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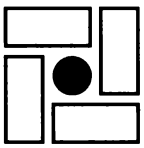

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Ecological–Demographic Characteristics of Natural Populations of *Plantago major* L.

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Abstract—Age structure was analyzed in 45 cenopopulations of *Plantago major* L. from different habitats of Russia. Modal spectrum was calculated for populations of *P. major*. The characteristic of the ecotope was given by three scales of Ramenskii: richness, moistening, and changeability of moistening of the soil. A clear interrelationship was determined between demographic characteristics and elements of the ecotope. It was established that subspecies *P. m.* ssp. *major* and *P. m.* ssp. *pleiosperma* occupied rather different habitats.

Plantago major is a perennial herbaceous polycarpic plant with short rhizome and a cluster of roots. It has a monopodial-rosette type of shoot formation (Serebryakova, 1977, 1988; Komarova, 1987). Leaves are ovoid-oval stalked. Generative shoots (scapes) are formed as axes of the 2nd, rarer of the 3rd, order and are leafless as a rule. The root system is formed by adventitious roots outgoing from a short vertical rhizome.

At present, the division of species *P. major* into two subspecies is widely accepted: *P. major* ssp. *major* Pilger and *P. major* ssp. *pleiosperma* Pilger (Pavlova, 1923; Pilger, 1937; Molgaard, 1976; Van der Aart, 1985; Van Dijk, 1989; *Plantago* ..., 1992). Typical plants of *P. m.* ssp. *pleiosperma* differ from ssp. *major* in their leaves, which are pressed down to the soil. Leaves are lanceolate-oval, often with an unevenly serrated margin at the base of the leaf blade, which is not characteristic of ssp. *major*. Generative shoots of ssp. *pleiosperma* are suberect and plagiotropic in their basal part, whereas they are orthotropic in ssp. *major* (Figs. 1 and 2). The number of seeds in a boll is the only reliable criterion for differentiating the subspecies: from 4 to 13 in *P. m.* ssp. *major* and 14 and more in *P. m.* ssp. *pleiosperma*.

The question of subspecies status of ssp. *major* and ssp. *pleiosperma* has not been completely solved, because these forms are not isolated geographically, and are often "mixed" ssp. *major*–ssp. *pleiosperma* populations are found, especially in agrocenoses (*Plantago* ..., 1992). At the same time, the existence of genetically predetermined differences between the forms ssp. *major* and ssp. *pleiosperma* is undoubted (*Plantago* ..., 1992).

Up to now, the subspecies were not practically differentiated in Russian population–ontogenetic researches. In foreign investigations, the population–ontogenetic approach was not used in the determination of subspecies; only absolute age was determined sometimes (*Plantago* ..., 1992).

This work is intended to describe the age structure of cenopopulations (CP) of *Plantago major* L. under different ecological conditions, both taking into account its differentiation into subspecies and without distinguishing subspecies.

MATERIAL AND METHODS

Intensive sampling was performed in contrasting habitats in the territory of the Republic Maryi El (Volzhskii, Zvenigovskii, Orshanskii, Medvedevskii, Novotor"yal'skii, and Yurinskii raions). Individual populations were investigated in the vicinity of the cities of St. Petersburg, Pushchino-on-Oka, Gorno-Altaisk, and in the Apastovskii raion of Tatarstan (Zhukova *et al.*, 1993). In total, 45 populations of *P. major* were studied from 1991 to 1994.

Standard geobotanical descriptions were performed in the phytocenoses under study. The plant lists obtained were analyzed, and the abundance was graded by the scales of Ramenskii (Ramenskii *et al.*, 1956) with the use of the program complex ECOSCALE (Komarov *et al.*, 1991) by the method of weighted mean center of interval.

In every population, 10 to 30 provisional plots 0.5 × 0.5 m were established for the determination of age structure. They were allocated randomly or regularly (over every 3 m). Determination of ontogenetic (age) states of *P. m.* ssp. *major* (Fig. 1) was based on diagnoses and keys developed by Zhukova (1983a, b). Ontogenesis of ssp. *pleiosperma* was given for the first time (Fig. 2).

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Fig. 1. Ontogenesis of *Plantago major* ssp. *major*.

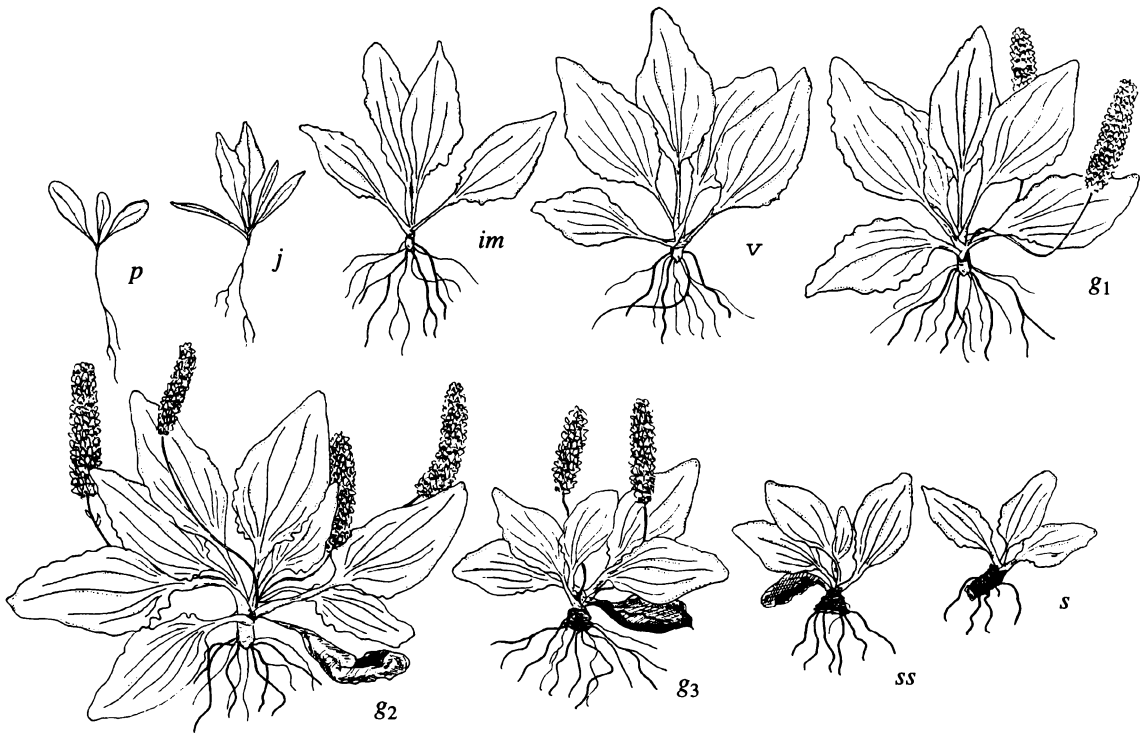

Fig. 2. Ontogenesis of *Plantago major* ssp. *pleiosperma*.

Table 1. Characteristics of the age structure in 45 cenopopulations of *P. major*

Type of cenopopulation	Number of cenopopulations	Density, ind. per 0.25 m^2	Coefficient of age status Δ	Recovery index I_r, %
Invasive	1	35.8	0.031	–
Young normal (with domination of *j* in pregenerative period)	14	13.4–148.4	0.055–0.280	56.0–1157.0
Young normal (with domination of *im*)	10	1.6–178.0	0.098–0.297	44.0–375.0
Young normal (with domination of *v*)	10	3.7–48.8	0.118–0.355	56.2–992.0
Mature normal	4	1.5–49.5	0.209–0.452	74.0–415.0
Aging normal	4	39.4–70.7	0.216–0.665	31.5–1215.9
Old normal	2	16.5–48.9	0.467–0.560	131.1–783.0

Previously received (1981–1984) data from the stationary transects in the floodplain of the Bol'shaya Kokshaga River (Republic Maryi El) were used for the characteristics of the dynamic processes in populations of *P. major*.

The density of seedlings per 0.25 m^2, and the ratio of number of seedlings to total number of cenopopulation, were determined by analyzing the demographic structure of cenopopulations. Shares of pregenerative, generative, and postgenerative fractions were accounted separately. Coefficient of age status Δ (Uranov, 1975) and recovery index I_r (Zhukova, 1987) were calculated. The modal (basic) range of the age structure of populations of *P. major* was created on the basis of the whole totality of data (Zaugol'nova, 1976, 1994; *Tsenopopulyatsii rastenii* ..., 1988).

Subspecies in populations were determined by the generative plants. In these plants, the number of seedbuds in a seedboll from the central part of the ear was calculated with fresh and preserved material. Twenty-three out of forty-five cenopopulations were used in the separate study of subspecies. The volume of the material was decreased, because at the beginning the work was not aimed at the differentiation of subspecies, and determination of subspecies from the herbarium samples was very difficult.

Statistical analysis of data obtained was performed with the AGESITES and AGETIMES programs (Zhukona *et al.*, 1992) and STAT, developed by V. L. Toropov at Maryi State University.

RESULTS AND DISCUSSION

Age composition is one of the most significant characteristics of population, which determines its stability and sustainability.

Rabotnov (1950) first has established the idea of the classification of plant populations by their age structure. He outlined the invasive, normal, and regressive types of populations. A more detailed classification was suggested by Uranov's school (Zhukova, 1967; Uranov and Smirnova, 1969). According to the latter, the young (v, g_1), mature (g_2), aging (g_3), and old (ss) populations were distinguished among the normal populations by the domination of the adult ontogenetic groups. This corresponded to particular stages in the development of the population flow.

The results of the study of age structure in populations of *P. major* suggested that the great majority of cenopopulations were normal and able to self-maintenance through seeding (Table 1). There was one invasive cenopopulation. Regressive populations were not found. Of 44 normal cenopopulations, 34 cenopopulations were young, 4 were mature, 4 were aging, and 2 were old. Among normal cenopopulations, 15 were full-membered, and 29 were not full-membered.

Of the 23 cenopopulations of *P. major* for which the subspecies were determined, 5 cenopopulations were "pure," represented exclusively by ssp. *major*, 8 were "pure" represented by ssp. *pleiosperma*, and 10 contained both subspecies. It should be noted that we considered "pure" and "mixed" cenopopulations that are the totalities of the individuals of the species within the certain phytocenosis. In this case, some cenopopulations could undoubtedly belong to one population and be situated meters to tens of meters apart.

Maximum numbers of types of cenopopulations were determined under coexistence of subspecies and minimum number in "pure" ssp. *major*.

The only invasive population was found in 1993, in a floodplain hay-meadow near the village Nolya Vershina in the Medvedevskii raion of the Republic Maryi El. The maximum in its age structure fell within the group of individuals in the immature state (Δ = 0.031). The density of population was relatively high, comprising 35.8 individuals per 0.25 m^2.

We subdivided young normal cenopopulations (a total of 34) with the account of local maximum in the fraction of young growth (Table 1). As the maximum displaced from the *j* to *v* ontogenetic group, the values of coefficients of age status increased regularly from 0.05 to 0.35. The density of populations varied significantly, and the largest range of this characteristic was observed in populations with their maximum in the immature

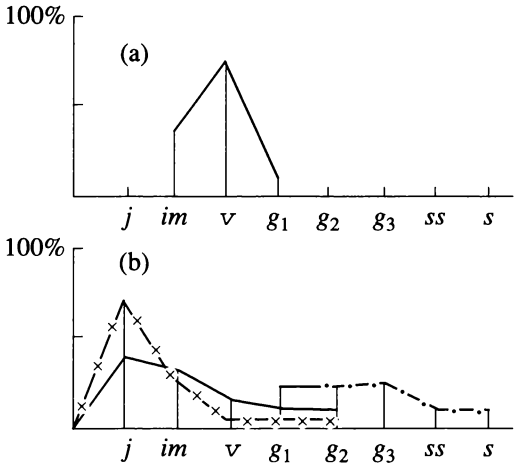

Fig. 3. Age specters of populations of *Plantago major* in (a) hay- and (b) pasture-meadows: (——) 1981, (–·–·–) 1983, (–×–×–) 1984.

group. It comprised here 1.6 to 178.0 individuals per 0.25 m^2. The recovery indices of most young normal cenopopulations were sufficiently high—up to 1157% (Pushchino). Of all studied cenopopulations, 64.7% had recovery index more than 100%, which attested to their relatively successful processes of self-maintenance. The minimum value of the recovery index (44.0%) was determined in the Orshanskii raion, in a population on the pathside in a rye field.

It seems likely that as populations developed and entered the mature normal state, competition between plants intensified. The density of separate cenopopulations decreased to 1.5, but it was capable of attaining 49.5 individuals per 0.25 m^2. Their coefficient of age status reached 0.45. Recovery indices were somewhat lower than in the previous type of population (Table 1).

Aging and old cenopopulations were characterized by a further increase in their coefficients of age status; in this case, the maximum values in aging populations were even slightly above (0.665) the level for old ones (up to 0.560). This situation could be explained by the appearance of a new wave of recovery in the flow of population; such a possibility was confirmed by high recovery indices (up to 1215.9%).

Table 2. Characteristics of the age structure in 23 cenopopulations of *P. major* with accounting of their subspecies composition

Subspecies composition	Density, ind. per 0.25 m^2	Coefficient of age status Δ	Recovery index I_r, %
"Pure" ssp. *major*	11.2–48.0	0.118–0.269	191–292
"Pure" ssp. *pleiosperma*	7.4–121.4	0.067–0.418	44–506

The analysis of data for all populations on the interrelation between demographic characteristics has shown the existence of hard negative correlations between the coefficient of age status and the density of seedlings ($r = -0.55$, $p < 0.001$), density of plants in pregenerative fraction ($r = -0.81$, $p < 0.001$), and recovery index ($r = -0.71$, $p < 0.001$). At the same time, a positive correlation was between the coefficient of age status and the density of generative ($r = 0.80$, $p < 0.001$) and postgenerative ($r = 0.31$, $p < 0.05$) fractions.

The described correlations remained for young normal populations, whereas the only statistically significant coefficient for old and aging populations was that between the age and number of plants in the pregenerative period ($r = -0.88$, $p < 0.05$).

Correlations close to the statistically significant ones at the 5% level were revealed only for young normal cenopopulations: between density of cenopopulation and the coefficient of age status ($r = -0.37$, $p = 0.051$) and between density and the recovery index ($r = 0.33$, $p = 0.056$). This suggested a clear negative dependence between the intensity of the phytogenic field of the population and the intensity of the processes of self-maintenance. This was supported by the following biological regularity: the older the population is, the slower the processes of seed reproduction are due to the deficit of resources and space. This was confirmed also by the negative correlation between relative parts of seedlings and the generative fraction in all populations ($r = -0.55$, $p < 0.01$), between relative parts of generative and pregenerative plants ($r = -0.89$, $p < 0.001$), and between generative plants and the recovery index ($r = -0.82$, $p < 0.001$).

The expeditions of 1981–1984 provided information on the population dynamics of great plantain in pasture meadows in the Bol'shaya Kokshaga River floodplain that could support this assumption (Fig. 3). Typical lefthanded range was described in 1981 in a young normal population of *P. major* with the maximum in a group of juvenile plants. The age status of these populations sharply increased around 1983 because of the participation of g_3, *ss*-, and *s*-groups, and also because of the complete absence of the fraction of pregenerative individuals, and the population became old normal. This state could be considered as the end of a large wave in the population flow (Uranov, 1975). In 1984, the appearance of a new wave of recovery restored the age structure characteristic of the young normal population. Hence, dynamic phenomena in the populations of *P. major* had an obviously successional character which corresponded to the explerent strategy of this species in the pastures.[1]

A young normal population of *P. major* with its maximum in a virgin group was also found in hay-meadows of Bol'shaya Kokshaga in 1981. In the years

[1] Translator's note: Explerents are plants which have a low ability to form cenoses, but can rapidly occupy free territories, even if for a short time known as R-strategists.

that followed, participation of *P. major* in this community sharply decreased. The density of the population decreased to such a degree that the obtained sample was insufficient for the assessment of age structure of the population. In this case, *P. major* demonstrated the traits of a patient.[2]

In Table 2, the characteristic is given of the age structure of 23 cenopopulations, taking into account their subspecies composition. The range of the variability of all demographic characteristics is the largest under the coexistence of subspecies.

The sufficient volume of material on the age structure of populations of great plantain from different points of the area allowed us to calculate a modal range that could be considered as a generalized characteristic of the dynamic equilibrium state of the population, which it tried to attain after the deviation under the external effects. Full-membered populations and populations with the absence of senile individuals were used in the construction of the range. The inclusion of the latter into the calculation was explained by frequent finishing of the ontogenesis in the subsenile state and low abundance of this group in all ecological states. The modal range of *P. major* had a typical lefthanded character, with maximums in juvenile and young generative groups (Fig. 4). This supported once again the dominance of the young normal cenopopulations.

Subspecies occupied relatively different habitats: *P. m.* ssp. *major* was found on roadsides, forest paths, slopes of ravines, and pastures and hay-meadows; *P. m.* ssp. *pleiosperma* was found on frequently inundated territories and in agrocenoses. They occurred together on alluvial sands, river terraces of high levels with short-term overflowing, and in some associations of floodplain hay-meadows. These data were in good agreement with the results of Dutch researchers (Van Dijk, 1989, *Plantago* ..., 1992).

The grades of an ecological series determined by analysis of geobotanical descriptions could serve as the units of measurement of ecological conditions in habitats. For this purpose, Ramenskii *et al.* (1956) developed ecological scales by the richness (*NS*), moistening (*FE*), and changeability of moistening (*VE*) of the soil. *P. major* could reach the 5th to 24th grades in the scale of soil richness (Ramenskii *et al.*, 1956). The analysis of our geobotanical descriptions with use of the program complex ECOSCALE has shown that studied cenopopulations of the greater plantain occupied the central position in ecological series by the richness of the soil: 8.6 to 17 grades. This reflected a relatively narrow range of growth conditions: from poor (mesotrophic) (1 cenopopulation) to relatively rich (38), rich (5) and slightly solonchak (1) soils. As a rule, they were unsalinized alluvial meadow, lowland meadow and other slightly leached soils with pH from slightly acid (pH 5.5–6.5) to slightly alkaline (pH 7.5–8.3) levels.

[2] Translator's note: Patients are the plants that survive under stress conditions due to their resistance known as S-strategists.

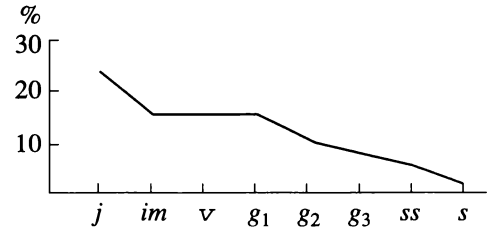

Fig. 4. Modal range of *Plantago major.*

They are mainly sandy, sandy-loamy, and loamy soils. Subspecies of *P. major* did not differ in their requirements for soil fertility.

Ramenskii established 120 grades in the ecological series of soil moistening. Great plantain reached 50th to 96th grades in the scale of moistening (Ramenskii *et al.*, 1956), which corresponded to the right part of the ecological series excluding wet habitats of the amphibious and aquatic plants. Within our research, greater plantain was found in habitats covering almost the entire range of conditions, including maximum values (88.0–89.9). In the range of minimum values, the presence of this species was determined at the grade 44.5. This, the only population with moistening of the mean grade, characteristic of conditions of the feather-grass steppe, belonged to the "mixed" type with expressed domination of ssp. *major* (93.1%). Other habitats were distributed by the scale *FE* in the following manner: fresh meadow (8 cenopopulations), moist meadow (26), wet meadow (6), and bog–meadow (1) moistening. The listed habitats ranged from dry to wet and from boggy meadows to forests, which correspond to the drained habitats of the forest zone.

It is significant that all "pure" populations *P. m.* ssp. *major* grew on soils with wet meadow moistening (grades 64.5 to 74.0). At the same time, ssp. *pleiosperma* was found also in more wet habitats: on soils with wet meadow and bog–meadow moistening. Of great interest was the habitat of ssp. *pleiosperma* on the sandy beach of the Volga River in the village of Zvenigovo, where the high water level in the river was supported (by the Novocheboksarskaya Hydroelectric Power Plant) often to the beginning of July. In this case, the development of vegetative and generative organs of the plant occurred immediately under the water. The leaves of the plants of this ecotype were long-petioled, wide-lanceolate, reddish, and covered by a coating of blue–green algae. The unevenness of the edges of the leaf blades was almost absent. Generative shoots were orthotropous, as opposed to those characteristic of the subspecies. The rhizome was, as a rule, very long and curved (Fig. 5). The processes of self-maintaining were difficult in this period: the density was no more than 4.8 plants per 0.25 m^2, age status 0.35, and recovery index 44%. As the water receded, young growth appeared intensively. Total density increased to 54.4 individuals per 0.25 m^2, and coverage of the cenopopulation reached

Fig. 5. Morphological features of *P. m.* ssp. *pleiosperma*. "Aquatic" ecotype, the plant of the middle age generative state.

more than 60%. Hence, within one growing season *P. m.* ssp. *pleiosperma* could show both patient and explerent features, depending on the environmental conditions.

It should be noted that the plants of the habitat under discussion were, as a rule, in *v*-, g_1-, and g_2-states in the submerged period. This could indirectly suggest that in habitats in the center of the European part of Russia, the lifetime of the individuals of this subspecies could be no less than two years, which contradicts the findings of Dutch researchers who classified this subspecies as annual (Van der Aart, 1985; *Plantago* ..., 1992). Great plantain can reach, by the scale of changeability of moistening (*VF*), 6 to 19 grades (Ramenskii *et al.*, 1956). In our study, we had 6.5 to 15.5, which corresponded to very changeable (5 cenopopulations), moderately changeable (35), and changeable–secure (5) water nutrition. Very exchangeable moistening is characteristic of meadows of river floodplains and lowlands, inundated in spring and drained by the river in summer. Habitats with secure, changeable, and moderately changeable moistening are widely distributed in the humid climate of the forest zone and are favorable for the development of most species of meadow plants.

Spearman's coefficients of rank correlation were calculated in order to assess the interrelations of characteristics of ecotope conditions (Sachs, 1976). Of them, only one coefficient was statistically significant by three scales of Ramenskii (*FE*, *NS*, *VF*): between soil richness and changeability of moistening (for 42 cenopopulations $r = 0.81$, $p < 0.001$, for 34 young cenopopulations $r = 0.44$, $p < 0.01$, for other 8 normal cenopopulations $r = 0.90$, $p < 0.01$). Other correlation coefficients were close to zero.

A positive dependence between the density of cenopopulation and soil richness ($r = 0.11$; $p < 0.025$) and a negative correlation of the changeability of soil moistening with coefficient of age status ($r = -0.35$, $p < 0.05$) were found in the analysis of the interrelations of demographic parameters with the peculiarities of the ecotope. This confirmed that *P. m.* ssp *pleiosperma*, inhabiting phytocenoses and groups with relatively high changeability of soil moistening, was an annual or biennial plant, and thus formed predominantly young normal populations.

CONCLUSION

The use of the concept of discrete description for the ontogenesis of *P. major* revealed a high degree of age heterogeneity of populations. A high degree of dependence was found between demographic characteristics and their relationships with factors of ecotope. *P. major* could change the type of strategy and manifesting features, both patient and explerent, depending on the environmental conditions and economical use of the phytocenoses with participation of this species. In this case, ssp. *pleiosperma* was the most labile. Subsequently, for the complete description of the population structure of species *P. major*, it will be necessary to analyze in detail the age and spatial structures of cenopopulations belonging to different subspecies, to determine the degree of differentiation of proper subspecies, to sample material throughout the area, and to improve ecological characteristics of the intraspecific taxa and of consortive links, including the specific character of seed and pollen transport and functioning of seed pool. Only a complex study performed by population ecologists, geneticists, and biocenologists would allow us to solve this problem.

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