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Experience in Using Ecological Phytoindication Scales for Revealing Unfavorable Factors at the Boundary of Species Distribution

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Abstract—The ecological phytoindication scales proposed by Tsyganov (1983) were used for characterizing biotopes at the northern limit of the distribution of three nemoral species: *Ajuga reptans, Asarum europaeum,* and *Pulmonaria obscura.* Regional ecological amplitudes of the model species were determined. The environmental factors approaching the lower limit of species amplitudes in Tsyganov's scales were classified as unfavorable.

Key words: ecological phytoindication scales, range boundary, *Ajuga reptans* L., *Pulmonaria obscura* Dumort., *Asarum europaeum* L.

In many species of the nemoral floristic complex (*Tilia cordata* Mill., *Asarum europaeum* L., *Ajuga reptans* L., *Pulmonaria obscura* Dumort., etc.), the northern limit of distribution is now within the middle taiga zone of the Komi Republic. These species have been preserved in the northeastern European part of Russia since the time of the Holocene thermal optimum, and their ranges have similar outlines of their northern boundaries (Yudin, 1954; Martynenko, 1976). New research methods made it possible to develop a new approach to the description of peculiarities of species habitats at the range boundary and identification of factors restricting species distribution. Notwithstanding different views on the ability of the factors to partially compensate one another (Goryshina, 1979; Tsyganov, 1983), specialists agree that the life activities and distribution of a species are limited by the factor which is "at a minimum" with respect to the environmental demands of this species. Ecological phytoindication scales represent one of the methods for identifying unfavorable factors "at minima."

The purpose of this work was to describe specific features of growing conditions for several nemoral species at the northern limit of their distribution in the middle and, partly, southern taiga subzones of the Komi Republic and to identify possible unfavorable factors with the aid of ecological phytoindication scales.

A variety of such scales has been developed to date. Their characteristics and applications were described in many studies (Ramenskii *et al.*, 1956; Samoilov, 1973, 1986; L'vov, 1979; L'vov *et al.*, 1987; Didukh *et al.*, 1991; Didukh and Plyuta, 1993, 1994; Prokop'ev, 1993; Zaugol'nova *et al.*, 1995, 1998). For this work, we chose the range scales proposed by D. N. Tsyganov (1983), which characterize plants in relation to ten environmental factors: temperature regime (*Tm*), ombroregime (*Om*), regime of continentality (*Kn*), cryoregime (*Cr*), soil moistening (*Hd*), salt regime in biotope soils (*Tr*), soil acidity (*Rc*), variability of soil moistening (*fH*), soil nitrogen supply (*Nt*), and illumination–shading regime in the community (*Lc*). These scales indicate the ecological amplitudes of more than 2000 plant species in the subzone of coniferous–broad-leaved forests, including species occurring in other plant zones.

METHODS

Nemoral species *Asarum europaeum, Ajuga reptans*, and *Pulmonaria obscura* were chosen as model species. The study was carried out at the northern limit of their distribution: in the Sysola, Vychegda, and Letka river basins located in the middle and, partly, southern taiga subzones of the Komi Republic. Middle taiga forests represent the zonal type of vegetation, and associations with green mosses represent the main group of associations. Fir–spruce bilberry forests on highly podzolic soils prevail. Haircap-moss (*Polytrichum*) spruce forests on peaty podzolic gley soils are common in the central parts of watersheds. Bilberry–wood sorrel, wood sorrel, and wood sorrel–small fern fir–spruce forests are associated with river valleys and southern slopes. The association of wood sorrel–spruce forest is the central association of southern taiga forests in the Komi Republic. Nemoral species are sometimes found in southern areas of the middle taiga subzone and in the herbaceous cover of southern taiga forests.

According to ecological amplitudes indicated in Tsyganov's scales, model species have similar requirements for soil fertility and nitrogen supply but differ in

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Table 1. General and regional ecological amplitudes of model species

Scale	Scale range, grades	General ecological amplitude on Tsyganov's scales (1983)			Regional amplitude in the middle taiga subzone of the Komi Republic		
		Ajuga reptans	*Asarum europaeum*	*Pulmonaria obscura*	*Ajuga reptans*	*Asarum europaeum*	*Pulmonaria obscura*
Thermoclimatic (*Tm*)	1–17	4–13	6–12	5–12	6.5–7.9	6.8–7.9	7.0–7.8
Climate continentality (*Kn*)	1–15	3–13	5–11	4–12	8.5–9.5	8.4–9.5	8.6–9.2
Ombroclimatic (*Om*)	1–15	5–11	7–9	7–11	7.6–8.8	8.0–8.9	8.3–10.1
Cryoclimatic (*Cr*)	1–15	6–11	5–10	5–11	5.8–7.4	5.6–7.2	6.1–6.9
Soil moistening (*Hd*)	1–23	11–15	11–15	9–16	11.9–14.6	11.4–14.1	12.0–13.9
Soil fertility (*Tr*)	1–19	3–9	3–9	3–9	5.1–7.4	4.8–6.9	5.4–6.3
Soil acidity (*Rc*)	1–13	1–11	7–11	7–11	5.7–7.8	5.4–7.8	6.1–7.5
Soil nitrogen supply (*Nt*)	1–11	5–9	5–9	5–10	4.9–6.3	4.6–6.2	4.9–6.3
Variability of moistening (*fH*)	1–11	–	–	5–7	4.2–5.7	4.4–5.7	4.5–5.7
Illumination in the community (*Lc*)	1–9	3–7	4–9	1–9	3.3–5.4	3.8–5.4	4.3–5.2

tolerance limits along the axes of other factors (Table 1). These differences include species requirements for illumination in the communities, cryoregime, and soil acidity. *Ajuga reptans*, unlike *A. europaeum* and *P. obscura*, can grow on very acid soils and is more sensitive (by one grade) to the severity of winter conditions. *Asarum europaeum* is more shade-tolerant than other model species (Goryshina, 1979). *Pulmonaria obscura* has a wide amplitude with respect to the illumination factor.

Specific ecological features of habitats and regional amplitudes of model species were determined by analyzing original geobotanical descriptions made according to conventional procedure and the materials of previous years from the phytocenarium of the Institute of Biology (Komi Research Center), kindly presented by Dr. V.A. Martynenko and Cand. Sci. (Biol.) S.V. Degteva. The communities containing the three model species were described in the Letskii, Priluzskii, Koigorodskii, Sysol'skii, and Syktyvdinskii raions of the Komi Republic. These were herbaceous pine forests; tall-grass fir forests; wood sorrel–fern, cowberry–green moss, and herbaceous spruce forests, including a tall-grass forest near a brook; tall-grass, nemorose-herbaceous, and woodreed birch forests; nemorose-herbaceous, woodreed, tall-grass, and herbaceous aspen forests; dropwort–speckled alder forests near brooks and speckled alder forests near roads and in overgrown clearings. The abundance of *A. europaeum* in these communities was estimated at one to three grades, and that of *A. reptans* and *P. obscura* did not exceed two grades on Drude's scales. Ninety geobotanical descriptions (44 with *A. europaeum*, 66 with *Ajuga reptans*, and 33 with *P. obscura*) were analyzed, including the descriptions of hayfields, sown meadows, clearings, and road banks. Such a sample of descriptions can be regarded as sufficient, because it adequately represents different types of habitats of model species.

The data of geobotanical descriptions were processed using the Ecoscale program (Zaugol'nova *et al.*, 1995). The index of the regime was calculated for every factor by the method of weighed mean center of the range using the formula

$$Y = \sum(a_i \times x_i/n),$$

where Y is the mean regime value of an environmental factor, grades; a_i is the estimate of species abundance; x_i is the mean value of species tolerance to this factor; and n is the number of species the data on which are provided in the description.

Mean values of the factors in the study region were calculated for model species and were used for characterizing biotopes. Regional ecological amplitudes of the species (Samoilov, 1986) were determined from the minimum and maximum values of the factors and compared with the ecological amplitudes on Tsyganov's scales. Factors at or beyond the lower limit of ecological amplitude were regarded as unfavorable. At such values of these factors, the coefficients of satisfactoriness of environmental conditions for the species (Tsyganov, 1983) were zero. The factors whose values approached the conventional optimum of the species (the center of ecological amplitude on Tsyganov's scales) were considered favorable. The values of the soil acidity factor were converted from grades into quantitative physicochemical parameters.

RESULTS AND DISCUSSION

The results shown in Table 2 allowed characterization by Tsyganov's scales (1983) of environmental conditions in *A. reptans, A. europaeum,* and *P. obscura* habitats at the limit of their distribution in the middle and, partially, southern taiga subzones of the Komi Republic. The species compositions of individual geo-

Table 2. Characteristics of model species ecotopes in the middle taiga subzone of the Komi Republic

Parameter	Scale									
	Tm	*Kn*	*Om*	*Cr*	*Hd*	*Tr*	*Rc*	*Nt*	*fH*	*Lc*
					Ajuga reptans					
x	7.38	8.87	8.40	6.76	13.18	5.90	6.65	5.50	5.05	4.50
m	0.03	0.03	0.03	0.04	0.07	0.06	0.05	0.04	0.04	0.06
CV, %	3.3	2.5	2.7	4.9	4.1	8.6	5.5	5.5	6.2	10.8
					Asarum europaeum					
x	7.31	8.96	8.46	6.55	13.23	5.66	6.60	5.39	5.11	4.67
m	0.04	0.04	0.03	0.06	0.07	0.06	0.08	0.06	0.05	0.05
CV, %	3.6	2.7	2.0	5.6	3.5	6.7	7.5	6.9	6.2	7.4
					Pulmonaria obscura					
x	7.32	8.96	8.55	6.57	13.32	5.71	6.66	5.52	5.06	4.78
m	0.03	0.03	0.05	0.03	0.06	0.03	0.06	0.04	0.05	0.04
CV, %	2.6	1.7	3.5	2.9	2.6	3.2	5.4	4.5	5.1	4.8

Note: (*x*) mean value, grades; (*m*) standard deviation; (*CV*) variation coefficient, %. For designations of scales, see Table 1.

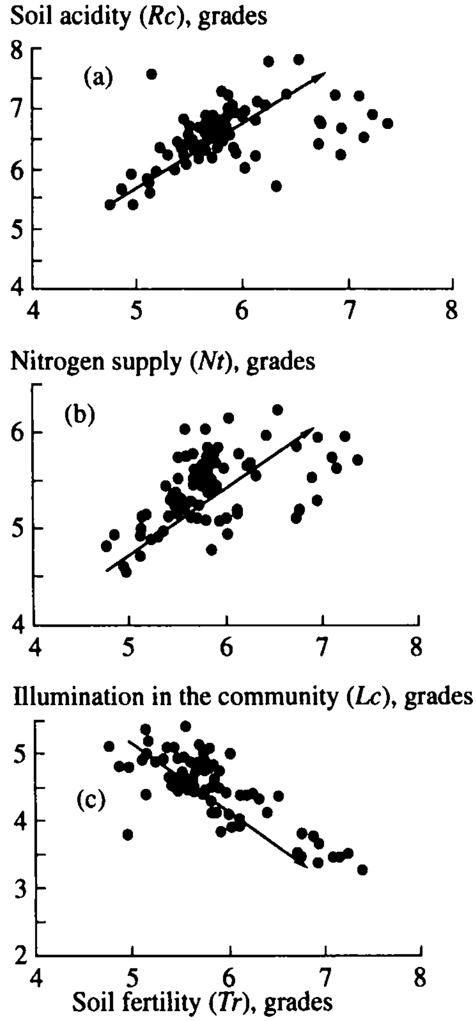
botanical descriptions were analyzed by 72–100% with the aid of Tsyganov's ecological scales, which provided for the sufficiently objective ecological characterization of biotopes.

The habitats of model species in the region are characterized by the following values of environmental factors. The values of climatic factors correspond to the boreal–subboreal thermal zone and the continental type of continentality, ombroregime is close to the subhumid type, and cryoregime of the habitats corresponds to the type of temperate winters. The species grow on slightly acid and neutral soils (pH 5.0–6.5, average 5.8), which correspond to the relatively poor type on the soil fertility scale and to the poor type on the nitrogen supply scale. Moisture content in habitats corresponds to the moist forest–meadow type, and moistening is variable but sufficient. On the illumination–shading scale, the habitats of *A. reptans* and *A. europaeum* correspond to the type of light forest regime (light coniferous, small-leaved, and severely disturbed dark coniferous communities).

The distribution pattern of ecological characteristics of the communities along the axes of soil acidity, fertility, nitrogen supply, and illumination (figure) showed that the soils of mixed and, especially, small-leaved forests with the prevalence of *Populus tremula* L., *Betula pubescens* Ehrh., *Betula pendula* Roth., and *Alnus incana* (L.) Moench. contain more nitrogen and are more fertile and less acidic. Comparing characteristics of different community types with the ecological amplitudes of species, it was found that conditions in the aforementioned communities most closely approach the conventional ecological optimum of model species in the middle taiga subzone of the Komi Republic.

The ecological amplitude of every species on the range scales (including Tsyganov's scales) comprises the set of its regional amplitudes, and any of the latter is usually no more than a small part of the total ecological amplitude. As the spectrum of habitats suitable for the normal growth and development of model species is reduced at the boundary of their range and the study area is relatively small (limited to the middle taiga subzone), the regional sectors of *A. reptans, A. europaeum*, and *P. obscura* amplitudes (Table 1) proved to be narrower than their complete ecological amplitudes on Tsyganov's scales.

These regional sectors for the middle taiga subzone of the Komi Republic were compared with the ecological amplitudes of species for the coniferous–broadleaved forest subzone according to Tsyganov's scales (1983). The results showed that the values of some factors studied in the present work are close to the lower limit of species tolerance, with minimum values often falling below this limit. These factors or their combination probably exert unfavorable influences limiting the development of species at the boundary of their range. Among climatic factors, which are generally favorable for the model species, the severity of the winter period is apparently the limiting factor for *A. reptans*. The analysis of soil factors showed that the mean values of nitrogen supply were close to the lower tolerance limit of all the three species, and the values of soil acidity were at a minimum for *A. europaeum* and *P. obscura*. Severe cold winters and competition for nutrients, nitrogen in particular, between tree stands and the herbaceous layer were also mentioned as the factors limiting the spread of nemoral species to the north and northeast (Gorchakovskii, 1968; Karpov, 1969; Polozhii and Krapivkina, 1985). The interaction between the factors of soil acidity and fertility is well known: nem-



Distribution patterns of model species habitats with respect to the axes of different factors: (a) soil acidity, (b) soil supply with nitrogen, and (c) illumination in the community. Ordinates show soil fertility. Arrows indicate the direction of changes from dark coniferous to mixed and small-leaved communities.

oral species are less adapted to consuming nutrients from acid soils than taiga dwarf shrubs and grasses (Rabotnov, 1979; Yushchenkova, 1990).

At the northern boundary of distribution, the ecological amplitude of *A. europaeum* slightly expanded at its lower limit with respect to the factor of illumination in the community. In the study area, this species is usually found in better illuminated communities, compared to the coniferous–broadleaved forest subzone (in coniferous–small-leaved and small-leaved communities and, sometimes, in forest meadows and clearings). The type of illumination in these communities corresponds to that in light forests and semienclosed areas.

Based on the regional amplitudes of model species in the middle taiga subzone of the Komi Republic, it is possible to determine more accurately their ecological amplitudes on Tsyganov's scales. When regional amplitudes by the factors of cryoregime (*Cr*), soil acidity (*Rc*), nitrogen supply (*Nt*), and illumination in the community (*Lc*) are included in the total ecological amplitudes of model species (Table 1), lower limits of the latter are displaced. Thus, amplitudes of all the species slightly increase (by 0.1–0.4 of a grade) owing to the displacement of the minimum point toward soils with a lower nitrogen supply; the ecological amplitude of *A. reptans* expands by 0.2 of a grade toward more severe winter conditions, and that of *A. europaeum*, toward growing conditions with a greater illumination intensity. The amplitude of *P. obscura* increases by 0.5 with respect to the factor of variation in moistening; i.e., the species tolerates less variable moistening than that indicated in the scales. The most pronounced increase in ecological amplitudes is observed in *A. europaeum* and *P. obscura* (by 1.6 and 0.9 grades, respectively) owing to the displacement of the minimum point toward more acid soils. Defining ecological amplitudes of the species is important for improving the accuracy of subsequent calculations by Tsyganov's scales.

CONCLUSION

The method of ecological phytoindication scales made it possible to characterize ecologically the habitats of *A. europaeum, P. obscura,* and *A. reptans* at the boundary of their range in the middle and, partly, southern taiga subzones of the Komi Republic and to identify communities satisfying their ecological requirements to the greatest extent.

Factors and their combinations unfavorable for individual species were revealed with the aid of ecological scales proposed by Tsyganov (1983). Some of them are common for all the model species (nitrogen deficit), whereas others are specific, such as cryoregime for *A. reptans*, soil acidity for *A. europaeum* and *P. obscura*, and a low variability of moistening in the communities for *P. obscura*. These are the unfavorable environmental factors approaching the "minimum" with respect to the ecological amplitude of the species. Some factors have previously been mentioned among those limiting the spread of nemoral species to the north and northeast.

The ecological amplitudes of model species on Tsyganov's scales (1983) can be elaborated and defined more precisely on the basis of regional amplitudes determined in this work.

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