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Variation in the Number of Cotyledons in Scotch Pine in the East of European Russia

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Abstract—Population variation in the number of cotyledons in Scotch pine seedlings was studied within a part of species range in the east of European Russia. Four zones were outlined, each comprising several population groups differing in the average number of cotyledons. The observed variation of this character is explained by the history of species dispersal in the Holocene. The boundaries of migration zones coincide with the external boundaries of population groups identified previously (Vidyakin, 1991b, 1995).

Studies on regularities of the formation of natural populations and the populational structure of species are important for solving complex biological problems, primarily for understanding the essence of the species, criteria of species identification, principles of organization, intraspecific systematics and taxonomy, and for assessing the size, boundaries, and interactions of populations. The investigation into the population structure of tree species, in particular of pine, is just beginning, but the available data show that this structure is complex and ordered into a hierarchical system of areal elements of various ranks (Mamaev and Makhnev, 1982, 1983a, 1983b; Semerikov, 1986; Makhnev, 1987).

In previous studies performed in eastern European Russia (Vidyakin, 1991b, 1995), we used indices of cone shape (ICS) and cone apophysis shape (ICAS) to identify corresponding areal entities of Scotch pine (*Pinus sylvestris* L.) trees, which were provisionally given a population rank. Subsequent investigations showed that these entities were actually groups of populations, as within each of them, according to phenes of generative organs, smaller subdivisions of the species were distinguished. It was concluded that the latter are populations proper, which have the genetic basis and are the elementary evolutionary units of the species. We analyze population structure with respect to each character separately (Vidyakin, 1991a) and regard the population as a natural historically formed unit whose structure reflects various processes and phenomena in their development (Glotov, 1975).

Investigation of the population structure of the species by few characters produces unreliable results (Mamaev, 1970), and, hence, the maximum possible number of characters should be involved in analysis (Yablokov and Larina, 1985). In the present paper, we describe the results of studies on variation in the number of cotyledons in relation to the previously revealed

population-group structure of the species (Vidyakin, 1991a, 1991b, 1995).

The number of cotyledons in coniferous species within their ranges demonstrates clinal variation associated with latitudinal-zonal and meridional-provincial transformation of natural factors (Sukachev, 1928; Chuang Shi-Tsui, 1969; Pravdin, 1975; Prokazin *et al.*, 1975; Shutyaev, 1979). There have been virtually no attempts to elucidate the relationship between a character and the population structure of species, as virtually no schemes of the distribution of populations within species ranges were available. The only such scheme was composed by Mamaev (1970) for Scotch pine in the Ural part of its range.

MATERIALS AND METHODS

The study was performed on Scotch pine seedlings grown from seeds of different geographic and ecological (with respect to forest types) origin. The seeds of different geographic origin had been collected in 70–100-year-old stands in Arkhangelsk, Vologda, Kostroma, Kirov, and Nizhegorodskaya oblasts, Komi and Mari El Republics, and Tatarstan, Chuvashia, and Udmurtia, i.e., in the area between 56–65° N and 46–54° E (Vidyakin, 1991b). The greatest number of samples was taken from forests of Kirov oblast and Udmurtia (subzones of middle and southern taiga and coniferous-broadleaved forests). On felling areas, ten cones were collected from each of 70–80 trees in the most common forest types. For each sampling site, a pooled sample was prepared before sowing, in which seeds were mixed proportionally to productivity of trees.

To analyze ecological (by forest types) variation in the number of cotyledons, cones and seed samples were obtained in the same way, except that cones were col-

Table 1. Distribution of Scotch pine seedlings with respect to the number of cotyledons in cultures grown from seeds collected in different forest types (Urzhum forest farm, Tse-pochkinskoe forestry)

Forest type	Number of seedlings						
	number of cotyledons						total
	3	4	5	6	7	8	
Cowberry pine forest	0	9	87	169	44	3	312
Bilberry pine forest	0	6	77	160	39	3	285
Wood sorrel pine forest	0	6	84	181	49	3	323
Total	0	21	248	510	132	9	920

lected in different forest types found within the same stand.

All seed samples were sown in a greenhouse under the same growing conditions. After germination, the number of cotyledons was counted in 200–450 plants grown from each geographic and ecological seed sample.

Statistical data processing was performed by means of *G*-test (contingency tables) and three-level nested ANOVA (levels: migration zone, group of populations within the migration zone, and population within a group of populations; model II; unequal sample sizes) (Sokal and Rohlf, 1995; Rohlf and Sokal, 1995).

RESULTS AND DISCUSSION

Analyzing geographic variation, it is methodologically important to find out if the observed variation

depends on ecological conditions of growth, whose integral reflection is the forest type. Table 1 shows variation in the number of cotyledons in cultures grown from seeds from different forest types found in the Urzhum forest farm (Tse-pochkinskoe forestry). Similar results were obtained for seeds collected in Kirsinskoe (Peskovskoe forestry) and Kirovskoe (Adyshevskoe forestry) forest farms. Summing up the *G* values and the degrees of freedom by three contingency tables (for three populations), we obtain $G = 1.715$ ($df = 15$, $P > 0.9995$). Thus, samples from the same population are very homogeneous, and growing conditions do not influence the variation of this character.

Table 2 and the figure show the data on geographic variation in the number of cotyledons. Materials on population groups Luza (2), Vetluga (4), Svechinskaya (9), and Zelenodol'sk–Kama (15) are absent or insufficient. Samples are arranged in the table according to the average number of cotyledons in seedlings) from each migration zone. The results of ANOVA for these data are presented in Table 3.

It is seen that interpopulation variation within each population group was not revealed. Moreover, the mean square for populations (according to the structure of the ANOVA model, comprising population variance and error variance) proved to be smaller than the mean square (variance) of the error. Although this may be a result of random fluctuation, two facts deserve special attention. First, two-way ANOVA was performed separately for nine groups of populations (three groups are represented in our material by only one population). In eight of them (except the population group from Severnye Uvaly), mean squares for a population were

Table 2. Distribution of Scotch pine seedlings with respect to the number of cotyledons in different populations

Migration zone	Number of seedlings							Average number of cotyledons
	number of cotyledons						total	
	3	4	5	6	7	8		
First	0	102	1005	2101	475	22	3705	5.81
Second	0	177	1177	1562	222	5	3143	5.59
Third	11	379	784	429	46	4	1653	5.08
Fourth	7	158	612	475	26	0	1278	5.28

Table 3. Results of three-level nested ANOVA for the number of cotyledons in Scotch pine

Level	Sum of squares	Degrees of freedom	Mean square	<i>F</i>	<i>P</i>
Migration zone	721.970	3	240.6565	344.00	≪0.001
Population group	6.296	9	0.6996	1.32	0.22
Population	4.703	24	0.1960	<1	ns
Error	5154.471	9742	0.5291	–	–

Note: As for the population $F < 1$, we follow the rule for pooling mean squares (Sokal and Rohlf, 1995) and test the significance of a population group by dividing the mean square 0.6996 by $(4.703 + 5154.471)/(24 + 9742) = 0.5283$; ns means that the effect of the factor is nonsignificant.

smaller than the corresponding squares of errors. Second, we used the *G*-test to analyze homogeneity of populations in each group by comparing sample distributions (contingency tables). Summing up *G* values and degrees of freedom for all groups, we obtain $G = 14.048$ at $df = 72$. This means that the probability of accidentally obtaining the same or greater homogeneity is less than 10^{-9} ! It should be noted that the corresponding probability for seeds from different forest types (Table 1) is also low: $P < 0.0005$. This may be evidence for a certain systematic bias in estimating the variation of populations within a population group. Its probable reason is that populations within the group were chosen very carefully to avoid sampling from the hybrid zone between neighboring groups, i.e., outside of a certain "pure" group. The observed effect deserves special investigation.

The effect of the population group within the migration zones, as they are organized in Table 3, is also statistically nonsignificant.

The map-scheme (figure) demonstrates a certain orderliness in the distribution of population groups with identical average numbers of cotyledons. Four zones can be distinguished in the investigated part of the species area.

The first zone (the average number of cotyledons 5.81) is located in the lower and middle reaches of the Vyatka River, on the right bank of the Kama River, and the left bank of the Volga. It stretches from southeast to northwest and comprises the Kiknur, Lower Vyatka, Udmurt, Buretskaya, Zvenigovo–Kokshaiskaya, and Mari–Vyatka–Uvaly groups of populations. This zone is separated from neighboring zones only by the northern boundary (other boundaries are beyond the region of studies). We suppose that the southern boundary of the zone is situated far away, as indicated by the available seedling samples from seeds collected on the right bank of the Volga in Chuvashia. Here, the average numbers are as follows: Kirskaa forest farm, 5.88; Ibsresinskii forest farm, 5.88; and Shemurshinskii forest farm, 5.79. These seeds originated from areas located 80–120 km south of the study region. In the west, the boundary appears to lie along the left bank of the Vetluga River. This is confirmed by a sample of seedlings from seeds collected in the Tonkinskii forest farm (Nizhegorodskaya oblast), in which the average number of cotyledons is quite different (5.55). As no seeds were collected on the left bank of the Kama River, we do not know how far away from the region of studies the eastern boundary of the zone is situated.

The second zone (average 5.59), which comprises the Central, Yug, and Northern Dvina groups of populations, is also generally extended from the southeast to the northwest. The map shows that these population groups are spatially separated and have no common boundaries. However, we assume that the Northern Dvina group is connected with the Yug group somewhere outside of the investigation region, and the Yug

group borders on the Central group. The boundary between the Yug, Central, and Northern Uvaly groups was drawn arbitrarily, as there were only a few sample plots (Vidyakin, 1991b). To outline this boundary more precisely, additional sample plots are being established in the middle Moloma River basin and in the Yug–Luza interfluvium.

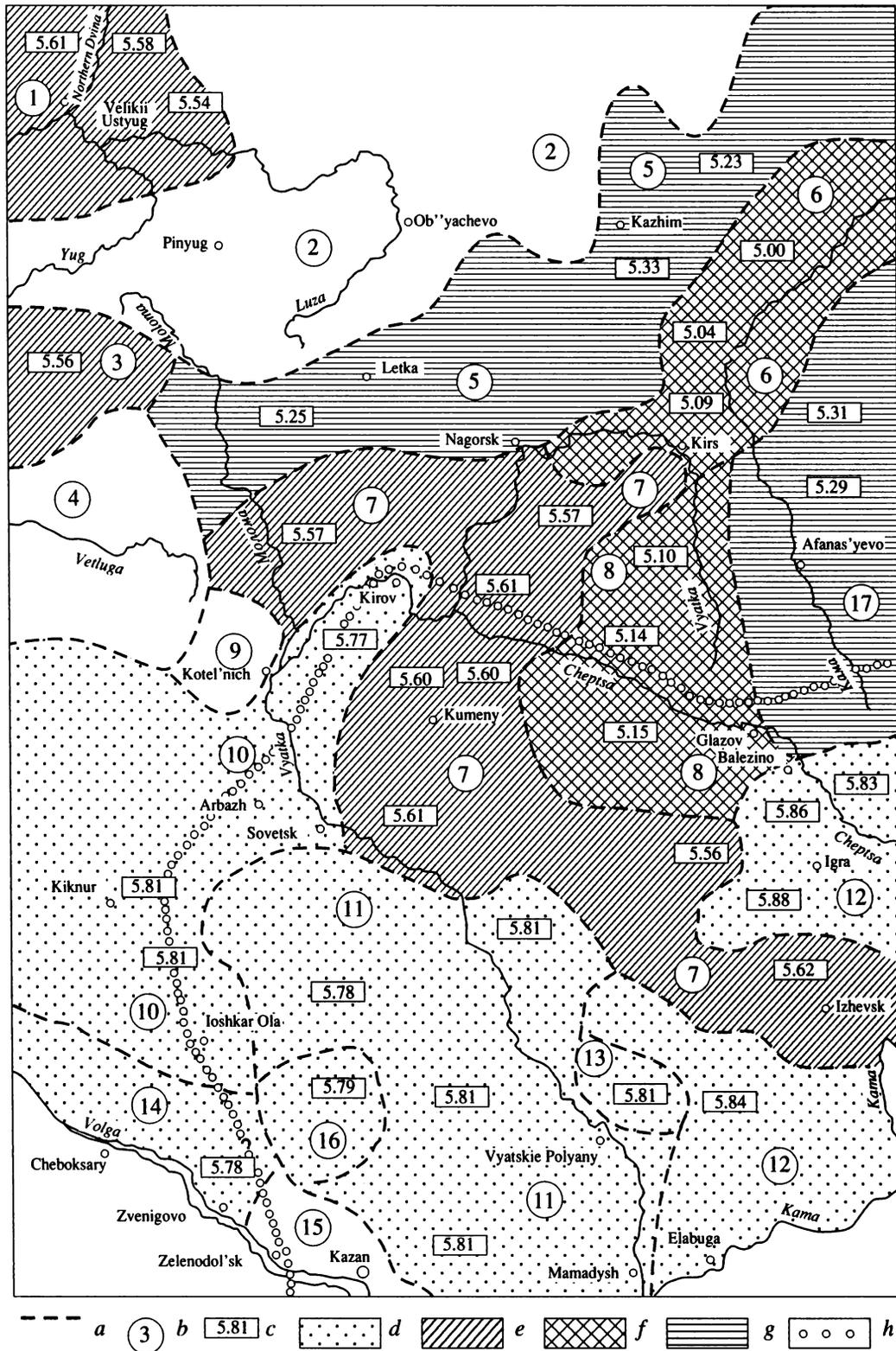
The third zone (average 5.08) comprises the Chepetskaya and Kaiskaya population groups. It covers the middle reaches of the Cheptsya River, the upper reaches of the Vyatka River, and the basin of the Kama, where the river turns from the northwest to the northeast. The zone extends from the northeast to the southwest.

The fourth zone (average 5.28) includes the groups of populations of the Northern Uvaly and the Upper Kama Upland.

The number of cotyledons changes according to the population–group structure of the species, rather than clinally (depending on the latitude and longitude of the site of seed origin). For example, average numbers of cotyledons at the latitude of the city of Kirov change from the west to the east in the following way: 5.68, 5.77, 5.61, 5.10, 5.29; and from the north to the south, along the Pinyug–Cheboksary line: 5.58, 5.54, 5.25, 5.57, 5.81. A weak tendency toward clinal latitudinal variation in the character is observed only within limits of each of the aforementioned zones. In the third zone, for example, the average number of cotyledons changes from the north to the south in the following way: 5.00, 5.04, 5.09, 5.10, 5.15. The distance between the first and the last samples is 250 km. Thus the variation gradient of the character is 0.06 per 100 km.

We believe that the observed structurization of the Scotch pine range may be explained by specific features of species distribution in the Holocene. The influence of the migration zone, the upper-level factor in the hierarchical structure shown in Table 3, is highly significant statistically.

It is known that in the Pleistocene there were several glaciation periods in the territory of European Russia: Likhvin, Dnieper (the greatest), and Valdai glaciations (Lavrova, 1952). There were no forests in the zone of continuous glaciation or at some distance from it, in the so-called periglacial zone (Sukachev, 1938; Kats, 1952; Gorchakovskii, 1953, 1969). In this time, woody vegetation grew in glacial refugia situated beyond the periglacial zone, in areas with relatively favorable conditions for forest growth. It was thought (Frentsel, cited from Pravdin, 1964, 1975) that woody vegetation in the Pleistocene survived in glacial refugia in southern Europe, the Carpathians, middle Russia, Middle and Southern Urals, and middle Siberia. It is supposed that the refugia for larch were in the Middle and Southern Urals (Neishtadt, 1957); for cedar, in the Altai piedmonts (Povarnitsyn, cited from Neishtadt, 1957); and for pine, in the eastern Carpathians (Vul'f, 1944). In the interglacial periods and the Holocene, as climate became warmer, the glacier retreated to the north, and



Map-scheme of Scotch pine variation with respect to the number of cotyledons in the east of European Russia. Population groups (according to Vudyakin, 1991b, 1995): (1) Northern Dvina, (2) Luza, (3) Yug, (4) Veluga, (5) Severnye Uvaly, (6) Kayskaya, (7) Central, (8) Chepetskaya, (9) Svehinskaya, (10) Kiknur, (11) Lower Vyatka, (12) Udmurt, (13) Buretskaya, (14) Zvenigovo-Kokshayskaya, (15) Zelenodol'sk-Kama, (16) Mari-Vyatka Uval, (17) Upper Kama; (a) boundaries of population groups; (b) population group numbers; (c) average number of cotyledons in the population. Migration zones: (d) First, (e) Second, (f) Third, (g) Fourth; (h) the southern boundary of the ice sheet in the period of the Dnieper Glaciation (according to Shernin, 1955).

vegetation migrated from the glacial refugia (Lavrenko, 1930; Sukachev, 1938; Kats, 1952; Gorchakovskii, 1953, 1969).

At the peak of glaciation, a considerable part of the investigation region was covered with an ice sheet (figure), and the periglacial zone lay southeast of its margin (*Priroda...*, 1967). Therefore, pine was absent from the investigation region in this period (possibly, except for the left bank of the Kama River) and migrated there from neighboring refugia in the Holocene. The boundary of the maximum glaciation in this region is directed from the east to the west along the upper Kama River–Glazov–Chepts River–Kirov line, abruptly turns to the southwest and south, and then, beyond the investigation region, to Penza and the mouth of the Medveditsa River (a left-bank tributary of the Don River) (Gorchakovskii, 1953). Thus, pine could not survive west and southwest of the investigation region because of powerful glaciation extending far to the south. It was also absent in the south, as there was the periglacial zone adjoining the eastern margin of the glacier. The pine could migrate to the investigation region only from the southeast and east, i.e., from the Middle and Southern Urals and adjacent territories of the Preural and Transural regions, which were not affected by continuous glaciation (Vul'f, 1944). There are numerous indications to the presence of pine in these regions in the Pleistocene and the early Holocene (Gorchakovskii, 1953, 1969; Neishtadt, 1957; Khvalina, 1963; Ryabova, 1965).

Hence, the zones distinguished with respect to the average number of cotyledons in pine seedlings (Table 2) may represent the pathways of the postglacial species dispersal from refugia of the Southern and Middle Urals and the adjacent Preural and Transural regions (for brevity, subsequently referred to as Southern and Middle Ural refugia). It is supposed that such zones of woody plant migration actually exist and are possible to discover in the species range with the aid of genetic markers and phenes (Iroshnikov *et al.*, 1989). However, we do not know of any studies dealing with their mapping. The migration zone is an aggregate of population groups having common natural-historical background associated with the dispersal of the species from one center under the influence of climatic changes. We regard it as a structural subdivision of the highest rank in the population hierarchy of the species.

Our data obtained within a limited part of the Scotch pine range suggest that the dispersal of this species proceeded from different centers. Their geographic location can only be identified provisionally. The contour and general direction of the first zone suggest that pine migrated to this territory from the Southern Urals via two routes: the first (southern) lay along the line Vyatskie Polyany–Ioshkar Ola–Sovetsk–Kirov, and the second (northern), Votkinsk–Igra–Balezino. The second zone, also generally extending from the southeast to the northwest, reflects migration from the refugium that was probably located on the territory of present-

day Bashkortostan. From there, pine migrated in the direction Izhevsk–Kumeny–the Chepts River mouth–the lower Moloma River–the upper Yug River–Velikii Ustyug–the source of the Northern Dvina river. The third and fourth zones reflect the direction of pine dispersal from two probable refugia in the Middle Urals. These zones generally extend from the northeast to the southwest. The refugium from which the pine migrated along the Kama River to the upper reaches of the Vyatka River and the middle reaches of the Chepts River (the third zone) was probably located west of the refugium from which the dispersal of pine proceeded in two directions (the fourth zone): over Northern Uvaly toward Kazhim–Letka to the middle reaches of the Moloma River and along the Upper Kama Upland toward the upper reaches of the Kama River.

Each zone occupies a large territory characterized by an exceptionally high environmental heterogeneity. Therefore, the general gene pool of the ancestral population of a given refugium have apparently been differentiating in a long series of generations beginning from the moment of species appearance in the investigated part of its range in the postglacial period. This actually occurred, as follows from the data on ICS and ICAS (Vidyakin, 1991b, 1995). With respect to the number of cotyledons, the migration zone at the present stage of microevolution is an integrated system retaining the initial genetic structure.

If total variance in the number of cotyledons within the study area is taken as 100%, the variation of this character will be 83.5% within the same population, 0% between populations, 0.1% between groups of populations (not differing from zero statistically), and 16.4% between migration zones. The prevalence of the intrapopulation component in total variation mainly depends on specific features of genetic determination and expression of dimensional and quantitative characters (Mamaev, 1973; Semerikov, 1986). It is noteworthy that variation increases at the highest hierarchical level, which is determined by natural-historical factors. A similar tendency was previously noted in *Quercus robur* L. in the Caucasian part of its range for large territories ranked as geobotanical provinces and subprovinces (Glotov *et al.*, 1981).

The observed population structure of Scotch pine reflects the current stage of microevolution. It is quite probable that different vectors of natural selection in the parts of migration zones considerably differing in environmental factors will lead to differentiation of populational structure with respect to the number of cotyledons, and the areal elements equivalent to previously identified population groups will be segregated (Vidyakin, 1991b, 1995). Judging by characters that are less stable in the evolutionary aspect, it appears that this differentiation already proceeds, which is manifested in the subdivision of migration zones via partial spatial specification and stabilization of characters at different values.

CONCLUSIONS

(1) Distributions of the character "the number of cotyledons" in Scotch pine seeds from different forest types found in the same stand do not differ from one another. Four zones are distinguished within the investigated part of the Scotch pine range, each comprising several population groups that differ in the average number of cotyledons. Within zones, no significant differences between groups of populations and between populations are found.

(2) Variation in the character "the number of cotyledons" over the territory is explained by the history of species dispersal in the Holocene, which determined the formation of the observed migration zones. The boundaries of these zones coincide with the external boundaries of the previously identified population groups (Vidyakin, 1991b, 1995).

(3) A weak latitudinal clinal variation in the number of cotyledons is observed only within the limits of migration zones.

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