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Morphophysiological and Population Adaptations of *Ajuga reptans* L. at the Northern Boundary of Its Range

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Abstract—The results of comprehensive morphophysiological and population studies on *Ajuga reptans* L., a species of the nemoral floristic complex, at the northern boundary of its range (in the middle taiga subzone of the Komi Republic) are reviewed. Adaptations at the cell, organism, and biocenotic levels are revealed. The maintenance and survival of the species at the boundary of its range are provided for by its physiological plasticity, resistance to low temperatures, and multiple variants of ontogeny. Prognosis of *Ajuga reptans* future status under conditions of global climate change and expansion of anthropogenically disturbed areas is favorable.

Key words: *Ajuga reptans* L., northern boundary of species range, adaptation, functional plasticity, ontogeny, cenopopulations, life strategy

The adaptation of organisms to a changing environment is achieved through the rearrangement of a combination of characters at all levels of biological organization. As applied to the genotype, the concept of adaptation implies phenotypic plasticity, i.e., the ability of an organism to take on more than one alternative form of the morphological and physiological state and/or behavior in response to environmental conditions (West-Eberhard, 1989; Getty, 1996). The combination of morphophysiological, behavioral, population, and other features of a species provides for its survival in a certain environment.

Ajuga reptans L. is a nemoral species whose range embraces a vast territory of Western Europe, the western part of the Mediterranean, European Russia, the Caucasus, and the Urals. In the northeast of European Russia, it belongs to the relicts of the Holocene thermal optimum (Martynenko, 1976). It occurs in herbaceous aspen and birch forests, mixed coniferous–small-leaved forests, and meadows. *Ajuga reptans* is a stolon-forming herbaceous polycarpic with monocarpic semirosette shoots and belongs to summer–wintergreen species (Serebryakov, 1952). It reproduces by seeds and incompletely rejuvenated vegetative diaspores (Smirnova, 1987). It is known as a medicinal ecdysteroid-containing plant (*Rastitel'nye resursy…*, 1991; Alekseeva *et al.*, 1998) and is used for landscaping as an ornamental soil-covering species.

The biology of *A. reptans* in the ecotopically favorable zone of broadleaved forests has been studied fairly comprehensively (Rysina, 1973; Mikhailovskaya and Kuz'micheva, 1974; Komarova, 1986; Smirnova, 1987). However, the data on its physiological parameters are far less abundant (Bachmann *et al.*, 1994; Bachmann and Keller, 1995; Luk'yanova *et al.*, 1986; Masarovicova, 1997).

One of the methods for revealing the adaptive responses of plants and assessing their plasticity is the comparison of morphophysiological, biochemical, and other indices in representatives of the species from different parts of its range. The purpose of this work was to reveal the adaptive properties of *A. reptans* under conditions of middle taiga communities, at the northern boundary of its range. To this end, the structural, functional, ontogenetic, and population features of the species were studied.

METHODS

Studies were performed in the middle taiga subzone of the Komi Republic (between 60° and 62° N), at the northern boundary of the species range. This region is characterized by elevated plains that have moderately rolling or, in some areas, dissected topography, with cover loams or sandy loams underlain with moraine and with green-moss middle-taiga spruce and fir–spruce forests on highly podzolic soils. In recent decades, the primary forests have been largely replaced by the secondary spruce–aspen and spruce–birch communities due to strong anthropogenic effects (Pruchkin *et al.*, 1999). The climate of the region is excessively humid and moderately warm.

Specific features of *A. reptans* growth and development were studied in 32 natural cenopopulations growing in white alder groves, herbaceous aspen forests, birch forests, and mixed coniferous–small-leaved communities, forest margins, grass–herb meadows, felling areas, and roadside banks. Studies were performed between 1995 and 1998 using conventional methods of

Morphophysiological parameters of plants and population parameters of *Ajuga reptans* in different parts of its range

Parameters	Broadleaved forest zone	Middle taiga subzone
Physiological characteristics		
Photosynthetic rate, mg CO_2/dm^2 per hour	6.0–9.5**	2.5–4.5
Chlorophyll content, g/dm_2	4.40 ± 0.10***	2.15 ± 0.05
Soluble carbohydrate content, mg/g fresh weight	75–85**	20–30
Population parameters		
1. Cenopopulation element		
Biomass	3.0–3.5*	0.9–1.2
Height of assimilative surface, mm	150–200*	50–160
Root length, mm	40–80*	110–180
Vegetative growth rate, cm/year	30–50*	8–35
Potential annual production of vegetative primordia, pcs. per element	3–7*	0–4
Potential annual production of seed primordia, pcs. per element	100–250*	150–300
Duration of partial shoot ontogeny, years	2–3*	up to 6 and more
Duration of area retention, years	3–4*	2–6 and more
Developmental rate	Normal*	Cenopopulations
2. Cenopopulations		
Age spectrum	Generative age state dominates*	Immature age state dominates
Store of diaspores in the soil	Large	Small
Type of maintenance	Seed and vegetative*	Vegetative type is dominant, seed type manifests itself upon plant cover damage

Note: Data on the broadleaved forests zone are from studies by *Smirnova (1987), **Bachmann *et al*. (1994), and ***Masarovicova (1997).

cenopopulation research (*Tsenopopulyatsii rastenii…*, 1976; Smirnova, 1987; Zhukova, 1995). As a unit of count, we used an individual *A. reptans* plant (before the onset of vegetative propagation) or a partial shoot (after the onset). To obtain the quantitative characteristics of age states, we measured the length of the largest leaf in the rosette part of a shoot, the number of plagiotropic shoots, and their lengths after rooting.

Morphophysiological studies were performed in nature, in a spruce-aspen herbaceous forest, and on cultivated plants in the experimental plot near Syktyvkar (62°52' N). Carbon dioxide exchange in mature summer- and wintergreen leaves was studied using an Infralit-4 infrared gas analyzer (Sivkov and Nazarov, 1990) at temperatures and illumination of 5–35°C and 4–500 W/m^2 of photosynthetically active radiation (PAR), respectively. The cardinal points of light and temperature curves of photosynthesis were determined as described by Garmash and Golovko (1997). The values presented in the paper are the averages of six to ten curves.

The chlorophyll and carotenoid contents in leaf blades were estimated spectrophotometrically (Shlyk, 1971), in five replications. Soluble hydrocarbons were analyzed by HPLC with modifications proposed by Glyad (1999); free amino acids were determined in an AAA-T339M analyzer (Mikrotechna-Praha, Czechoslovakia), in three replications.

RESULTS AND DISCUSSION

Structural–functional level. The results of comparative analysis (table) showed that *A. reptans* at the northern boundary of its range, in the taiga subzone, is characterized by a decreased photosynthetic rate. With respect to the rate of CO_2 absorption, this species is much closer to the plants of the boreal floristic complex (Starostina, 1983) than to those typical of broadleaved forests (Mitina, 1981).

The low rate of photosynthesis correlated with a reduced green pigment content in *A. reptans* leaves. This result agrees with the concept that the amount of chlorophyll in shade-loving plants decreases at higher latitudes, which is explained by changes in the light spectrum. It appears that some other factors should also be taken into account. In particular, this concerns the deficiency of nitrogen (the element essential for chlorophyll synthesis), which is explained by soil poorness and slow litter decomposition at low temperatures. At a low rate of CO_2 assimilation, *A. reptans* plants growing under the forest canopy in the middle taiga subzone accumulated approximately one-half less nonstructural hydrocarbons than plants from the central part of the range.

According to the parameters of light curves of photosynthesis (steepness and low values of adaptive radiation intensity and light compensation point) (Fig. 1) and the ratio of chlorophylls *a*/*b* < 3 in the pigment complex, *A. reptans* belongs to a group of shade-tolerant plants. Shade tolerance is determined genetically. This was confirmed in experiments with *A. reptans* plants from various ecotopes, which proved to be capable of adapting themselves to high illumination intensity (growth in culture) and retaining the properties of a shade-tolerant species (Dymova and Golovko, 1998a).

It should be noted that nemoral species in the broad-leaved forests zone can develop the properties of photopilic species and photosynthesize at a high rate in early spring, when the foliage of trees has not yet been formed completely (Mitina, 1981). We found that, under extreme conditions existing at the northern boundary of the *A. reptans* range, this nemoral species is incapable of absorbing CO_2 at a high rate in a light forest in spring. During the growing period, the rate of photosynthesis in leaves varied insignificantly (Fig. 2), which provided evidence for plant adaptation to the conditions of illumination in the middle taiga communities.

The photosynthetic apparatus of *A. reptans* is adapted to moderate temperatures of the middle taiga subzone and is capable of acclimating to weather changes during the growing period. During the season of 1997, with typical thermal conditions (average air temperature 11.6°C) but insufficient moistening (annual precipitation rate 260 mm), the range of temperatures optimal for photosynthesis was 8–16°C (Fig. 3b). At a saturating illumination of about 50 W/m^2 and the optimum temperature, *A. reptans* leaves photosynthesized at a maximum rate, assimilating 6–8 mg CO_2/dm^2 per hour. At a temperature of 6–7°C, this rate decreased by 20–40%; at temperatures exceeding 25°C, photosynthesis was strongly inhibited. The temperature optimum proved to change by 2–6°C depending on thermal conditions and moistening. Thus, during the moist growing season of 1996 (total precipitation 375 mm) and the warm growing season of 1998 (average air temperature 12.9°C), this optimum shifted toward higher temperatures (10–22°C) (Figs. 3c, 3d). Thus, the photosynthetic apparatus demonstrated functional plasticity and stability.

As in the central part of the area, the phenomenon of wintering with green leaves was clearly pronounced at the northern limit of *A. reptans* distribution. The leaves remained capable of photosynthesis in late autumn, after frosts, and in early spring, after wintering (Fig. 2). The overwintered leaves slightly differed from summer leaves in the rate and temperature dependence of photosynthesis (Figs. 3a, 3b). The assimilative apparatus remained functional at low temperatures, and this promoted the early onset of assimilative activity in the overwintered leaves. This adaptive strategy provided for plant growth in the spring–summer period (late May–early June).

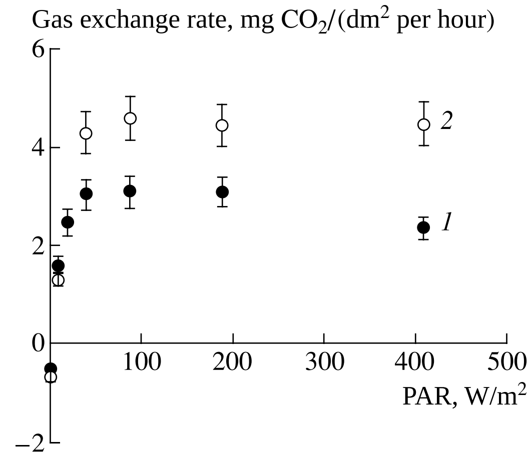

Fig. 1. Light dependence of photosynthesis in leaves of *Ajuga reptans* plants (*1*) growing under the forest canopy and (*2*) cultivated on a plot (June 1996, n = 6–10). PAR is photosynthetically active radiation.

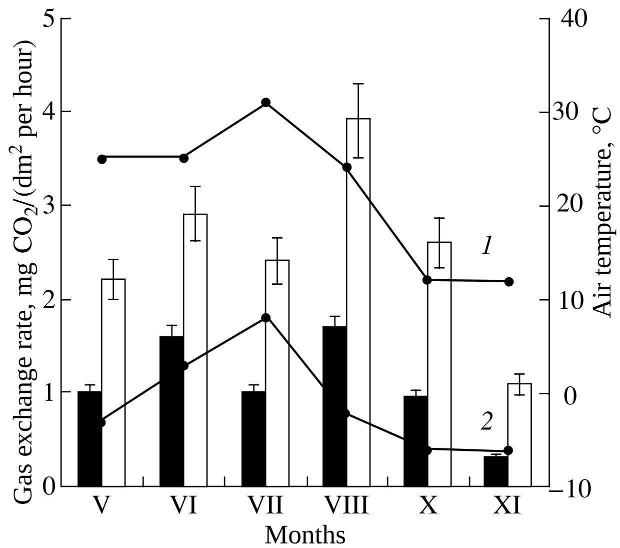

Fig. 2. Seasonal courses of photosynthesis in *Ajuga reptans* leaves and air temperature (1996, n = 6–10). Clear bars show the maximum rate of CO_2 absorption (P_{max}); filled bars show is the rate of CO_2 absorption at adaptive radiation intensity (P_{ari}); curves show (*1*) maximum and (*2*) minimum monthly average air temperature.

Cold tolerance and the maintenance of the photosynthetic apparatus in autumn were promoted by the accumulation of soluble carbohydrates (up to 35 mg/g fresh weight) and free amino acids (up to 2 mg/g fresh weight). In this period, the photosynthetic apparatus

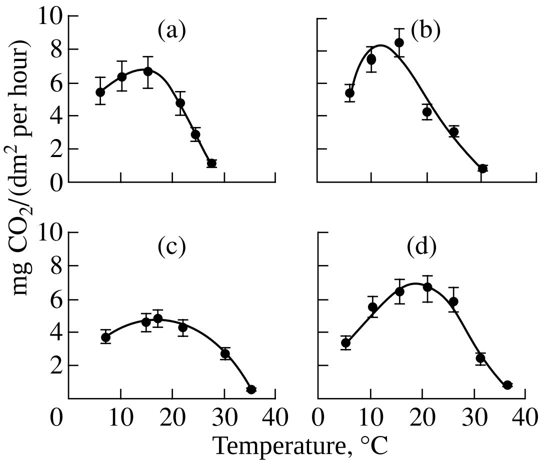

Fig. 3. Photosynthesis in *Ajuga reptans* leaves as a function of temperature in different years and growing seasons: (a) June 1997, wintergreen leaves; (b) June 1997, summer leaves; (c) July 1996; (d) August 1998 (n = 6–10).

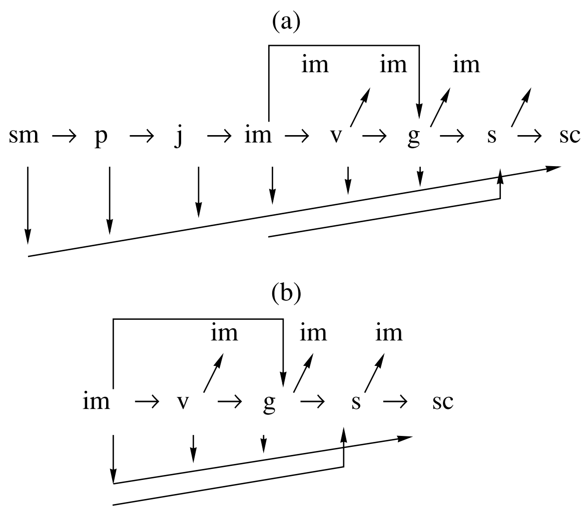

Fig. 4. Scheme of multivariant ontogeny of (a) *A. reptans* plant and (b) partial shoot in the middle taiga subzone. Age states: (sm) seeds, (p) sprouts and seedlings, (j) juvenile, (im) immature, (v) virginal, (g) generative, (s) senile, (sc) dying.

underwent some structural–functional rearrangements manifested in a decrease in the number of grains in thylacoids (less than 10) and the size of chloroplasts, starch hydrolysis, and partial degradation of chlorophylls and carotenoids (by 25–30%). The fact that *A. reptans* grows in the ground layer, where it is protected by the snow cover and litter, is very important for the survival of its wintergreen leaves. Species adaptation to subzero temperatures allows it to endure autumn frosts and winter cold.

Despite the low rates of photosynthesis (4–8 mg CO_2/dm^2 per hour), the assimilative organs of *A. reptans* were characterized by a relatively high respiration rate (1–3 mg CO_2/g per hour) during vegetation. Such rates are characteristic of many plants cultivated in the North (Golovko, 1999). The high respiratory capacity of these plants provide them with the amounts of energy necessary for growth in a cold climate.

Thus, the study of *A. reptans* at the functional level revealed its physiological plasticity, resistance to unfavorable environmental conditions, and high shade tolerance, which provide for the growth and survival of this nemoral species in the middle taiga subzone.

Organism level. As compared with southern plants, northern plants of *A. reptans* had smaller dimensional parameters (leaf length, the area of foliage surface, the number of stolons per partial shoot) and biomass (table). It is known that the distribution of resources in living organisms is aimed at improving their adaptation. The observed decrease in plant size and the number of growing vegetative structures may be regarded as an adaptive response to unfavorable ecotopic conditions, which promotes species survival in the North.

The study of *A. reptans* ontogeny at the northern boundary allowed us to distinguish four periods subdivided into eight age states: latent (seeds), pregenerative (seedlings, juvenile, immature, virginal), generative (generative state), and postgenerative (senile and dying states). A specific feature of the species is that the immature age state is prominent: the partial shoot in the form of leaf rosette with underdeveloped axillary buds exists for several years (Teteryuk, 1996).

Figure 4 shows the schemes of *A. reptans* ontogeny and the partial shoot. We observed the following variants: progression through all ontogenetic states in consecutive order, omission of one or several states, and plant death at different developmental stages. In addition, temporal variants (dynamic multiversality) of plant ontogeny were revealed, which were accounted for by dicyclic and polycyclic development of generative ramets. Analysis with regard to their actual age indicated that the partial shoot may develop at the normal rate or demonstrate dicyclic development, with flowering in the second year of life (Fig. 5). This is typical of plants from the central part of the range. In the study area, dicyclic development took place rarely, only under the most favorable ecotopic conditions. Most ramets developed slowly, with a delay in the immature and virginal age states; genets demonstrated a delay in the juvenile, immature, and virginal states. Flowering occurred in the third year of life or later. Similar changes of developmental cycles in different parts of the species range were described in *Poa annua* L., *Cochlearia arctica* Schlecht. Ex DC, and *Androsace septentpionalis* L. (Goryshina, 1979).

It is considered (Zhukova, 1995) that the existence of multiple variants of ontogeny increases the adaptive potential of species. The decreased vital activity of northern plants and unfavorable edaphic conditions of their natural habitats in the middle taiga subzone cannot provide for a sufficiently high rate of biomass accumulation and may be responsible for a delayed devel-

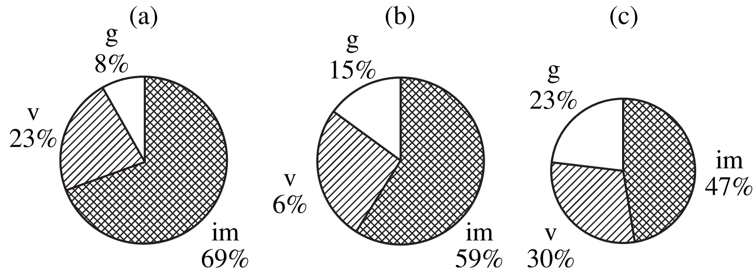

Fig. 5. Rates of development of *Ajuga reptans* partial shoots in the middle taiga subzone: (a) ramets in the second year of life, (b) third year of life, and (c) of conventional age over three years.

opment of the species. The polycyclic development of most ramets and genets, the prominence of the immature age state, and their multivariant ontogeny, which involves different rates of progression through the age states, may be regarded as an ontogenetic adaptation of the species to conditions of the North.

Population level. Our studies provided data on the *A. reptans* age spectrum in the middle taiga subzone (Fig. 6). This basic spectrum is shifted to the left due to the prevalence of the immature age group, as most of the partial shoots demonstrate polycyclic development. It differs from that obtained in the subzone of broadleaved forests, where generative plants prevailed (Smirnova, 1987). This fact reflects general trends in the development of a species at the boundary of its range.

The age spectrum provided evidence that the change of *A. reptans* generations in the middle taiga subzone is retarded, the activity of seed and vegetative reproduction is decreased, and their relative significance for the maintenance of species cenopopulations has changed in favor of vegetative reproduction. In white alder groves, small-leaved forests, and mixed coniferous–small-leaved communities, we revealed a relatively high proportion of virginal plants with the maximum possible number of stolons (two to four in the study area), whereas genets occurred very rarely.

Seed reproduction plays no significant role in maintaining the density of species populations at the boundary of its range, but it allows the species to form a reserve of viable diaspores, colonize new remote areas, and survive in critical situations (*Tsenopopulyatsii rastenii…*, 1988). The most favorable ecophytocenotic conditions for the maintenance of *A. reptans* cenopopulations by seed reproduction exist in anthropogenically disturbed areas, such as hayfields, felling areas, and roadside banks. In the age spectra of such cenopopulations, the generative age group accounted for up to 35%, and seedlings and juvenile individuals were present.

Thus, our studies provided evidence for a change in the basic age spectrum of the species at the boundary of its range and a decrease in the activity of seed and vegetative reproduction. The leading role in the maintenance of cenopopulations proved to belong to vegetative reproduction, which is more energy-efficient and provides for higher survival in the progeny.

Biocenotic level. One of the aspects of species adaptation to the environment is its “behavior,” or life strategy. There are several classifications of the types of plant behavior (Ramenskii, 1971; Grime, 1979; Mirkin, 1985; Smirnova, 1987). They are based on three main types of strategy: competitiveness, tolerance, and reactivity.

In the zone of broadleaved forests with ecotopically favorable conditions for the model species, special and general (phytocenotically significant) characteristics of behavior were determined (Smirnova, 1987). *Ajuga reptans* belongs to species with the reactive life strategy, which are characterized by the minimum period of growth confined to a certain territory (area retention), active reproduction, and a high rate of expansion to new habitats. In the middle taiga subzone, we observed a decrease in the biomass of cenopopulation components, the height of their assimilative surface, and the rates of their development, accompanied by an increase in the period of area retention by ramets (table). The rate of expansion to new habitats was lower than in the central part of the range. This is evidence that the life strategy of *A. reptans* at the northern boundary of its distribution became less reactive and more tolerant under the effect of unfavorable ecological and phytocenotic conditions. The signs of species tolerance manifested themselves more strongly in mature aspen

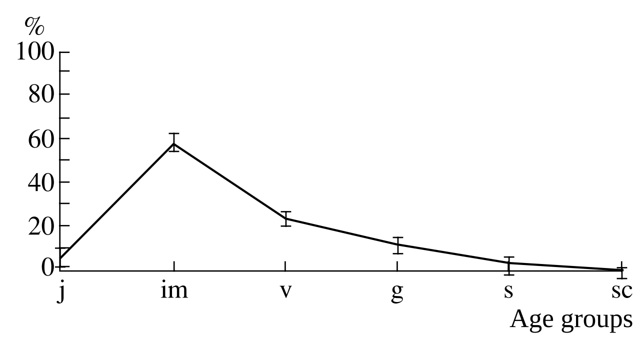

Fig. 6. Basic age spectrum of *Ajuga reptans* cenopopulations in the middle taiga subzone.

groves, birch forests, and mixed coniferous–small-leaved communities and less strongly in disturbed communities, such as those on roadside banks and in felling areas.

CONCLUSION

The maintenance and survival of the nemoral species *A. reptans* at the northern boundary of its range were promoted by adaptations on the cell, organism, population, and biocenotic levels. The species became adapted to conditions of the North due to its physiological plasticity, acclimation of the photosynthetic apparatus to conditions existing in middle taiga forests, and cold tolerance. Its multivariant ontogeny and a long period of growth in the pregenerative state allow *A. reptans* to maintain its abundance in the environment where metabolic processes cannot provide for biomass accumulation at a high rate, which leads to a decrease in plant size, the number of vegetative structures, and the intensity of seed and vegetative reproduction. Morphophysiological and population characteristics of the species at the boundary of its range affected its life strategy.

Studies on cultivated *A. reptans* showed that this species is capable of an accelerated development in the middle taiga subzone on conditions of high illumination intensity and the lack of competition for environmental factors (Dymova and Golovko, 1998b). This indicates that relatively low temperatures and a short growing season are not the main factors limiting the growth, development, and expansion of the species. Specific features of *A. reptans* development in its natural habitats are probably accounted for by the combination of unfavorable edaphic conditions (poor podzolic soils) and interspecific competition for nutrients.

The results of this research indicate probable trends in the development of *A. reptans* as a species under conditions of global climate change. It is expected that temperatures at northern latitudes will increase by 3–7°C and the CO_2 concentration in the atmosphere will become two times higher. On the basis of morphophysiological characteristics and physiological plasticity of *A. reptans*, it may be assumed that the expected changes will be favorable for the photosynthetic function and, hence, the growth and development of plants. The ever-increasing size of anthropogenically disturbed areas will also be favorable for the expansion of this species, which is characterized by the reactive life strategy, beyond the present-day boundaries of its range.

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