CONCEPTUAL MODEL OF SPRUCE POPULATION GEOGRAPHIC DIFFERENTIATION ON THE RUSSIAN PLAIN ACCORDING TO PHENE OF SEED SCALE FORM AND GROWTH RATE

Rumyantsev D. E., Chernishenko O. V., Sirotova A. A.

Mitischi filial of Bauman Moscow State Technical University,
141005, Moscow region, Mitischi, 1-st Instituskaya street, 1, LT3, Russia

Abstract

According to our hypothesis increase of forest exploitation intensity must have lead to selection inside the population directed to primary reproduction of sharp scale forms of spruce. The portion of variations with round seed scales is larger in areas with rare fires than in surrounding stands. Modern structure of spruce populations on Eastern-European plain does not reflect the structure of spruce populations according to phenoform of seed scales in geographical gradient after glacier contraction.

Keywords: *Eurasian spruce species, microevolution, drought resistance, growth rate, seed scale form, anthropogenic impact, natural selection, history of agriculture*

Seed scales variability of spruce forming Eurasian boreal forests has attracted attention of many scientists. It was found that the sharpest scale variations of spruce which were determined as Norway spruce (P. abies Karst.) covered the western part of habitat while the eastern part had only round scale variations determined as Siberian spruce (P. obovata Ledeb.). Spruce with intermediate form of seed scales defined as P. fennica Regel grows in intermediate part of the habitat. Besides, part of the habitat occupied with P. fennica Regel shows considerable population polyformism in respect of seed scale form (Fig.1).

D. N. Danilov was one of the first to study seed scales variability of spruce covering Eastern-European Plain. He measured the angle of seed scales in different populations of spruce and came to conclusion that from The Urals to western borders of Russia features of Norway spruce are increasing constantly and gradually, whereas features of Siberian spruce are decreasing.



Fig. 1. Sharp scale and round scale forms of spruce from Darwin reserve (Yaroslavl region)

To explain this phenomenon E.G.Bobrov [1] used principles of introgressive hybridization. An introgression means interspecific crossing at the border zone of the habitats and the back crossing of the hybrid breed with its recurrent parents.

L.F.Pravdin [24] stated and summarized in his monograph principles of introgression as the main reason for the fact that Siberian spruce does not grow on the Eastern-European Plain, and pointed out the role of natural selection in this process: "Having studied macro remains and data obtained from the pollen analysis we may judge that within post-glacial and interglacial periods Siberian spruce covered the territory as far as Moscow region where it almost does not occur nowadays. The cause of it is not in relations between Norway spruce and Siberian spruce or competition between these species but mainly in rules of variability in breed hybridization and inheritance. In post-glacial period glacier contraction was followed by spreading Siberian spruce from south-east and later Norway spruce from south-west and in the border zone of habitats the hybridization occurred. Hybrid breed of spruce being subject to variability occupied new ecological niches and after natural selection only those forms having the most suitable ecology and physiology for certain environmental conditions survived in population. Besides, the hybrid breed proved to be better adapted to the new ecological niches than parent species".

Conclusion made by Pravdin is based on the idea that different forms of spruce have different ecophysiological characteristics. Romeder and Shenbakh (1962) hold that such feature as seed scales form hardly depends on background adaption of species and new forms of trees are unlikely to be the result of natural selection. However, it was repeatedly noticed that gradient of seed scales variability is connected with the gradient of climatic factors changeability. On the basis of calculated coefficient of correlation between seed scales coefficients in populations and climatic characteristics in different parts of habitat P.P.Popov (2005) made the following conclusions:

"During natural selection climatic factors form populations with different biological parameters of spruce features. Under lower temperatures populations with shorter cones, higher narrowing coefficient of seed scales and less elongated top part of cone are formed. On the contrary, higher temperatures and consequently longer vegetation period as well as higher level of rainfall are favorable for forming populations with longer cones, more elongated seed scales and lower coefficient of narrowing at that". At the same time, the author inclines to the idea of "non-adaptive" role of seed-scale form. In order to combine both standpoints that are mutually exclusive for the first sight he offers a hypothesis that genes, which seed scales form depends on, can also determine certain ecophysiological characteristics being able to influence the ability of spruce to adapt to climatic factors. Thus according to this hypothesis although the form of seed scales does not influence the ability of trees within population to adapt to local climatic regime, owing to correlative variability (Darvin, 2001) gene pool of the population as far as seed scales are concerned is formed as a result of natural selection aimed at adaptation to local climatic conditions.

However, after L.F. Pravdin (1975) it was noticed in the monograph summarizing the results of joint researches of S.A.Mamaev and P.P.Popov (1989) that form of seed scales is not a biologically neutral feature. "Earlier fall of seed occurring in western part of habitat in September and sometimes later is a distinctive feature of Siberian spruce while seeds of Norway spruce (f. acuminata) remain longer in cones and fall late in winter. It is mainly connected with the structure of scales which dehisce slowly due to their largeness and soft texture. Climate of Central Europe (damp autumn, snowy winter with light frost, high air moisture) where stands of this variation (f. acuminata) are mainly concentrated also contributes to later dehiscence of cones. Seeds of other variations of Norway spruce with shorter scales fall much earlier. Slow dehiscence of scales and consequently later fall of seeds in comparison with Siberian spruce in this case is determined by soft climate of habitat of these variations of Norway spruce, later beginning of morning frost and slow drying of cone tissue. As a result Norway spruce seeds partly remain in cones till the end of winter".

Is it possible that terms of cone dehiscence influence substantially the ability of population to survive in different climate conditions? First and the most obvious assumption is related to their influence on seeds wintering. Perhaps in more severe Siberian winters the forms, which seeds winter under snow, survive better.

What arguments in favor of this hypothesis can we put forward? In mild European climate there are variations, the seeds of which winter both under snow and on it. However, in Siberia severe winters (presumably) limit the quantity of seeds survived, the seed scale form structure and consequently cone dehiscence synchronism structure is invariable. Nevertheless, we do not know facts proving low spruce seed germination being the result of frost influence.

The problem seems to be very complicated, and despite of the fact that many scientists tried to solve it, by now we can only agree with V.N. Sukachev, because as well as in the beginning of last century, it is "very difficult now to explain the connection between round scales of *P.exelsa* L. kind and low temperature conditions" though we can see obvious relation of round scale spruces distribution in Europe and cold climatic conditions (Sukachev, 1928). In our opinion, the conceptual model presented below gives simple and rational explanation to this problem and to the complex of related ones.

The first assumption may be supported by the idea that successful wintering is not necessarily connected with different resistance of seeds to the influence of climatic factors. Seeds remaining in cones of the tree form the ration for a number of animals and first of all for squirrels (Volkov, 1971; Kaletskaya, 1968). Thus great number of squirrels may theoretically be the factor of selection favorable for variations with falling seeds. Ration of mouse-like rodents includes seeds wintering under snow; consumers of soil seeds are able to eat 99% of spruce seeds even in highly productive year (Volkov, 1971). In Europe with low number of squirrels and high density of mouse-like rodents, the result of selection could be the increase in population of portion of spruce variations with seeds wintering on the trees.

We can suggest one more hypothesis explaining biological importance of terms of cone dehiscence and seed falling. Analyzing eco-biological aspects of alternation of pine by spruce I.S.Melekhov and A.A.Listov (1980) noticed that semination distance of Common pine and Norway spruce differs greatly because of different cone dehiscence terms. Pine cones dehisce in May or June and seeds fall when there is no blanket of snow and spreading of seeds over thin crust of ice is impossible. That is why seminition distance of pine seeds is 50-100metres. Seeds of Norway spruce fall in March or April and are spread over snow crust at the distance of 300 metres or more (according to M.E.Tkachenko at 8-10km). According to other estimations, spruce seeds can be spread over snow crust at the distance up to 500m in the forest and up to 1000m at open spaces (Urda, 1988). At the same time, maximum distance of spruce seeds emission in the stands is up to 150-200m (Urda, 1988). Thus we can suppose that gradient of seed scale form variability may be connected with selection on seeds spreading distance.

In what cases may spruce variations spreading seeds at considerable distances have advantage in struggle for survival over variations spreading seeds not far from mother tree? Firstly, in cases when there is much "free life space" and variations will compete for it. At the same time, variations with long distances of seed spreading will propagate faster. The second case is when on local areas all trees in population of all age categories are eliminated. Variations with short distances of seed spreading will perish together with their breed at that.

These conditions are created because of frequent fires. Variations with short distance of seed spreading will be "dislodged" by fires, undergrowth will perish with mother canopy and slashes will be sown with seeds from distant areas not touched by fires. First of all slashes will be sown with sharp scale variations of spruce with cones dehiscing in March and spreading seeds over thin crust of ice over snow at long distances from mother tree. Obviously, spruce is not always able to reforest on slash without alternation of species, but birch wood without spruce undergrowth is in fact also "free life space" for spruce seeds.

Having accepted this supposition that seems to be logical we need to examine its consequences and check their correspondence to facts. If the speculative consequences of a theory are confirmed by facts, it may be a criterion of its truth.

The first speculative consequence is that the portion of variations with round seed scales is larger in places with rare fires than in surrounding stands. Besides, in humid places spruce seeds wintering in forest floor, that is typical for round scales variations, are consumed by animals less intensively. Thus

according to V.A.Volkov (1971) within spring, summer and autumn after rich yield of spruce seeds in 1965 96% of soil seeds were consumed in wood sorrel spruce forest and in composite spruce forests while in bilberry scrub forest the figure was only 50%. So round scales variations have more chances to produce breed particularly in humid ecotopes both because of different seed spreading and different ability to survive.

In fact number of researches observed that round scales variations grew in water-logged ecotopes (Panin, 1957; Moskvitin, 1959; Milutin, 1963; Urkevich and others., 1974; Pismerov, 1999). This could also be a result of differences in drought resistance and water resistance of spruce with different seed scales forms, but the results of our dendroclimatic researches do not prove this hypothesis, that was discussed in more detail earlier (Rumyantsev, 2004).

The second consequence is that clear cutting affects ecosystem of spruce forest in a similar way as fire: mother canopy as well as opened undergrowth perish. That is why dramatic increase of intensity of clear cuttings in this area must result in total decrease of portion of round scale variations in population.

Sharp increase in amounts of clear cuttings occurred in areas to the west from Moscow after 1861. It was caused by general growth of commercial production after abolition of servage and first of all by construction of rail roads making markets available (Yakushev, 1946; Tsvetkov, 1957). Bishop Nikanor, being the contemporary of this process, set forth some of his observations regarding certain connections between it and railroads construction. These observations were reprinted in “Vestnik” newspaper edited by F.A. Gilyarov (1 december 1884, № 71) and further in 1886 – in an article of Russian philosopher K.N. Leonov as a big quotation (Leonov, 2007). We also will allow quite a big quotation, because it shows very convincingly the mechanism of clear cuts increase in connection with railroads construction. Bishop Nikanor wrote the following: «Does the modern velocity spend the power? No doubt, huge one… Let’s take steam. Great amount of water, iron and fuel is spent for its production. Even though there is plenty of water in Russia, but to get it much iron and fuel is needed as well. And even though there is plenty of iron ore in Russia, but to produce iron, apart from everything else, great amount of fuel is needed! So, fuel and fuel… It is not long ago since the first steam machines for power and movement have been introduced, … but not only forests in England are exhausted,…but also coal deposits are running out… What do we see in Russia? It was now living generation that saw untrodden, almost immense thicks of the forests, and now? On the area from Orenburg to Odessa an observant traveler cannot see any young forest. This traveler used to see dense forests of thousand year huge trees, suitable for ships and other things. Everything is devoured, especially near railroads”.

This is one more evidence of the contemporary person regarding processes which took place in Russian plain forests after 1861. M.E. Saltykov-Schedrin in his book “Blagonamerennye rechi” (“Right-minded speeches”) published in 1876 pays particular attention to drastic increase of forest exploitation intensity after 1861: “Forests here were continuous, virgin: there were no customers for the forest. Because there was nothing to do with it. The only ones who used forest, and at that for free, were serf peasants, who made pitch, tar, tubs, cups, spoons and other chip products. Now peasants are not allowed to go to landowners forest, forest trade declined and of course forest could become dead capital both for the landowners and for the region, but here came railroads, which considerably increased availability of the markets. And together with the first news about the railroads there appeared people of former “prasols” (cattle-dealers), “kabatchiki” (bar keepers), stewards and mayors and other village business people, which came by racing sulky to landlords and offered their services in cuttings. The landlords were enthusiastic. “To sell, to sell! – they cried in chorus – to sell and run then!”.

I am walking or driving by and do not recognize anything. Here, on this very place, there used to be a continuous wall of forest; now there are huge spaces on both sides of the road covered with stumps. The landlord sold the forest for nothing; the merchant cut it for nothing; the peasant grazed cattle on the clearing for nothing. No one grudges anything; no one looks forward; everybody tries to catch what he can in the moment. And now, this disorder started not long ago, and the surrounding looks naked, almost hopeless, stumps, stumps and stumps; somewhere thin willow-bush".

According to our hypothesis, increase of forest exploitation intensity must have lead to selection inside the population directed to primary reproduction of sharp scale forms of spruce. And in fact comparison of data about modern phenotype structure of spruce population in such areas as Tver region (Tatarinov, 1987) and Bryansk region (Milutin, 1963) with the observations made by the first researches shows disappearance of round scale forms and increase of sharp scale forms portion. In other words, spruce stands having reached maturity by the second part of XX century were formed in the conditions favorable for sharp scale spruce forms; chronologically period of their forming concurs with the time of drastic increase of forest exploitation in the second part of XIX century.

Belovezhskaya puscha (Belovezha) witnessed the same situation. V.V.Tatarinov (1980) wrote: «Nowadays number of sharp scale subspecies increases on the territory of Belovezhskaya puscha. Sharp scale forms here account for about 54%, though 60 years ago I.K. Pachoskiy pointed out predominance of obtuse scale forms. Probably individuals of *var. acuminata* bearing now by that time didn't reach bearing age». It should be noticed that after these Pachoskiy observations Belovezha had a period of intensive (not to say destructive) exploitation (Semakov, Strelkov, Melnik, 2004). In August 1915 area of Belovezhskaya puscha was occupied by German troops. The Germans started to cut down intensively valuable old stands. Six sawmills were built for wood processing and 325 km of narrow-gage railroads were created for its transportation. Over two years the invaders transported to Germany 4.5 million cubic meters of wood. After the First World War as a result of Rizhskiy agreement between Poland and Russia the Puscha passed to Poland's ownership, however intensive forest exploitation continued by the English company «Century European Corporation» according to concession agreement. It was only in 1930 when the Polish government cancelled the contract after paying forfeit, but by that time huge areas of old stands were cut down.

This example proves once again that intensive clear cuttings are favorable for more intensive reproduction of sharp scale forms rather than round scale. The same process, connected in our opinion with selection according to distance of seeds spreading, was stated by the comparison of seed scale forms in tree stands of different age in Kostroma region: the results of the research showed predominance of round scale forms in older (120-180 years) stands (Shutov and others., 2006). Here (and others, 2006) the facts are given that explain this phenomena - when ripe and old spruce stands were formed (1820-1880) the forests in Kostroma region were excessively destroyed. Dubuk (1918) wrote the following about forests in Kostroma region in the second part of XIX century: «Forests of different yield quality, giving sawing products were cut completely, and what was not suitable, crooked forests of low yield quality, were left undisturbed. Magnificent spruce ramens are spoiled with the stock of 60 or more taxation fathoms per arpent, and low "mokhry" and understocked "subolot" are growing on, not looking good to the eye.

Another consequence of this conclusion is that modern population structure must reflect the degree of district disturbance by felling. To check this supposition we used data by P.P. Popov (1999) regarding geographic variability of seed scale form coefficient in spruce populations. Share of ripe coniferous stands area in relation to total area of ripe stands of Minselkhoz (Ministry of Agriculture) (Forest fund…, 1999) was chosen as a criterion of felling intensity. Correlation coefficient between two sequences of data is 0,80. The data sequences are shown at fig.2.

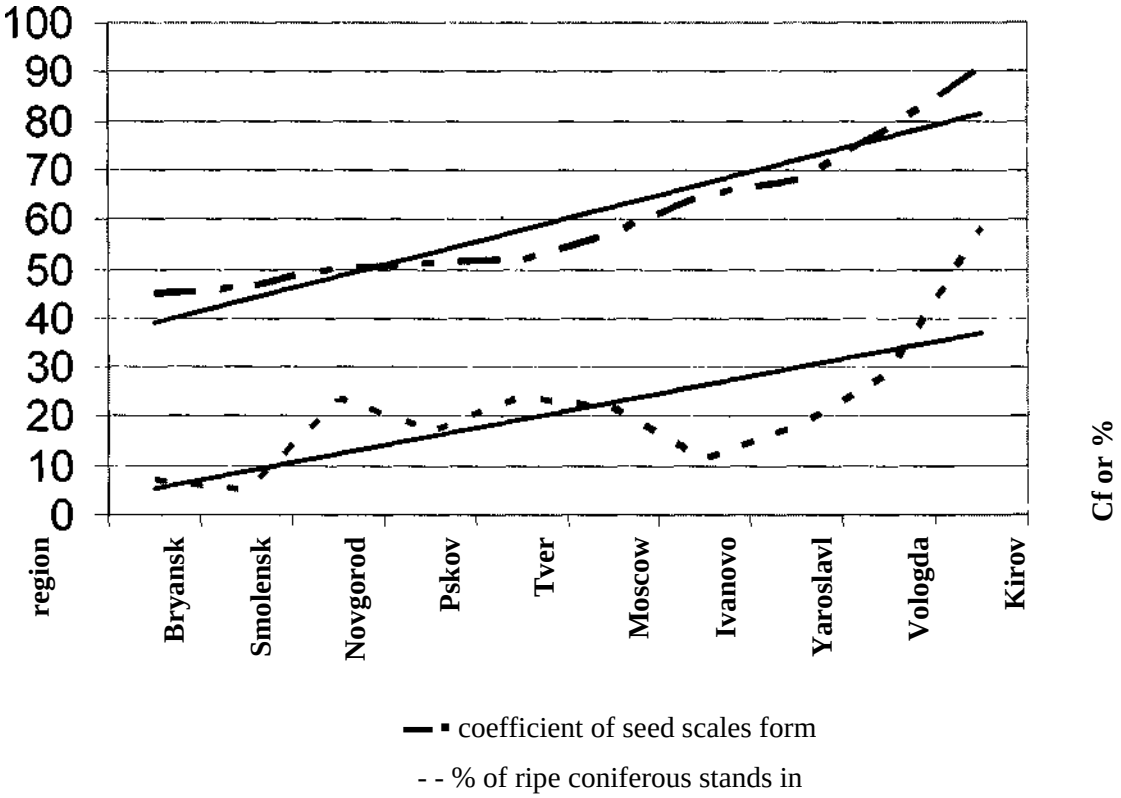


Fig. 2. Relationship between structure of spruce population (according to P.P.Popov) and intensity of forest exploitation in the region. Solid line shows linear trends.

Using data of P.G. Melnik (Melnik and others., 2004) we also found high connection between the data sequences - correlation coefficient is 0,70. Data sequences are shown at fig.3

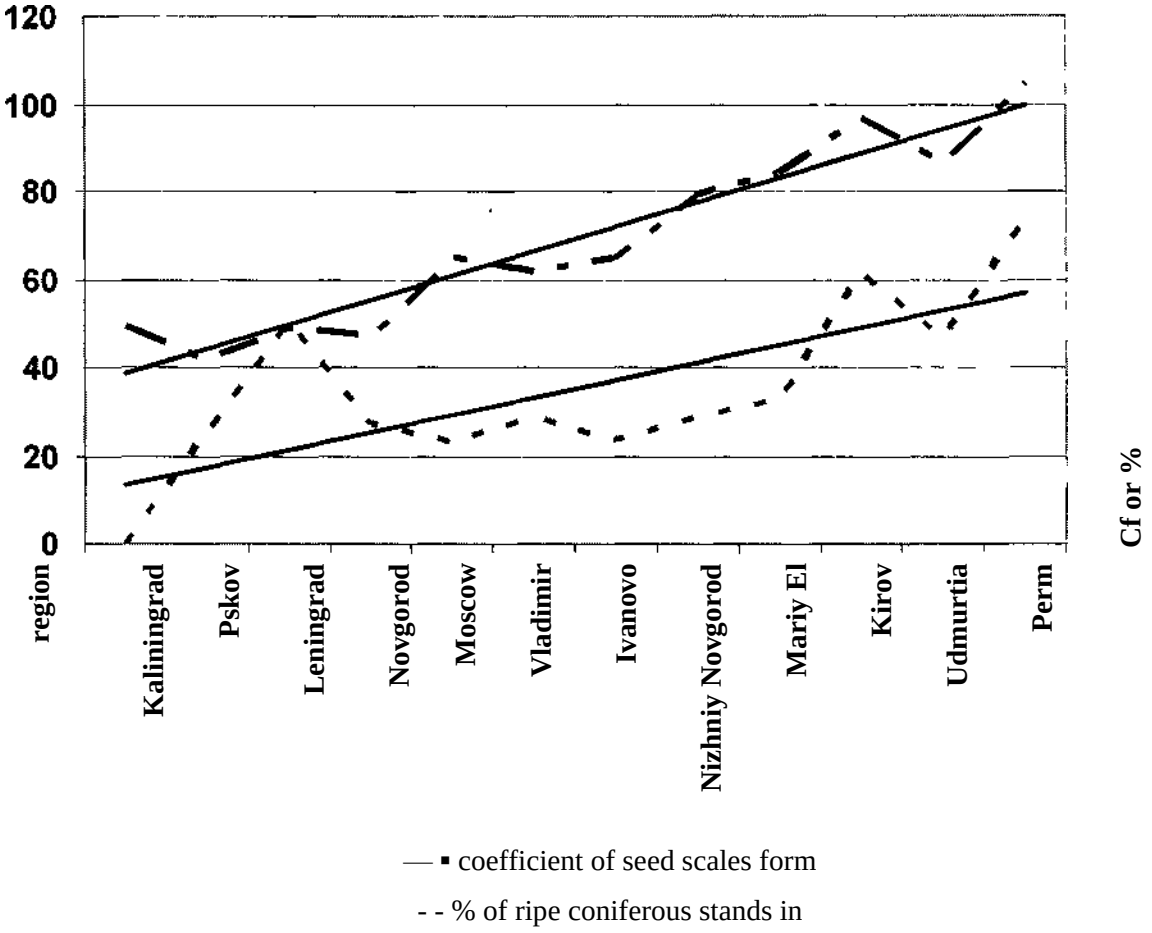


Fig. 3. Relationship between structure of spruce population (according to P.G.Melnik) and intensity of forest exploitation in the region. Solid line shows linear trends.

While choosing criterion of degree of area disturbance by cuttings our main idea was the following. Historically forest management in The USSR in rural forests was much less systematic (Kozhukhov and others, 2001), and that is why lack of most valuable stands (ripe coniferous) in their structure in a certain region is mostly caused by anthropogenic influence on spruce forests in the last centuries. The structure of Natural Resources Ministry forests is more smoothen in accordance with the needs of continuous and sustainable forest management and less suitable for such assessment purposes.

If we refer to the modern structure of spruce population according to phenoform of seed scales within one region, we may underline strong relation between this structure and density of human population in the beginning of XIX century. Data showing this connection in Kostromskaya region (Shutov and others., 2006) is displayed in table 1.

Table 1. Connection between modern phenotypic structure of spruce forest in Kostroma region and density of human population in the beginning of XIX century.

District	Density of population, number of people per square verst	Coefficient of modern structure of spruce population in the district according to phenoform of seed scales
Nerekhtinskiy	47,6	3,3
Kostromskoy	37,9	3
Soligalichskiy	17,7	2,4
Kologrivskiy	11,3	2,2

Increase of coefficients presented in the table reflects increase of portion of sharp scale variations in spruce population in a certain district. There is a strong connection between the increase of human population density and growth of portion of sharp scale variations in population.

Dependences found in Kostroma region (Shutov and others., 2006) and Karelia (Scherbakov, Scherbakova, 1984; Iljinov, 1998) between geographic variation of spruce according to seed scales form and agroclimatological zoning are in our opinion just the effect of different districts suitability for forestry and of history of natural selection in spruce populations related to it. Epos “Kalevala” testifies that area of Karelia where this dependence is quite strong must have experienced long period of slash and burn agriculture (Grekov, 2004). K. Kuusela (1991) pointed out that slash and burn agriculture was used on 50-75% of forest lands on the territory of contemporary Finland in XVIII-XIX century. This percentage is lower in northern areas and higher in southern ones. Speaking about territory of Karelia, we can expect the same trend.

The third consequence. When settling ecotope not occupied by spruce population apical growth speed of a tree will be significant in its survival and further breeding. It was G.F.Morozov (2004) who underlined that: “Biologically the purpose of apical growth is to allow a tree to use sunlight without hindrance. Growth speed is very important in competition between trees both of different species and the same ones. Trees with higher individual intensity of growth become dominant while others are suppressed”. Thus genes determining fast growth of young trees must occur more often in the same genotypes as genes determining dehiscence of cones in March (sharp form of seed scales).

For understory growing under forest canopy fast apical growth is not important because it can not overtop mother trees. On the contrary, slow growth requiring fewer resources is more favorable as in this case understory will grow longer and consequently there are more possibilities that tree of upper story will die and living space will not be occupied. Are there any facts proving this idea? Actually it is known that faster growing breed of population has sharper and longer seed scales (Mamaev, Popov, 1989; Popov, 2005). Besides, it is also confirmed by our data, stated in clause 5.4.

We may assume that this hypothesis is true because it is confirmed in practice. So we can show how Norway spruce spread over Eastern-European Plain emphasizing the role of natural selection directed at adaptation to anthropogenically changed environment in forming modern population structure.

The earliest Eastern-Slavonic state was recorded in VI century in the Carpathians in population of Volhynia (duleby) (Grekov, 2004) and probably in V-VII centuries Slavonic population migrated to the north and north-east (Gudz-Markov, 1997). Settling the western part of Eastern-European plain Slavonic tribes used slash and burn agriculture, and names of months in traditional Slavonic calendars (Polish, Czech, Ukrainian, Belarusian) may prove this fact. The first month when trees were cut was called “sechen” (from the word “sech” – to cut), the second month – when cut trees get dry – “sukhiy” (from the word “sukhoy” – dry); the third – when trees are burned to obtain ashes – was called “berezozol” (from the words “bereza” – birch and “zola” – ashes), then comes “traven” (“trava” – grass), “kveten” (“kvity” – flowers), “serpent” (“serp” – sickle), “veresen” (“vreshi” – to thresh). Traditional names of months used by Chuvash people are connected with their agricultural practice, by

Yakut people – with fishery, by Kazakh people – with cattle-breeding (Grekov, 2004). Thus we can say that increase of Slavonic population is proportionate to increase of intensity of clear cuttings. At the same time in cut-over-land tillage the field is used only for several years and then it is left and forested again. Also due to prescribed burnings forest fires became more often and area of slashes increased. Hence environment became more favourable for reforestation of sharp scale variations of spruce in comparison with round scale ones. And spruce populations with the sharpest scales are generally located on the territory of the earliest Eastern-Slavonic state, i.e. on the areas where the described selection mechanism took place for the longest period of time.

In terms of the problem discussed rather valuable are the observations of A.Pecherskiy (P.I. Melnikov), the author of novel "V lesakh" ("In the forests"), confirmed also by D.N. Kaigorodov (Kaigorodov, 2004). The following abstract shows their idea of forest environment transformation by Slavonic colonists: "In old times "kandoviye" (virgin, old growth) forests were grown in the Hills (hilly bank of Volga river), where the Mordovians were living. These folks like primeval forests and dark groves; no one of them will disturb a tree without need; to fell the forest in vain is a big sin for them; their ancient law says that the forest is the God's house. To destroy the forests means to offend the God, to ruin his house means to draw down the punishment on you. This is how a Mordovian thinks, and this is how the Cheremisy and the Chuvashes think…A Russian is not the same: he is the enemy of the forest; to fell a century-old tree in order to make an axis or horse shaft from a branch, to break a tree suitable for nothing, to bark a lime, to dry out a birch releasing the juice or peeling the bark for heating – no matter for him. He can even cut centenary oaks only to pick up acorns from them to feed the pigs. In old years when Russia was fighting for the lands with ancient tribes it used to destroy the forests unmercifully as enemy's fortress. And this habit is still alive; and now on the Hills where indigenous Russian people live, not cross-breed with foreigners, but of pure Slavonic breed, there are no more forests – only groves somewhere, bushes and dwarf birches…"

Settling Slavonian people on this area and further rise of density of their population must have caused one more holocoenotic effect, that is considerable shrinkage of squirrel population and growth of mouse-like rodent population. This effect increases the ability of seeds of sharp scale variations (wintering in cones) to survive and decreases this ability in seeds of round scale variations (wintering under snow).

Abu-Hamid, Spanish-Arabian writer of XI century, visited Eastern Europe and described commodity-money relations among Slavonian people of that time (Antic Russia, 2005): "They effect settlements by squirrel skins without fur which are not of any use. If the skin has head and feet, every 18 skins cost one silver dirham… And for one such skin one can buy a good round bread enough for a strong man. All kinds of goods can be bought for them: slaves, gold, silver… When they (skins) are spoiled in their houses people bring them torn in sacks to a special market…thread them on strong strings…And nobody can reject them, for them people sell and buy". It can hardly be false that such kind of money relations caused shrinkage of squirrel population and the author indirectly proves this because in the exchange people used worthless skins but only squirrel ones which was checked by head and feet. Obviously decrease of squirrel population lead to survival of high percentage of seeds wintering in cones.

Apart from squirrel Slavonic people traded in ermine, marten and fox fur (Niderle, 2000). Decrease of population of these species eased pressure on mouse-like rodent populations. Sowing of cereals in the forest extended their forage reserve, made it more stable and must have been conductive to increase of their population. That is why less portion of seeds of round scale variations of spruce wintering on forest floor survived.

Data of M.L.Kaletskaya (1968) prove that number of marten and number of mouse-like rodents of slightly disturbed biocenose are closely connected. At the same time, number of marten does not really influences number of squirrel (Kaletskaya, 1968; Volkov, 1971). That is why decrease of number of squirrel caused by hunting was not balanced by extermination of martin.

In addition, growth of mouse-like rodent population in forests near settlements could not be offset by appearance of such species as cat in a system of biocenose. Number of cats was not high in Slavonic

settlements otherwise the statute book “Russkaya Pravda” (Russian Truth) would not impose severe punishment for their killing. Archaezoological material found on the territory of Slavonic settlements of III and V centuries A.D. located in Vladimir region confirms our hypothesis: many bone remains prove intensive hunting for squirrel and marten in the settlement while bone remains of cat were not found [Russkaya Pravda].

It may be assumed that the reason of increase in number of mouse like rodent in the forests near settlements might be to some extent set off by appearance of such species as cat in the system of biocenosis. However, historical evidence shows that number of cats in Slavonic settlements was not high. For example, archaezoological materials from the Slavonic settlements of III and V centuries AD located on the territory of Vladimir region prove that there was squirrel and marten hunting, but bone remains of cats are not found there at all (Krylovich, 2006). It is important to note that in statute book “Russkaya Pravda” issued in IX century (information from www.hist.msu.ru) a cat is not mentioned among domestic animals, which proves at least that it was rare in IX century. The law book of XIV century called «Mitropolichje Pravosudiye» (“Metropolitan Justice”) (information from www.hist.msu.ru) sets the following system of penalties for stealing domestic animals: «For a pigeon 9 koun, for a duck 30 koun, for a goose 30 koun, for a swan 30 koun, for a crane 30 koun, for a cat 3 grivna, for a dog 3 grivna, for a female horse 60 koun, for an ox 3 grivna, for a cow 40 koun, for a “tretjak” 30 koun, for a “lonschina” half of grivna, for a “tel” 5 koun, for a male ship - nogata, for a pig, for a female ship 5 koun, for a male horse - grivna, for a colt 6 nogat». Grivna consisted of smaller money – kouns (marten skins) and nagats (fox skins), so we can understand from the text that cat was more valuable than such important for peasant farms animals as horse and cow, and it again proves that it was rare in Ancient Russia.

Thus there are strong reasons to assume that with settlement of Slavonic people on Eastern-European plain ecological environment became more favourable for those spruce variations with seeds wintering in cones on trees and being able to spread over crust of snow at long distances, that is for sharp scale variations and less favorable for round scale ones. Undoubtedly, spruce with different forms of seed scales freely produced hybrids and it caused not total substitution of round scale variations by sharp scale ones, but forming hybrid spruce with intervening structure of seed scales. In general ideas presented in the article agree with the concept of potential and modern growth in forests of Eastern Europe (Smirnova and others., 2006), that can serve as another proof of its truth.

In conclusion, we may say that modern structure of spruce populations on Eastern-European plain does not reflect the structure of spruce populations according to phenoform of seed scales in geographical gradient after glacier contraction because later it could depend on settlement of Slavonic people on this territory. We should mention here that clear cuttings were almost not conducted in areas with higher ground humidity (Shutov and others., 2006), and that is why these territories served as refugiums for spruce populations with structure similar to those before human interference but such population structure was characteristic only for humid ecotopes. It is variability of seed scales forms of spruce of old stands growing in humid ecotopes looked at from geographical point of view that may give more objective information about introgressive hybridization between Norway spruce and Siberian spruce in post-glacial period.

REFERENCES

1. Bobrov E.G. Introgressive hybridization in genus *Picea* // Theoretical basis of species changeability and coniferous species population structure. Sverdlovsk: ГТС AN SSR. 1974. – P. 60−66.
2. Volkov V.A. Value of marten and spruce seeds consuming animals in southern taiga stands. Abstract of a thesis. Cand. Sc. {Biology}. L.: LTA, 1971 – 20p.
3. Grekov B.D. Kievskaya Rus’. M.: OOO “Publishing House AST”, 2004. – 671p.
4. Grozdov B.V. Dendrology. M.-L.: Goslesbumizdat, 1960 – 356 p.

5. Gudz'-Markov A.V. The Slavs' history. M.:VINITI, 1997. – 488 p.
6. Dabilov D.N. Seed scales variability of *Picea excelsa* // Botanic journal. T. 28. №5. 1943. – P. 191−195.
7. Darvin Ch. "Origin of Species". 2nd edition, add. SPb.: Nauka. 2001. – 126 p.
8. Ancient Rus', IX century-1263 / Vladimir Petrukhin. M.: Astrel', 2005. – 192 p.
9. Il'inov A.A. Intraspecific variability and population structure of *Picea×fennica* (Regel) Kom. In Karelia. Abstract of a thesis. Cand. Sc. {Agriculture}– S.-Pb.:1998. – 25 p.
10. Kaigorodov D.N. Talks about Russian forest. Coniferous forest. Broad-leaved forest. – SPb.: FormaT, 2004 – 304 p.
11. Kaletskaya M.L. Revisited changes in squirrel and marten number in Darvin reserve.// Works of Darvin state reserve, Edition VIII, 1968. – P. 28−56.
12. Kozhukhov N.I, Korotkov S.A., Rumyantsev D.E., Bondarenko V.V., Stonozhenko L.V. Sustainable development of agrarian forests and increase of management efficiency in them. // Forest Economic Vestnik. №2. 2001. – P. 28−33.
13. Krylovich O.A. Archeozoological materials from medieval settlements Vishenki III and Ves' V (Vladimirskaya region, Suzdalskiy district) // Dynamics of modern ecosystems in holocoen. Materials of Russian Scientific Conference. – M.: KMK, 2006 – P.116−122.
14. Kuusela K. Boreal forests dynamics. SITRA, 1991 – 212p.
15. Leont'ev K. N. Bishop Nikanor about harm of railroads, steam and generally about dangers of too fast life. // East, Russia and Slavdom/ Konstantin Leont'ev. – M.: Эксмо, 2007 – C.670-677.
16. Forest fund of Russia (according to data of forest fund state recording as of 1 January 1998) / Reference book. M.: VNIIClesresurs, 1999. – 650 p.
17. Mamaev S.A., Popov P.P. Siberian spruce in the Urals (intraspecific variability and population structure). M.: Nauka, 1989 -104 p.
18. Melekhov I.S., Listov A.A. Some aspects of replacing pine by spruce on European North of the USSR // Lesovedeniye, №3. 1980. – P. 42−51.
19. Melnik P.G., Rubanskaya O.V., Protskaya A.V. Seed scale form variability and population geographic structure of spruce habitat in Central and Eastern Europe // Materials of IV International conference of young scientists "Eurasia Forests – Eastern Carpathians". – M.: MGUL. 2004. – P. 169−171.
20. Milutin L.I. Bryansk region spruce forms, their forestry and economic value. Abstract of a thesis. Cand. Sc. {Agriculture}. Krasnoyarsk: 1963 – 20 p.
21. Morozov G.F. Selectas. – M.: VNIILM. 2004. – 57 p.
22. Moskvitin A.V. Spruce in forest-steppe zone of Mordovia. – Saransk: Mordovskye knizhnoye izdatelstvo, 1959 – 48p.
23. Niderle L. Slavonic antiquities. – M.: "Aletaja", 2000. – 590 p.
24. Panin V.A. Forestry peculiarities of middle taiga spruce forms in European part of the USSR. // Young foresters to forty years of Great October. M.: Technical and scientific society for agriculture and silviculture, 1957 – P.48 - 58.
25. Pismerov A.V. Floral peculiarities of primary forests (Russian Plain and Transurals). // (Rus.) URL: http://www.ecoline.ru/news/JUL97/JUL.txt [16 December 1999].
26. Popov P.P. Spruce on the East of Europe and in Western Siberia: population and geographic changeability and its silvicultural value. Novosibirsk: Nauka, 1999 – 169p.

27. Popov P.P. Norway spruce and Siberian spruce: structure, integration and differentiation of population systems. – Novosibirsk: Nauka. 2005. – 231 p.
28. Pravdin L.F. Norway spruce and Siberian spruce in the USSR. M.: Nauka, 1975 – 176 p.
29. Pravosudiye Mitropolichye // www.hist.msu.ru/ER/Etext/RP/prp.html (23 September 2007)
30. Prostrannaya Russkaya Pravda // www.hist.msu.ru/ER/Etext/RP/mp.html (23 September 2007)
31. Romeder E., Shenbah G. Genetics and selection of forest species. – M.: Selkhozizdat. 1962. – 268 p.
32. Rumyantsev D.E. Results of dendrochronological analysis of spruces with different seed scale forms // Collection of scientific articles by candidates of Moscow state forest university. Scientific work.- Issue. 315 (3). M.: MGUL, 2002. – P.96-98
33. Rumyantsev D.E., Aleksandrova M.S. Dendrochronological diagnostics of separate ecological properties of Picea species // Main Botanic Garden newsletter. Issue. 190. M.: Nauka, 2006. – P.87-93.
34. Saltykov-Schedrin M.E. Blagonamerennyje rechi. M.: Pravda, 1984 – 640p.
35. Semakov V.V., Strelkov A.Z., Melnik P.G. Forestry excursion to Belovezhskaya Puschya. M.: MGUL, 2004 – 72 p.
36. Smirnova O.V., Bakun E.U., Turubanova S.A. Ideas of potential and restored vegetation cover of Eastern Europe forest belt. // Forest Science, 2006, №1 – P. 22−33.
37. Sukachev V.N. Forest species: their systematic and phytosociology. Coniferous – M.: Novaya derevnya, 1928. – 81 p.
38. Tatarinov V.V. Comparative analysis of spruce populations phenotype changeability in spruce forests communities in central part of Russian Plain. // Botanic Journal, 1987, T.72, №2 – P. 229-238.
39. Tatarinov V.V. Spruce interspecific changeability on south-west boarder of its continuous habitat // Population researches of plants in reserves. M.: Nauka. 1989. – P. 19−33.
40. Tkachenko M.E. General silviculture. – L.: Goslestechizdat, 1939. – 746 p.
41. Urda I.F. Plants dissemination and paleo- and bio-geography issues. Kiev: Naukova dumka, 1988 – 198 p.
42. Tsvetkov M.A. Change of forests amount in European Russia from late XVII century to 1914. M.: AN SSSR, 1957 – 213 p.
43. Shutov V.V., Sazhin V.S., Novikov A,N., Kozhurin S.I., Shelepov V.V., Varpholomeev V.E., Ryzhova N.V., Dudin V.A., Urzov G.N., Bagaev E.S., Kudryavtsev V.A., Korneev I.A., Ustjuzhanin A.V. Kostromskaya region forests: contemporary condition and prospects of forest use. – Kostroma: KGTU, 2006. – 179 p.
44. Scherbakov N.M., Scherbakova M.A. Ecological and genetic adaptations of Spruce in Northern conditions. // Adaptation of woody plants to critical environmental conditions. Petrozavodsk, Karelia branch of AN SSSR, 1984 – P.78-89.
45. Urkevich I.D., Golod D.S., Parfenov V.I., Sidorovich E.A., Chubanov K.D. Multiformity of woody plants in Belorusskaya SSR forests // Theoretical basis for interspecific changeability and population structure of coniferous species. Sverdlovsk: UNC AN SSSR, 1974 –P.51-59.
46. Yakushev M.R. Forests of Smolensk Region (materials on history of regional forests). Smolensk: SKNII, 1946 – 85 p.