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Response of Scots pine (*Pinus sylvestris* L.) seedlings to different climatic conditions and their adaptation peculiarities

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The influence of climatic conditions on seedlings of different Scots pine (*Pinus sylvestris* L.) populations was investigated. The same soil used outdoors allowed to evaluate the sensitivity of populations to transfer and their adaptability. The population formed in the most continental conditions (Labanoras) essentially differed from the other populations. The population formed in the maritime conditions (Telšiai) demonstrated the most negative reaction to new climatic conditions. The southern medium continental population (Veisiejai) occupied an intermediate position. Seedlings of the most continental population (Labanoras) grew best in Sûduva-Dzûkija highlands, while seedlings of maritime (Telðiai) and medium continental (Veisiejai) populations preferred autochthonous locations.

In the same growth conditions were ascertained differences in the genetic adaptation of population traits and characteristics in the juvenile stage (nursery). Therefore, selection of families in populations is more efficient than selection of populations. In more favourable conditions (nursery) a greater variation of growth and biological productivity indices is observed, thus selection in the nursery is more efficient on population, family and individual levels. The population from the most continental conditions exceeded by growth and biological productivity traits the seedlings from maritime and southern medium continental populations. Seedlings of the population formed in the maritime conditions showed a bad growth and lowest biological productivity traits. The survival of seedlings from families of different populations decreased from the north to the south: seedlings of the maritime population were superior for this trait than seedlings from the eastern most continental and southern medium continental populations.

Key words: Scots pine, autochthonous population, climatic conditions, genetic adaptation, ecological adaptation

INTRODUCTION

Material on the geographical variation of populations, transfer effect and adaptation of populations under new growth conditions is rather abundant. Transferred ecotypes first of all suffer from physiological disorders due to new growth conditions, which happen to be different according to growth duration, its onset and finish, light intensity, day length (photosynthesis), substratum moisture content, circulation time and the level of nutrients. Height increment of ecotypes increases from the north to the south up to the optimal region of the species. Afterwards, moving south in the same direction, the growth of ecotypes decreases [1]. Therefore, transfer of progenies from marginal regions is undesirable, because changes in climatic conditions have a negative effect on plants [2–4]. Eco-genetic studies of Lithuanian populations ascertain rather big differences in the growth of progenies of different Lithuanian populations; however, clinal differences in population transfer inside Lithuania are insignificant [4–7].

Most investigators [1, 8–11] confirm that geographic ecotypes differed by growth duration and increment size. Ramanauskas [12] has found that among populations there exists biological isolation, because sporification (flowering) of Scots pine in southern Lithuania occurs 6 days earlier than in northern Lithuania and 12 days earlier than in the coastal plain.

Intensive accumulation of organic matter is explained by a more active photosynthesis under the influence of microclimatic conditions. Seedlings grown in a nursery were characterised by a greater aboveground portion and root weight as compared to those grown outdoors [13]. The growth rate of seedlings of the first year was mostly dependent on the weight of small roots and their length [13, 14].

Studies of the growth rhythm of progenies allow to ascertain reliably the level of trait inheritance from parent trees, their genetic determination and recombination, as well as to reveal the norm of genotype reaction to environmental conditions [15]. Quantitative and qualitative changes of biotic and abiotic factors create selection of differing strength, leading to changes in the genetic structure of the population. The best survival is characteristic of those one-year-old seedlings the origin of which is related to a relatively short vegetation period and the sum of efficient temperatures being lower or close to growing conditions [8, 16]. The literature sources admit that the main condition for a successful growth of progenies is the correspondence between seed origin and growth conditions [13].

The work was aimed to ascertain the influence of transfer to other geographical regions on the progenies of Scots pine populations important for Lithuania.

MATERIALS AND METHODS

To ascertain the differences of populations in separate eco-climatic regions, mature pure pine stands of similar site class and stocking level, growing on the N_{bl} site, were selected in natural Scots pine populations of Telšiai, Labanoras and Veisiejai. Seeds were collected in stands and seedlings were grown in the Dubrava nursery outdoors and in the greenhouse. Additionally, seedlings of the mentioned populations were grown in the place of their origin: in the nurseries of Telðiai, Ðvenèionëliai and Veisiejai forest enterprises.

Each population was represented by 50 trees, from which 150 cones were collected. The cones were scaled and seeds were distributed according to size into fractions.

Trial I

To evaluate the reaction of seedlings to different climatic conditions, the fractionated seeds were sown using a stencil (3 × 3 cm) in small dishes (90 × 120 × 120 mm) in the place of origin of each population: in the nurseries of Telðiai, Ðvenèionëliai and Veisiejai forest enterprises. The soil was brought from the Dubrava nursery. Each population was represented by a mixture of 2800 fractionated seeds of 50 families and each natural forest region by 8400 seeds.

Trial II

Seeds of 150 families of all the three populations according to weight fractions were separately sown using a stencil (5 × 5 cm) outdoors in the Dubrava nursery and in a greenhouse. The trials were done with four replications.

The peculiarities of the Telšiai, Labanoras and Veisiejai populations were studied according to seed progenies. Two types of methods were applied:

1. Transfer of population progenies into different eco-climatic regions allowed evaluating the response of a population to new ecological conditions and the level of population adaptation. The novelty of this study consisted in the same soil used in three natural forest regions, which due to differences in climatic conditions outdoors allowed evaluating the sensitivity to transfer and adaptability of the populations. No such experiment had been done in Lithuania before.

2. Transfer of population progenies to one eco-climatic region allowed evaluating the genetic properties of population families. Variability studies of population traits and characteristics revealed differences in genetic adaptation, which became vivid after transfer into uniform growth conditions.

The height of seedlings was measured with a 0.1 cm and stem diameter with a 0.1 mm accuracy. The seedlings were dried at a temperature of 103 ± 2 °C for 17 ± 1 hours (standards used at the Forest Seed Control Station). Electronic scales were used for weighing with a 0.01 g accuracy.

Statistical analysis of the data was done applying the methods of genetic studies of forest tree species [17]. Variance analyses of growth characters were calculated according to the following model:

$$Y_{jlk} = m + P_j + S_l + B_m + E_{jlk},$$

where Y_{jlk} is the observed value on a k-th tree from the l-th family in the j-th population, m is the overall mean, P_j is the effect of j-th population, S_l stands for the effect of the l-th family within j-th population, B_m is the effect of repetition (block), E_{jlk} is a random residual of the jl-th observation, assuming normal distribution.

The ecological plasticity of each population was calculated in the eco-climatic regions according to the following model [18]:

$$X_{ij} = m + r_i I_j + d_{ij},$$

where X_{ij} is the observed value on i-th population in the j-th eco-climatic region, m is the overall mean, r_i is the regression coefficient of i-th population, I_j is the index of environment (ecological) conditions in the *j*-th eco-climatic region, d_{ij} is the variance of *i*-th population in the *j*-th eco-climatic region.

Population variation components were calculated for all traits by the following formula:

$$I_p^2 = \delta_p^2 / (\delta_p^2 + \delta_e^2),$$

where I_p^2 is the population variation component, δ_p^2 is the population variance, δ_e^2 is the intrapopulation (error) variance.

Family variation components were calculated for all traits by the following formula:

$$I_s^2 = \delta_s^2 / (\delta_s^2 + \delta_e^2),$$

where I_s^2 is the family variation component, δ_s^2 is family variance, δ_e^2 is intrafamily (error) variance.

Family heritability was computed according to the following formula:

$$h_{išg}^2 = 4\ \delta_s^2 / (\delta_s^2 + \delta_e^2),$$

where $h_{išg}^2$ is family heritability, δ_s^2 is family variance, δ_e^2 is intrafamily (error) variance.

Statistical analysis was done using MEAN (MS EXCEL), GLM (STATISTICA 5.5).

RESULTS AND DISCUSSION

Influence of different climatic conditions on the growth and adaptation of seedlings of different populations. In three forest natural regions used by us, the same soil allowed to assess the reaction of progenies of the populations studied to the environment under new climatic conditions. The results of analysis of variation components showed that the variability of the latter traits was more influenced by local climatic conditions (92.4–99.6%) than by the population (0.4–7.6%) itself. Differences in the traits of one-year-old seedlings on population level are reliable in different natural forest regions (p = 0.0001–0.03).

Differences in the geographic variability of the populations in each natural forest region showed the following regularity: one-year-old seedlings of the Labanoras population surpassed by their growth rate seedlings of the Telšiai and Veisiejai populations. According to height increment, seedlings of the general sample of Labanoras population in the place of their origin by 7.8% (Fig. 1a) surpassed the seedlings of Telšiai population. In the natural forest regions studied, seedlings of Telšiai population grew worse and were characterized by a greater variability of growth indices. Similar results were obtained by Áàðíèøêèñ [11], Abraitis and Eriksson [19], who have stated that very often the growth of northern provenances is worse than that of southern ones. A different adaptation character of individual populations was observed. The general adaptation character is typical of Labanoras population families, because their progenies grew evenly well in all native regions. The Veisiejai population is very close: its one-year-old seedlings were marginally slow in growth rhythm. A low general adaptation character was typical of Telšiai population, thus, it is suitable to grow only in its provenance. This population showed a rather high specific adaptability, because it most strongly reacted to the changed climatic conditions.

Influence of outdoors and greenhouse conditions on the growth and adaptation of seedlings. Different populations growing in one place outdoors were analysed on three levels (population, family and within a family), and the peculiarities of genotypic variation of individual populations were ascertained. A study carried out at the same time in a greenhouse showed a provoked reaction of population progenies (seedlings) to changes in environmental conditions. Results of analysis of variation components showed that the variation of traits of seedlings studied outdoors and in the greenhouse was more strongly influenced by environmental conditions (85.0–92.5%) than by the family (7.5–15.0%). Differences in the traits of one- and two-year-old seedlings on population level and among families as well as within a family among individuals were statistically reliable (p = 0.0001–0.02). Results of correlation analysis showed that growth correlation on population level remained similar in the greenhouse and outdoors (correlation of ranges according to seedling height (r = 0.85–0.99; p = 0.01–0.05) and stem diameter (r = 0.86–0.98; p = 0.01–0.05), *i.e.* seedlings of Labanoras population grew better as compared to the seedlings of other populations.

The regulation assessed in different natural forest regions on the population level was repeated in this trial as well (Figs. 1b and 1c). The differences in height increment of seedlings from large seeds between Labanoras and Telšiai populations are more pronounced in the greenhouse (one-year-old 26%, two-year-old 55%) than outdoors (one-year-old 15%, two-year-old 47%). The greatest differences in stem diameter increment of seedlings of the same seed fraction among the populations were observed in the first year outdoors (8%) and in the second year in the greenhouse (32%).

The greatest differences in the height and stem diameter increment of one-year-old seedlings from large seeds estimated among families within a population in the greenhouse comprised respectively 119% and 38% (Veisiejai population) and outdoors 24% and 10% (Labanoras population).

A similar tendency was observed in two-year-old seedlings. Differences in the growth indices studied revealed growth differentiation of the families from different populations, which in the families of one-year-old and two-year-old seedlings was greater according to height than according to stem diameter. Similar results were presented by Danusevièius [8] who determined different growth rates of the families of yellow pine in the initial stages of its ontogenesis.

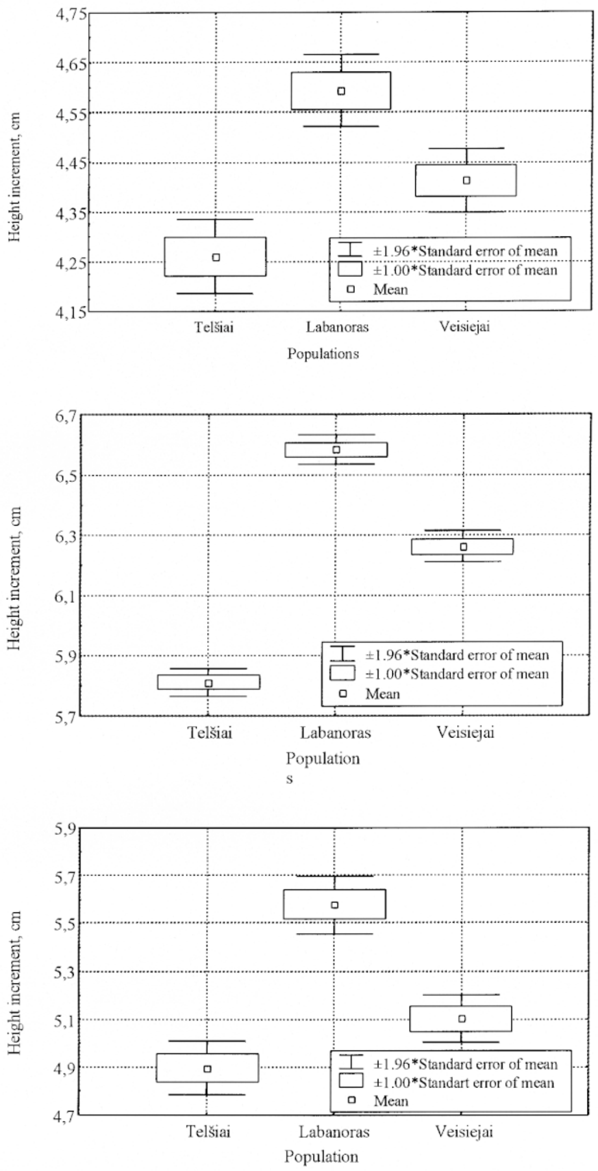

Fig. 1. Height increment of population seedlings under new climatic conditions (*a*), in the greenhouse (*b*) and outdoors (*c*)

In the greenhouse, among individuals within a family the greatest difference in height increment of one-year-old seedlings from large seeds was assessed to be 12–35% (Labanoras population), while outdoors it reached 22–29% (Telšiai population). It shows that under better growth conditions increment differentiation is higher. Studies have shown that the variation of growth traits among families within a population is far greater than on interpopulation and individual levels. A higher variability of the traits of seedlings grown in the greenhouse, ascertained in our study, reveals the homogeneity of growth conditions and a favourable microclimate, the influence of which in the juvenile stage leads to a different reaction of various population families to environmental conditions. Due to a greater range of variation of trait family means in populations, selection of families would be more perspective. Similar results were obtained by Pliûra and Gabrilavièius [7], Danusevièius [8].

In the greenhouse, height increment inheritance ($h^2_{išg}$ = 0.598) of one-year-old seedlings remained the highest in Labanoras population and stem diameter increment inheritance ($h^2_{išg}$ = 0.524) in Veisiejai population. The height ($h^2_{išg}$ = 0.335) and stem diameter ($h^2_{išg}$ = 0.409) increment inheritance coefficient was lowest in Telšiai population. A similar tendency was repeated studying two-year-old seedlings, where similar height ($h^2_{išg}$ = 0.323–0.581) and stem diameter ($h^2_{išg}$ = 0.373–0.513) increment inheritance ranges were assessed (Table). Each ecotype of Scots pine, having acquired modified traits and properties in ontogenesis, can sustain them when transferred into other climatic conditions [20–22].

We have found a reliable correlation between height and geographical conditions of the place of origin of two-year-old seedlings from different populations. The height of seedlings is related to geographical latitude ($r = –0.48$; $p = 0.001–0.01$), eastern longitude ($r = 0.82$; $p < 0.001$) and altitude ($r = –0.13$; $p = 0.001–0.01$). A stronger dependence of height and stem diameter in the studied populations was revealed in seedlings from large ($r = 0.51–0.56$; $p < 0.001$) than from small seeds ($r = 0.29–0.56$; $p < 0.001$).

Along with the growth indices of seedlings of different populations, the weight variability of biological productivity parts was studied. Results of the analysis of variation components showed that the latter indices were more strongly influenced by microclimatic conditions (30.6–98.9%) than by the family (1.1–69.4%). The difference in indices of two-year-old seedlings on population level and among families within a population and among individuals within a family was statistically reliable ($p = 0.0001–0.03$).

Studies of the variability of biological productivity indices of two-year-old seedlings under different microclimatic conditions have shown that in the greenhouse conditions the greatest bioweight was accumulated by seedlings of Labanoras population. Representatives of this population had also a relatively greater weight of roots. Seedlings of this population were characterized by a better ratio of aboveground and underground weight (Fig. 2a). A similar regularity was observed outdoors, too. However, root development was weaker outdoors. Warmth is considered to be the main factor stimulating root development; therefore, soil scarification, allowing warmer air to enter it, may stimulate root development. Seedlings of the Telšiai population were characterized by the least weight of biological productivity parts in different microclimatic conditions and a greater aboveground weight variability outdoors. The populations studied showed that large seeds produced larger se-

Table. **Variance components and family mean heritability of traits of different population seedlings in the greenhouse**

Population	Trait	Seed size	Variance components, %		Family mean heritability
			Family	Other factors	
Telšiai	Height	Large	14.2	85.8	0.570
		Small	8.1	91.9	**0.323**
		General sample	11.5	88.5	0.462
	Diameter	Large	9.6	90.4	0.383
		Small	9.3	90.7	**0.373**
		General sample	9.4	90.6	0.378
Labanoras	Height	Large	14.5	85.5	**0.581**
		Small	8.4	91.6	0.334
		General sample	11.8	88.2	0.471
	Diameter	Large	10.3	89.7	0.402
		Small	10.7	89.3	0.428
		General sample	10.3	89.7	0.411
Veisiejai	Height	Large	14.3	85.7	0.573
		Small	8.5	91.5	0.341
		General sample	11.6	88.4	0.465
	Diameter	Large	12.8	87.2	**0.513**
		Small	9.8	90.2	0.393
		General sample	12.2	87.8	0.488

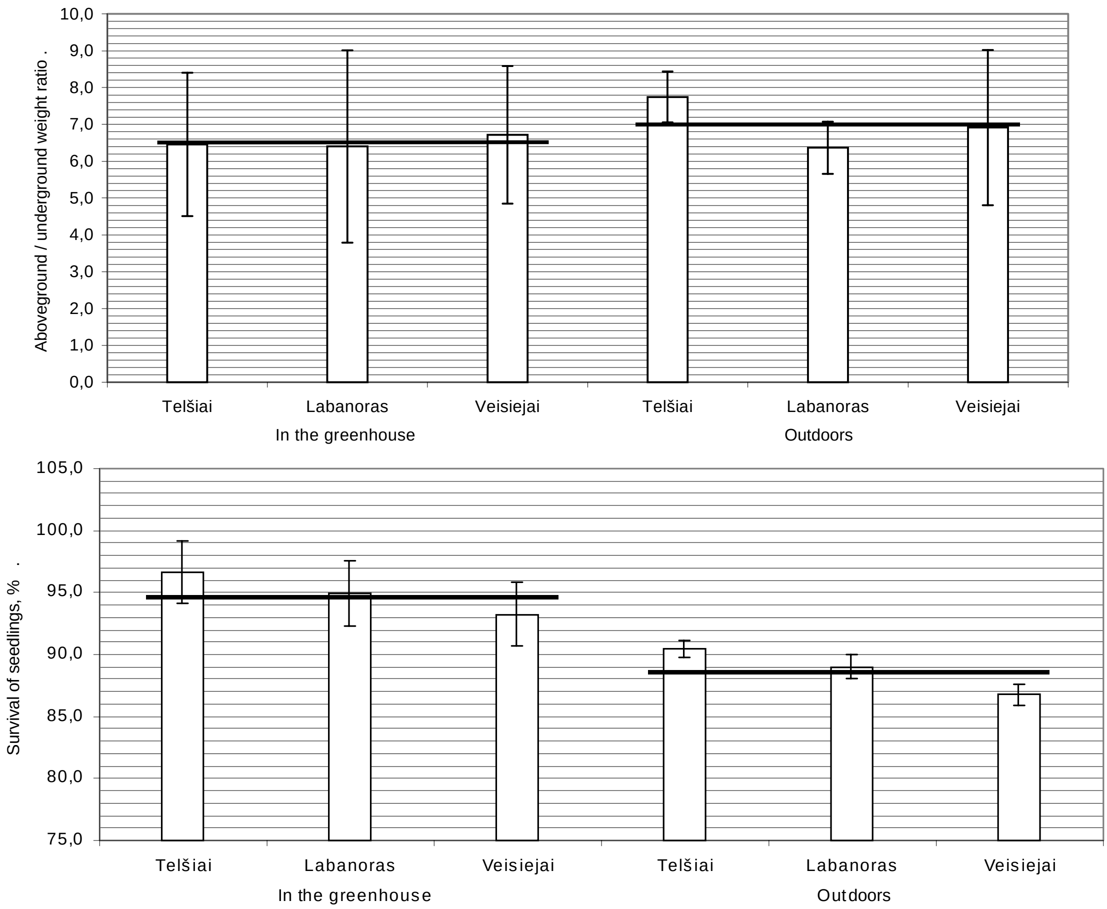

Fig. 2. The ratio of aboveground / underground weight (*a*) and adaptation (*b*) of different population seedlings in different microclimatic conditions. Bars show averages of ratio aboveground / underground weight and of survival of various population seedlings, vertical lines show standard deviation. Horizontal lines show average ratios of aboveground / underground weight and survival of different population seedlings in different microclimatic conditions

edlings. The greatest aboveground weight differences of the general sample seeds in the greenhouse and outdoors between Labanoras and Telšiai populations comprised respectively 27% and 45%, while the greatest differences in underground weight of the latter seed fraction reached respectively 32% and 75%. The larger weight of small roots ensured for the seedlings of Labanoras population an even development of the aboveground portion and better establishment.

Similar results were obtained by Smirnov [13], Baltruðaitienë [23]. The greatest differences in the weight of aboveground and underground portions of seedlings of the general sample seeds among families within a population in the greenhouse comprised respectively 117% and 328% (Labanoras population), while outdoors – 72% (Telšiai population) and 130% (Veisiejai population).

Under greenhouse and outdoors conditions, a stronger dependence of the biological productivity indices of two-year-old seedlings was more pronounced on family than population levels. A correlation between the weight of needles and roots was higher outdoors ($r = 0.98$; $p = 0.001–0.01$) than in the greenhouse ($r = 0.63$; $p = 0.001–0.01$), showing the vitality of seedlings.

Survival of the seedlings of population families. Analysis of the variation components showed that the survival of population families was more strongly influenced by microclimatic conditions (96.6–99.5%) than by genetic family peculiarities (0.5–3.4%). The differences of the variable on population level and among families within population was statistically reliable ($p = 0.0001$).

Seedlings grown in the greenhouse survived better than those grown outdoors. On population level, the best survival was recorded for the Telšiai and the worst the Veisiejai population. Two-year-old seedlings were characterised by a higher mortality than one-year-old seedlings. In the greenhouse the latter index in the first year comprised 5% and in the second year 14–23% the outdoors mortality being 10–13% and 23–30%, respectivelys.

The greatest differences of this variable for one-year-old and two-year-old seedlings between Telšiai and Veisiejai populations in the greenhouse comprised respectively 3.7% (Fig. 2b) and 11%, while outdoors the difference of two-year-old seedlings between the mentioned populations reached 10%. Studies of the survival of seedlings among population families ascertained the greatest survival differences of two-year-old seedlings in the Veisiejai (29%) while the least in the Telšiai (21%) populations.

Similar results reported by Danusevièius [8], Tcherepnin [24] show that the survival is best in the one-year-old seedlings the provenance of which is related to a short vegetation period and an efficient sum of temperatures, which is lower or close to the growth conditions. Resistance to frost in the early autumn is applicable to the indication of acclimatization during frosts of the first year and confirms better survival in the provenances of northern latitudes [25, 26].

Under different microclimatic conditions, reliable correlations with seed weight and geographical latitude were estimated. In the greenhouse, a correlation between the survival of seedlings and seed weight was stronger on the level of families ($r = –0.66–0.73$; $p < 0.001$) than populations ($r = –0.53–0.58$; $p < 0.001$). Outdoors, a strong correlation was ascertained between the survival of seedlings and geographical latitude ($r = 0.80–0.89$; $p < 0.001$), as well as population.

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PAPRASTOSIOS PUŠIES (*PINUS SYLVESTRIS* L.) POPULIACIJØ SËJINUKØ ATSAKAS Á SKIRTINGAS KLIMATINES SÀLYGAS IR JØ ADAPTACIJOS YPATUMAI

Santrauka

Straipsnyje iðtirtas klimatiniø sàlygø poveikis skirtingø paprastosios puðies populiacijø sëjinukams. Naujomis klimatinëmis sàlygomis panaudotas tas pats dirvoþemis atvirame grunte leido ávertinti populiacijø jautrumà perkëlimui bei ekologinës adaptacijos laipsná. Labiausiai þemyninëmis sàlygomis susiformavusios (Labanoro) populiacijos sëjinukai pagal poligeninius poþymius yra pranaðesni ir ið esmës iðsiskiria ið likusiøjø. Jûrinio klimato sàlygomis susiformavusi populiacija (Telðiø) labiausiai neigiamai reagavo á naujas augimo sàlygas. Vidutiniðkai þemyninë pietinë populiacija (Veisiejø) uþëmë tarpinæ padëtá. Labiausiai þemyninës populiacijos (Labanoro) sëjinukai geriausiai augo Sûduvos–Dzûkijos aukðtumose, o jûrinio klimato (Telðiø) ir vidutiniðkai þemyninës pietinës (Veisiejø) populiacijos sëjinukai – autochtoninëse vietose. Dël didesnio fenotipinio plastiðkumo Telðiø ir Veisiejø populiacijø sëjinukams bûdingas specifinis adaptyvumas. Telðiø populiacijos palikuonys, prasèiausiai augantys visuose tirtuose miðko gamtiniuose regionuose, tinkami auginti tik savo kilmës vietoje.

Vienodomis augimo sàlygomis nustatyti populiacijø poþymiø ir savybiø genetinës adaptacijos skirtumai. Dël didesnio poþymiø kintamumo ðeimø atranka populiacijos viduje yra efektyvesnë negu tarp populiacijø. Palankesnëmis mikroklimatinëmis sàlygomis (ðiltnamyje) pasireiðkia didesnë augimo ir biologinio produktyvumo rodikliø kaita, todël atranka ðiltnamyje efektyvesnë tarp populiacijø, ðeimø ir individø. Labiausiai þemyninë populiacija (Labanoro) augimo ir biologinio produktyvumo rodikliais pralenkia jûrinio klimato sàlygomis susiformavusios (Telðiø) bei vidutiniðkai þemyninës pietinës (Veisiejø) populiacijos atstovus. Pastarosios augimo sparta artimesnë rytinei labiausiai þemyninei (Labanoro) populiacijai. Jûrinio klimato sàlygomis susiformavusios populiacijos (Telðiø) sëjinukai auga prastai, jø biologinis produktyvumas maþiausias. Skirtingø populiacijø ðeimø sëjinukø iðlikimas maþëja ðiaurës pietø kryptimi: jûrinio klimato sàlygomis susiformavusios populiacijos (Telðiø) sëjinukai ðiuo rodikliu pranaðesni uþ rytinës labiausiai þemyninës (Labanoro) bei pietinës vidutiniðkai þemyninës (Veisiejø) populiacijos sëjinukus.