Ecological and morphological studies in the hybrid zone between *Pinus sibirica* and *Pinus pumila*

S. N. Goroshkevich, A. G. Popov, G. V. Vasilieva

Abstract. In the Baikal Region, there is no phenological isolation between Siberian stone pine (*P. sibirica* Du Tour) and Siberian dwarf stone pine (*P. pumila* (Pall.) Regel) since the timing of their 'flowering' coincides. Morphologically intermediate individuals, supposedly natural hybrids,occur not very often. In the west half of Stanovoye upland area four regions were investigated: Barguzinskiy, Baikalskiy, Verchneangarskiy and the Severo-Myiskiy mountain ridges. Interspecific natural hybridization was found to take place in several overlapping regions of the species' ranges; however there are some differences in frequency of natural hybrid occurrence between regions as well as within each region. Great numbers of natural hybrids are found only in a specific habitat which occurs rarely and occupies a relatively small area. At the north-east coast of Lake Baikal the lakeside zone is occupied by Siberian stone pine forests with moderate participation of Siberian dwarf stone pine in the undergrowth. The natural hybrid are widespread everywhere. The ratio of fructiferous Siberian stone pine, Siberian dwarf stone pine and natural hybrid was found to be approximately 300:10:1. About 90% of the examined natural hybrids took an intermediate position between the two parental species by most features (structure of needles, shoots, and crown), i.e. representing putatively the first generation hybrids. Therefore, in contrast to the parental species they are subjected to the destructive effect of snowbreak (broken off or dislocated from part of the root system). Like the Siberian dwarf stone pine the natural hybrid has specific root sources forming from latent buds. Therefore, the hybrids are not subjected to ageing, as well as have no internal limitation of age and size. Siberian dwarf stone pine, Siberian stone pine and their natural hybrid grow together in the Upper Angara delta in the bog regions. In the most productive sites the ratio of fructiferous Siberian dwarf stone pine, Siberian stone pine and natural hybrid amounts approximately to 60:3:1. The ratio of fructiferous Siberian dwarf stone pine and natural hybrid reaches about 20:1 in the less productive sites where Siberian stone pine is sterile. Analysis of cone structure showed that the natural hybrid have substantially increased in comparison with the species' mortality and aplasia of reproductive structures at all stages of the generative cycle, from differentiation of the seed-bearing scales to differentiation of the embryo. The portion of the ovules, which develop into the valuable seed with differentiated embryo, amounted in Siberian dwarf stone pine to 69%, in Siberian stone pine to 44%, and in natural hybrid to 25%. Thus, the fertility of natural hybrid in the Upper Angara Delta substantially decreased in comparison with the pure species; however, it was demonstrated that natural hybridization between Siberian dwarf stone pine and Siberian stone pine species occurred.
Keywords: *Pinus sibirica, Pinus pumila*, natural hybrids, introgression, hybrid zone

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Introduction

Natural hybridization in forest trees, including species of the family *Pinaceae* has been studied thoroughly. For example, there is extensive literature on hybridization between *Picea abies* and *P. obovata* as well as between *Larix sibirica* and *L. gmelinii* in Russia. In these cases the hybridizing species are quite similar with respect to taxonomy, morphology, and ecology. In the Lake Baikal region and in Transbaikalia the ranges of the Siberian stone pine (SSP) and the Siberian dwarf stone pine (SDSP) overlap. Morphological and ecological differences between these species are significant. Many researchers consider these species not to be closely related phylogenetically (Komarov 1927, Litvintseva 1974, Critchfield 1986). This is proven by data of biochemical (e.g., Krutovskii et al., 1990, 1994, 1995, Belokon et al. 1998, Politov & Krutovsky 2004) and molecular genetics (e.g., Liu et al. 2005). Therefore, the study of natural hybridization between SSP and SDSP promises interesting results. The possibility of natural hybridization between the two species was first suggested by Sukachev (1929). However, until quite recently only a few individuals of possible hybrid origin were described (Pozdnyakov 1952, Galaziy 1954, Molozhnikov 1975).

Genetic evidence of the hybrid origin of a single specimen of a putative hybrid was obtained by allozyme loci (Politov et al. 1999). Politov (1998) revealed and genetically proved a number of NH in several localities along the eastern Baikal coast.

We first described morphology of natural hybrids (NH) in the Khamar-Daban mountain ridge (Goroshkevich 1999, 2004). Individuals strongly intermediate between the two species by a complex of morphological traits characterizing life form, growth rate, shoot, needle and cone structure occurred along an elevation transect except for the upper 100-150 m. Growing together both species have coinciding flowering periods. The lack of phenological reproductive isolation allows these species to intercross. Analysis of the cone and seed structure in trees from the upper forest belt showed that in contrast to pure species NH have the highest levels of loss of seed-buds, seeds and embryos at all stages of reproductive structure development. For SSP every second seed-bud, for SDSP every tenth seed-bud and for NH only every fiftieth seed-bud developed to a sound seed. The aim of the present study is to investigate the natural hybridization in other regions including the occurrence and frequency of NH, crown structure analysis, as well as cone and seed structure in comparison with parental species.

Material and methods

During the period from 2000 to 2005 we undertook route studies in the northern part of the region where ranges of SSP and SDSP overlap including Barguzinskiy, Baikalskiy, Verchneangarskiy and Severo-Myiskiy mountain ridges, the southern and north-east coast of Lake Baikal, and the Upper Angara river delta (figure 1). During the route observations of the occurrence of the parental species and NH were recorded and temporary sample plots in selected sites were established. The two species and NH were identified based on two traits, namely habitus and the color of immature cones. Therefore, only adult trees bearing female cones were considered. Individuals with trunk other than upright and with green cones were attributed to SDSP, while trees with upright trunk and violet cones were attributed to SSP. All trees having no upright trunk but possessing violet cones were classified as NH. There were no trees with green cones and vertical trunks in populations.

Four zones of the western part of Stanovoye upland were investigated. Natural hybridization was found to take place across the region of the overlapping ranges, although frequency of NH occurrence greatly varied both among these locations and among individual sites within each region (figure 2).

The first region was the territory of Barguzinskiy nature reserve, and included the coast of Davsha Bay, the coastal plain and the central part of Barguzinskiy mountain ridge. A narrow lakeside zone, 40-50 m wide, is occupied by coniferous forests of different age and the various ratios between SSP and larch were

studied most thoroughly. SSP are numerous, and strong and abundant seed cone bearing was observed everywhere in this zone. In contrast, SDSP are scattered widely and are represented by single strong clones. In the year of observations we observed sufficient numbers of conelets, but mature cones were almost absent, and the few cones that were found were mostly deformed. Judging from the absence of traces on the bark, there were almost no mature cones in previous years either. Thus, SDSP in this site was not only very rare, but it bore few female cones. NH was widespread including huge old NH clones up to 10 m high and up to 40 cm in diameter. Seed production of NH was weak because most of them grew under the forest canopy. Only a few NH clones growing under more or less suitable light conditions showed normal cone crop. The current-year cone crop was medium, intermediate between the abundant cone crop of SSP and the very poor cone crop of

SDSP. Among strong seed cone bearing NH only half have mature cones. The ratio of seed cone bearing of SSP, SDSP and NH was
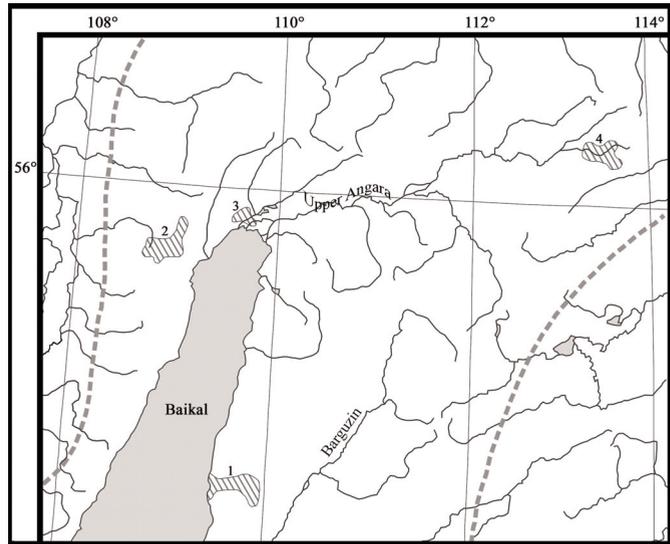

Figure 1 Study area. Dotted lines - western boundary of *Pinus pumila* range and eastern boundary of *Pinus sibirica* range. 1.Barguzinskiy nature reserve, coast of Davsha creek, coastal plain and central part of Barguzinskiy mountain ridge. 2. Central part of Baikalskiy ridge along the Baikal-Amur Railroad from Delbichinda station to Davan station; 3. Upper Angara delta and neighboring southern part of Verchneangarskiy ridge; 4. central part of Severo-Muiskiy ridge.
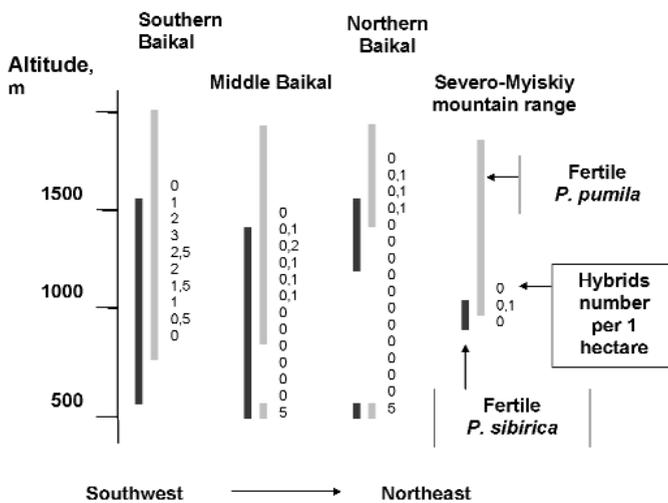

Figure 2 Parental species' distribution and natural hybrids' occurrence within studied regions

approximately 300:10:1.

Situated between Baikal Lake and the foot of Barguzinskiy ridge a relatively wide (25-30 km) plain is occupied by the conifers. SSP were widespread here, while SDSP are rarely spread under the forest canopy, especially in the middle part of this band at the same distance both from the shoreline and the mountains. Cone crop was virtually absent. SDSP are lacking in the bogs that occupy significant areas. NH was not found.

The Barguzinskiy ridge consists of three forest zones which replace each other within the altitude range from 500 m to 1,500 m: (1) SSP + *Larix sibirica*, (2) SSP + *Abies sibirica* and (3) *Abies sibirica*. Even at the bottom of the mountains the number of SDSP was higher in comparison with that on the plain. Seed cone bearing SDSP appear on a steep slope and in the river valleys from 750 to 800 m. The number of SDSP increase with altitude. In the river valleys at altitudes from 800 to 1,200 m there are strong thickets of SDSP amidst the SSP forest. *Abies* dominates in the upper part of the forest zone. SSP are present, but are represented by single (1-2 per hectare) strong trees at ages of 400-500 with normal seed production. In this part of the zone seed cone bearing SDSP are numerous. At altitudes from 1,400 to 1,500 m the subalpine zone of SDSP is clearly pronounced. A band 25-30 m wide along the route and an area about 5 ha in the subalpine zone of SDSP were investigated for occurrences of NH. Only two NH were found, one on the steep slope of the river valley at an altitude 950 m and another in the subalpine zone of SDSP at an altitude of 1,550 m.

The second study region is the central part of Baikalskiy ridge along the Baikal-Amur Railroad from Delbichinda station to Davan station. The area is characterized by almost the same forest zone distribution as the Barguzinskiy ridge. For the purpose of NH presence detection only the upper zones were investigated: SSP + *Abies sibirica* forests and higher. Total length of the routes was about 120 km, including the Goudgekit river valley from the river outlet to the river head, a wide band along the subway above the Baikalskiy tunnel of the Baykal-Amur Railroad, two elevation transects (to the north and to the south) from Baikalskiy Pass to the alpine zone, and western slopes of

the ridge towards Kunerma and Delbichinda River valleys. Only 9 NH were found, 7 of them were concentrated within one small plot (3-5 ha) in the extremely rare and virtually unique site (western part of Baikalskiy Pass, 950 m above sea level). In ordinary widespread sites there were practically no NH.

The third region is the Upper Angara river delta and neighboring southern part of Verchneangarskiy ridge. The Upper Angara delta is a vast area of about 350 km^2. The area of the wetland covered with woody plants can be conditionally divided into three parts. The first part contains sites with occurrences of SSP and occupies a negligibly small area (less than one percent of the total wetland area). These sites are the most elevated and productive. The investigated site was about 5 ha. All woody plants have post-fire origin at the age of 80-100 or less. There were only a few individuals of Scots pine, larch and birch and a little more SSP (20-30 per ha, heights of up to 10-12 m). SDSP was abundant and very strong reaching heights of up to 4-5 m. The ratio of seed cone bearing SDSP, SSP and NH was approximately 60:3:1. The most part of the wetland area is covered with woody plants and consists of low productive SDSP with heights of up to 1.5 m (zone 2). About 1 ha of such brushwood was investigated and it was found that many of even the strong and old SDSP, approximately 50%, do not produce seeds. SSP are represented by single sterile trees and heights of up to 2 m. NH were not found in that part of the bog. Approximately 1-2% of the third region was occupied by a transitional zone between the first and the second types of the vegetation (zone 3). In the parties' zone SSP were sterile, but occurred higher and more frequently in comparison with zone 2. Size and seeds' productivity of SDSP plants were intermediate between zones 1 and 2. NH were especially numerous. The ratio of seed cone bearing SDSP and NH was approximately 20:1.

The southern branches of Verchneangarskiy ridge neighboring the river delta are covered with the forest. Altitudinal forest zones are represented by larch-pine-birch forests from 500 to 800 m, larch-birch forests from 800 to 1,000 m, SSP + *Larix sibirica* forests from 1,000 to 1,200 m, *Larix sibirica* crooked forest from 1,200 to 1,350 m, and brushwood of seed cone

bearing SDSP from 1,350 m above the sea level. SDSP are widespread in the undergrowth across the forest zone but are absolutely sterile under such conditions. A poor cone crop was detected from 1,200 m above sea level. With regards to NH, a band along the route 25 m wide in the altitudinal range from 500 to 1,500 m was observed as well as an area of about 3 ha in the SDSP zone at an altitude around 1,400 m. Only 3 NH were found, one NH at an altitude of 1,000 m (the lowest timberline with SSP), the second one at an altitude of 1,400 m in the strong (height up to 4 m) brushwood of seed cone bearing SDSP, and the last one at an altitude of 1,500 m among small (about 1.5 m in height) SDSP.

The fourth region is the central part of Severo-Muiskiy ridge where SSP are located near the eastern limit of their distribution and occur only in valleys of medium size with big rivers, although quite fertile. At an altitude 700-800 m SSP are observed only in flood-plains of the Angarakan River as a small admixture in the larch-spruce forests (10-20% of total stand composition). In contrast, SDSP are a widespread keystone species. SDSP are fertile even in the subalpine zone up to 2,000 m a.s.l. In order to evaluate NH occurrence our route investigations envelop the part of the valley 40 km long and 500 m wide from the Kavokta River outlet to the large flowing lake in the upper reaches of Angarakan River (between the settlements of Tonnelniy and Razliv). In this site NH were found but were not numerous (1 individual per 5-10 ha). All NH were revealed only in the Angarakan River flood plain, i.e. under growth conditions where two parental species grow together.

Results and discussion

Thus, natural hybridization between SSP and SDSP occurred in all the investigated areas of the northern Baikal Region. NH were found in all plant formations where parental species were fertile. However, significant amounts of NH appear (or survive?) only within peculiar sites that occur rarely and occupy relatively small areas. Two hypotheses for explanation of this phenomenon are possible: (1) only these unusual conditions are optimal for cross-polli-nation of the parental species because of coin-cident flowering periods; (2) only under these unusual conditions where adaptation of parental species is complicated is there a rela-tively free niche occupied by NH. These two hypotheses are not alternative and can comple-ment each other. In further studies these hypotheses could be confirmed or rejected.

In the regions of widespread natural hybridization (North-Eastern Baikal coast and Upper Angara River delta) the majority of the studied NH (about 90%) were intermediate between parental species by most studied traits (structure of needles, shoots and crown etc.), i.e. they likely represent hybrids of the first generation. Such F_1 hybrids inherit only two of all studied traits according to domination rule, namely the color of ripening cones (violet color like in SSP) and the ability to produce specialized roots from latent buds (like in SDSP). About 10% of NH are characterized by prevalence of traits of one parental species; these individuals are putatively backcrosses. NH DNA research was conducted together with Japanese colleagues (Professor Y. Watano from the Chiba University). It was determined that all analyzed NH had mitochondrial DNA of SDSP and chloroplast DNA of SSP, indica-ting that natural hybridization is unidirectional. Analysis of the NH nuclear DNA was started.

Life-form morphogenesis of pure species and typical NH were analyzed using the popu-lation sample from the Baikal coast in the Davsha creek region. For the whole period of ontogeny, normal SSP have one straight verti-cal trunk. In rare cases when there are several trunks, they are in general straight and vertical, excluding the base of the trunk. At the juvenile stage a single trunk unambiguously dominates while skeletal shoots retarded in their growth, have uniform size and are mainly plagiotropic. With age trunk domination gradually decreas-es, it becomes selective, especially after the tree reaches the first forest layer. Lateral branch differentiation by size strongly enhances growth rate of most of those that are still lagging; some of the large branches, in contrast, emerge from trunk control and they reach the same growth rate as the trunk. In turn, on these branches, a limited number of

lateral branches comparable with them are produced. When a tree reaches 90-95% of its total height the bough basis of the crown's upper part consists of many relatively uniform trunk-branches of different ramification orders (from 1st to 8th). The verticality and straightness of the main trunk ensures high resistance to snow load. Only boughs in the middle part of the tree's crown can be regularly broken off under the influence of this factor. Maximum height of trees is 20-25 m.

Since early development stages SDSP have many relatively uniform TB, and their number permanently increases during the whole ontogeny period because of regular branching from common regeneration buds. Such crown structure forms because of weak but very selective domination of existing TB: all branches tend to dominate during the first 2-3 years of life reaching the same growth rate as the boughs and turns into TB with time, obtaining the ability to generate new TB of the next ramification order. All TB are scimitar-shaped, i.e. their proximal part is almost parallel to the ground and their distal part is almost vertical.
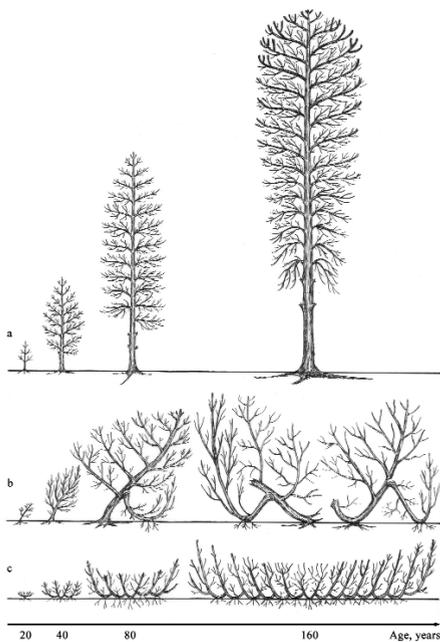

Figure 3 Crown morphogenesis in *Pinus sibirica* (a), *Pinus pumila* (c), and their natural hybrids (b).

As TB grow, a length of young scimitar-shaped part of the TB remains relatively constant, while its old horizontal part constantly increases. SDSP have a lot of specialized root sources produced from latent buds and are capable of intense ramification even at the latent stage of their development. Root sources become more active when TB reaches moss-lichen cover, and they proliferate and start rooting when TB come in contact with the cover. The crown of young trees has a more or less symmetrical cup shape with radial position of TB. Continuous increase of crown area with regular radial structure occurs due to centrifugal growth and branching of TB, and density and viability of branches decrease from circumference to the center. Ramification order, age and crown size are not limited by internal factors. Some, quite weak, signs of senescence of the local branching system are observed only in the center of the crown. The crown circumference invariably remains 'forever young'. SDSP have a mechanism of active natural pruning of any thickness of TB prior to winter. SDSP crowns always spend the winter under the snow cover. Maximum SDSP height (from 1.5 to 3.0 m depending on light and soil conditions) is reached at 100-150 years, and then height remains more or less constant.

From youth onwards, NH has just one trunk. The pattern of relationship between the trunk and lateral branches is intermediate between SSP and SDSP. NH selectivity of domination is revealed later than in SDSP, but significantly earlier than in SSP. Therefore, transition from a single-trunk to a multi-trunk status occurs not as early as in SDSP, but not so late as in SSP. Therefore, in NH, the TB 'cup' similar to that of SDSP appears to be located on the primary trunk with heights 0.5-1.5 m and TB themselves are not so numerous and uniform as in SDSP. NH transition to a multi-trunk status is not irreversible but not yet completely realized and weak and unstable domination of the initial trunk regarding TB of next branching order is retained. As a result, TB 'cups' are situated not in one horizontal plane such as in SDSP but in different ones. Most often above this elongated vertical 'cup' there is a feebly marked initial trunk that occasionally generates new TB. So, nevertheless, the whole branching system is concentrated to a certain degree around a

single axis. Initial NH trunks are never straight and vertical. Early in the trunk development, they turn scimitar-shaped but the curve degree is significantly smaller than that in the case of SDSP TB, where the distal part of the trunk is strictly vertical, while the proximal part is inclined on average by 30-45°. A mechanism of active TB natural pruning in NH in pre-winter period is weakly developed or absent, so that their crowns are located above the snow cover. Because of the occurrence of the main scimitar-shape curve, NH does not have tolerance to the snow load. As age and crown size increase, the tolerance to this factor decreases. This leads to unavoidable damage as the tree reaches heights of 4-5 m (rarely 6-7 m and higher). In general, breakage or reversing of roots on the side opposite to a scimitar-shape curve takes place. Usually the tree falls down not strictly in the plane of the curve but angularly, approximately ± 45° towards a curve plane. Under these conditions a certain part of the root system remains alive and is functioning normally. In most cases this is enough for a tree to survive, although the growth rate decreases. The fallen tree crown has insignificant damage. Many living branches contact the moss-lichen cover. NH has the ability to generate shoot-bearing root sources and, therefore, additional roots are not as pronounced as in SDSP; however it is enough for rooting of branches lying on the ground. Depending on their initial status, 2-3 years are necessary to activate root sources not yet ready to proliferate. After rooting, rejuvenation of branches and enhancement of their growth occurs. As a result, crown differentiation is drastically reinforced because the unrooted branches grow slowly. Abrupt change of a crown position in space has also other consequences. The 'cup' elevated above ground prior to falling now appears lying on the ground on its side. Almost all branches somehow change the direction of their growth which results in formation of complex and variable curves. Previous growth rate restores quite soon. However, such initially low NH crown resistance to snow load further decreases by secondary structure deformations after falling, and therefore, the destructive effect of snow breakage is progressive. The effect is exhibited not only in the falling of individual rooting TB with separation of root part but in the breaking of 'unnaturally' oriented TB still not rooting. The essential portions of these TB do not completely break off but only partly, with partially functioning vascular tissues. Most broken TB are rooting and thereby rejuvenating. As a result, one NH clone can occupy an area comparable to that for a SDSP clone. The fundamental difference between them is that the NH clone does not have a ring-radial structure inherent in SDSP clones. At early development stages the NH clone spreads out fan-shaped in the direction of the first falling of the initial trunk. The general direction is maintained during a long time period. For very old clones it is almost impossible to identify the position of the initial trunk and main spread direction. The NH usually reach a maximum height (5-7 m) before the first falling of their initial trunks. After that the height decreases to 2-3 m and then it is gradually set at maximum level since further falling and breaking of numerous TB do not concur. Both SDSP clones and NH clones do not have internal limits for age and size.

Cone crop, cone and seed structure were studied with the population sample from the Upper Angara delta. The SSP cone crop was weak because of small crown size and low number of female shoots. Even the oldest 100-year old trees had less than 10 female shoots and 15-20 cones. The SDSP cone crop was abundant; the oldest trees had on average 200-250 cones. NH was intermediate between the two parental species by both cone crop and tree height at the age when seed production starts: 0.5-1.0 m for SDSP, 1.5-2.0 m for NH, and 3-4 m for SSP.

Five cones were collected from 16 trees of each group (SSP, NH, SDSP). Cone length and maximum diameter were measured. In order to analyze a cone structure, scales were separated from the axis and were counted in proximal sterile, medial fertile and distal sterile zones. Structures of any size shaped like mature seeds and originating from seed-buds were considered as seeds. They were classified as 1) developed seeds of normal size, and 2) abortive seeds. Then the distribution pattern of seed size was determined using sieves with aperture diameters of 3-8 mm. Developed seeds were divided into 1) empty seeds, 2) seeds with underdeveloped endosperm, and 3) full seeds.

In the full seeds the presence of embryos and their status (differentiated or not) were detected, embryo number and length (determined as the part of the canal length occupied by the embryo) were measured as well. Full seeds with differentiated embryo were weighed. The significance of the differences between samples was evaluated using ANOVA (Scheffe test) at P-level 5%. The results are demonstrated in the table that also contains data obtained earlier in the study at Khamar-Daban Ridge. The same letters near values show that significant differences between the groups (SSP, NH, SDSP) in regard to the trait and region in question are absent.

NH cones were of intermediate size between the parental species both in the Khamar-Daban (KD) and Upper Angara delta (UAD). However, NH cone length was similar to the SSP ones (it is pronounced only in UAD), while NH cone diameter was more like the SDSP ones (it is pronounced in both regions, especially in UAD). For NH the total number of scales per cone was strictly intermediate between pure species. In the KD three cone zones ratios were not significantly different between SSP, SDSP, and NH. In the UAD there were no differences except for the fertile cone zone part. Proximal zone part was larger for SDSP, while distal zone part was larger for SSP; NH showed intermediate characteristics between the two parental species.

The initial number of seed-buds was maximal for SSP, minimal for SDSP, and strongly intermediate for NH. Traits listed in the table below the initial number of seed-buds characterize their developmental process. In the table, traits measured as absolute values (pcs.) show survival dynamics of seed-buds and seeds at every stage of their development. These traits alternated with traits that demonstrated losses in every stage of development as percentage of seed-buds or the number of seeds remaining at the onset of each stage. Analysis of these data showed the highest loss level for NH almost during all stages in both regions; but in UAD it was considerably lower than in KD. Lowest loss level was observed for SSP in KD and for SDSP in UAD.

Seed-buds partially perish at the earliest stage of development (before pollination). In mature cones such seed-buds are represented by flat remains. A portion of such seed-buds in KD was very high for SDSP and almost three times lower for SSP. NH was intermediate between the species. In UAD values for the same traits varied not so greatly, moreover, the value for NH was almost the same as that in KD, significantly higher for SSP, significantly lower for SDSP. In both regions gametophyte seed-buds mortality (i.e. portion of undeveloped seeds) was very high for NH and relatively low but approximately equal for parental species (though much higher in KD than in UAD). Bimodal distribution of seeds by size was typical for both parental species, seeds are clearly divided into small (undeveloped) and normal (developed); and there are no seeds of intermediate size. For all NH, seed distribution by size was continuous, i.e. seeds of intermediate size occurred as often as small and normal ones in general.

Seed-buds' mortality after fertilization (i.e. portion of empty seeds) was also maximal for NH. In KD for pure species, the value of this trait was equally low (6-8 times lower than for NH), in UAD it was common only to SDSP, while SSP in this respect did not differ from NH. The fraction of seeds with undeveloped endosperm in KD was 5 times higher for SSP and NH and 10 times higher for SDSP than in UAD. Losses for NH were maximal at this stage of development, too. Some seeds with normally developed endosperm had no embryos. Such seeds occurred very rarely in the pure species, particularly in SSP, and 10-20 times more frequently for NH. Seeds with undifferentiated embryos occurred 2-10 times more often in KD than in UAD. In both regions, especially in UAD, this portion for NH was significantly higher in comparison with pure species. Polyembryony was detected in all groups, but for NH the phenomenon occurred considerably more frequently (10%) than SDSP (3%) and SSP (1%). In comparison with SDSP, full seed weight of SSP was 2.4 (UAD) - 3.0 (KD) times larger. NH is strictly intermediate between species for this trait.

Thus, natural hybridization occurs fairly intensively between SSP and SDSP in UAD. There are 2-5% NH from the total number of seed cone bearing trees in all types of ecosystems where at least one parental species is fertile. For NH, cone and seed size is

intermediate between parental species. At all stages of the reproductive cycle, from differentiation of seed scales to differentiation of embryo, NH has higher mortality and underdeveloped levels of reproductive structures in comparison with pure species. Moreover, NH fertility in UAD appears to be many times higher (13-14 times) than it was estimated earlier based on the results of 1-year observations in KD (Goroshkevich, 2004). In UAD, NH produce normal seeds and under favorable conditions at least 1 seed-bud out of 4 develops into a full seed with differentiated embryo. The data allow us to assert that natural hybridization between SDSP and SSP is not limited by the first generation NH and looks like a real introgression of specific genomes.

Conclusions

Analysis of the obtained results allows us to draw the following preliminary conclusions.

Two species of 5-needle pines, namely SSP and SDSP, are genetically compatible; and they have similar flowering periods in the overlapping regions of their ranges.

Natural hybridization between SSP and SDSP takes place throughout the sympatric region. However, there are great differences between the regions and plant association types within region for NH occurrence.

By many morphological traits, NH are strictly intermediate between the species. Only two studied traits were inherited by hybrids as dominant ones, namely the violet color of maturing cones as for SSP and capacity to produce special root sources from the latent buds as for SDSP.

In some plant associations NH occupy a relatively free ecological niche in the second stand layer. Compared to the parental species NH have lower adaptability mainly due to low resistance to the snow load. Moreover, due to good regeneration ability of the crown and root systems NH are quite viable, e.g. able to propagate vegetatively.

In all regions the first generation NH clearly dominate among all NH. NH fertility is much lower than that of parental species, the increased seed-buds' mortality and increased rate of anomalies is observed at all stages of development of seed-buds into seeds. However, under favorable conditions up to 25% of NH seed-buds produce full seeds with differentiated embryo.

Investigation of natural hybridization between SSP and SDSP is just beginning; there is not much reliable data and many available facts can not be interpreted conclusively. However, even now there are reasons to suggest such phenomenon may be significant for the evolution of 5-needle pines including speciation.

Current phylogeny and classification of 5-needle pines are still at the stage of accumulating raw data. Systems based on different taxonomic features, both traditional and molecular ones, differ greatly from each other. Probably, this phenomenon is related to the reticulate character of evolution for this group of species, namely rotation of divergence cycles with following interspecific hybridization.

Acknowledgements

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Rezumat. Goroshkevich S.N., Popov A.G., Vasilieva G.V., 2008. Studii ecologice şi morfologice în zona hibridă dintre *Pinus sibirica* şi *P. pumila*. Ann. For. Res. 51: 43-52.

În Regiunea Baikal nu există o separare fenologică între Pinul siberian (*Pinus sibirica*) şi Pinul siberian târâtor (*P. pumila*) întrucât perioada înfloririi celor două specii coincide. Deşi, în zona respectivă pot fi identificaţi, nu prea frecvent, arbori cu caractere morfologice intermediare care probabil sunt hibrizi naturali. În jumătatea de vest a zonei muntoase Stanovoie, au fost investigate patru regiuni sau zone muntoase şi anume: Barguzinskiy, Baikalskiy, Verchneangarskiz şi Severo-Myiskiy. S-a constatat că hibridări naturale interspecifice au avut loc în diferite regiuni de contact ale celor două specii; totuşi, există anumite diferenţe în privinţa frecvenţei hibrizilor naturali atât în interiorul regiunilor cât şi între ele. Un număr mare de hibrizi naturali a fost găsit numai într-un anumit habitat care se găseşte foarte rar şi care ocupă o suprafaţă foarte mică. Pe coasta de nord-est a Lacului Baikal şi anume zona de pe malul lacului este ocupată de păduri de Pin siberian cu o participare moderată a Pinului siberian târâtor situat sub coroana celuilalt pin. Aici, hibrizii naturali sunt răspândiţi pretutindeni. În privinţa fructificării celor trei unităţi sistematice *P. sibirica* : *P. pumila* : hibrid a fost de aproximativ 300:10:1. Aproximativ 90% din hibrizii examinaţi sunt intermediari între cele două specii parentale în privinţa următoarelor caractere: structura acelor, creşterile şi coroana; cu alte cuvinte, aceştia, prezumtiv, reprezintă prima generaţie hibridă. În comparaţie cu speciile parentale, hibrizii suferă de rupturi de zăpadă. Ca şi pinul siberian târâtor, hibridul are capacitatea de a forma rădăcini din moguri latenţi. Pinul siberian târâtor, pinul siberian şi hibridul cresc împreună în zona mlăştinoasă a deltei superioare a râului Angara. În cele mai productive staţiuni, raportul de creştere a celor trei unităţi sistematice *P. sibirica:P. pumila:*hibrid a fost de aproximativ 60:3:1. În cele mai slab productive staţiuni, raportul de fructificare dintre Pinul siberian târâtor şi hibrid este de 20:1 în timp ce Pinul siberian este steril. Analiza structurii conului a arătat că proporţia de ovule care produc seminţe viabile (având embrionii diferenţiaţi) a fost de 69% la *P. pumila,* 44% la *P. sibirica* şi până la 25% la hibrid. Rezultă că fertilitatea hibridului în zona mlăştinoasă a deltei superioare a râului Angara este mult inferioară comparativ cu speciile pure; cu toate acestea s-a demonstrat că hibridarea naturală dintre Pinul siberian târâtor şi pinul siberian are loc.

Cuvinte cheie: *Pinus sibirica, P. pumila*, hibrid natural, introgresiune, zonă hibridă.

(Tradus de I. Blada)