in the nursery showing a better herbicide resistance. The difference materialized in numerical ratios of the forms in the nurseries and in their growth in the crops.

The above-quoted results of investigations of dissymmetric forms of the pine and the fir in North-Western Russia point with consistency to the fact that the L and D forms are adaptively non-equivalent and differ with certainty in such vital biological

parameters as the growing capacity, the seed yield capability, and the competitive ability. The regularities established by these studies have significant importance for population biology and forest selection.

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