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Morphological Polyvariance of Ontogeny in Natural Plant Populations

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Abstract—The main patterns of expression of the morphological polyvariance of plants are discussed: diversity of biormorphs, pathways of ontogeny, and disturbances of morphogenesis. The diversity of biormorphs of tap root plants in different ecological conditions has been analyzed in detail. Promising directions of future studies have been formulated.

Key words: plant populations, plant ontogeny, polyvariance of ontogeny, morphogenesis, biormorphs.

Nowadays, there are two approaches to understanding development. Ontogenesis is often restricted to embryogenesis. In such a narrow sense, the subsequent periods of life remain beyond the ontogeny and constitute the postontogenetic (postembryonic or postnatal) period. This is the traditional approach based on the Haeckel concept “Ontogeny is a history of embryo development.” Another, wider approach includes in the ontogeny both development (embryogenesis) and subsequent life until the completion of development as a result of aging and death.

The differences in approaches of different researchers appear to be determined by specific features of the objects and different principles of their organization: unitary in most animals and modular in plants, fungi, and some animals, such as sponges, hydroids, corals, and pearlwrorts. The modular organisms are characterized by the polar and metameric body structure and unlimited growth (Zaugolnova *et al.*, 1988; Bigon *et al.*, 1989).

Rabotnov (1950) proposed periodization of plant ontogeny on the basis of the wider approach, which was later substantially complemented and developed by Uranov (1975) and his students (Tsenopopulyatsii..., 1976; *Ontogeneticheskii atlas...*, 1997, 2000; Gatsuk *et al.*, 1980). Four periods and 12 ontogenetic states are now distinguished in the plant ontogeny. The periodization is based on the concept of biological age as the organism’s own time. The changes in ontogeny are an expression of development in time. Hence, any ontogenetic state can be considered as a measure of biological time. It is characterized by a set of morphological characteristic-markers, not inherent in earlier developmental stages, and the disappearance (full or partial) of the previous characters. Thus, the ontogenetic states can be considered the key moments of development characterized by specific features of morphogenesis, certain ratios of *de novo* formation and dying, morphobiologi-

cal markers, and specific physiologobiochemical processes. The efficiency of this approach has been confirmed by the results studying the ontogenies of more than 500 seed plants, more than 20 ferns (Shorina, 1981), and two lichens (Suetina and Zhukova, 1997; Mikhailova and Vorobeichik, 1999).

In the 1960s–1970s, different modifications of ontogenetic states were described (Sabinin, 1963; Tsenopopulyatsii..., 1976; Zaugolnova *et al.*, 1988). This phenomenon was called polyvariance of development (polyvariance of ontogeny). The polyvariance of ontogeny is realized at both the organismic (individuals and ramets) and suborganismic levels (polyvariance of the development of organs characterized by morphogenesis or partial ontogeny). Classification of different expressions of the polyvariance of ontogeny has been proposed and two supertypes are distinguished: structural (types: dimensional, morphological, and reproduction methods) and dynamic (types: rhythmological and development rates) (Zhukova and Komarov, 1990; Zhukova, 1995).

The aim of the present study was to analyze the morphological polyvariance of ontogeny in natural populations of plants of different biormorphs. This problem has been extensively studied on tree (Chistyakova, 1978; Istomina and Bogomolova, 1991) and herbaceous plants (Tsenopopulyatsii..., 1976; Zaugolnova *et al.*, 1988; Zhukova, 1995; Nukhimovskii, 1997).

The succession of life forms is observed in many plants during development. Even the trees begin their life and single-shoot herbaceous plants (germlings and, more rarely, juveniles), while lignified shoots appear only during the second–third year. This is a typical course of ontogeny, during which morphogenetic programs of organs are switched on at certain stages and, as a result, the biormorph as a whole develops. At the same time, the older organs die, which leads to particu-

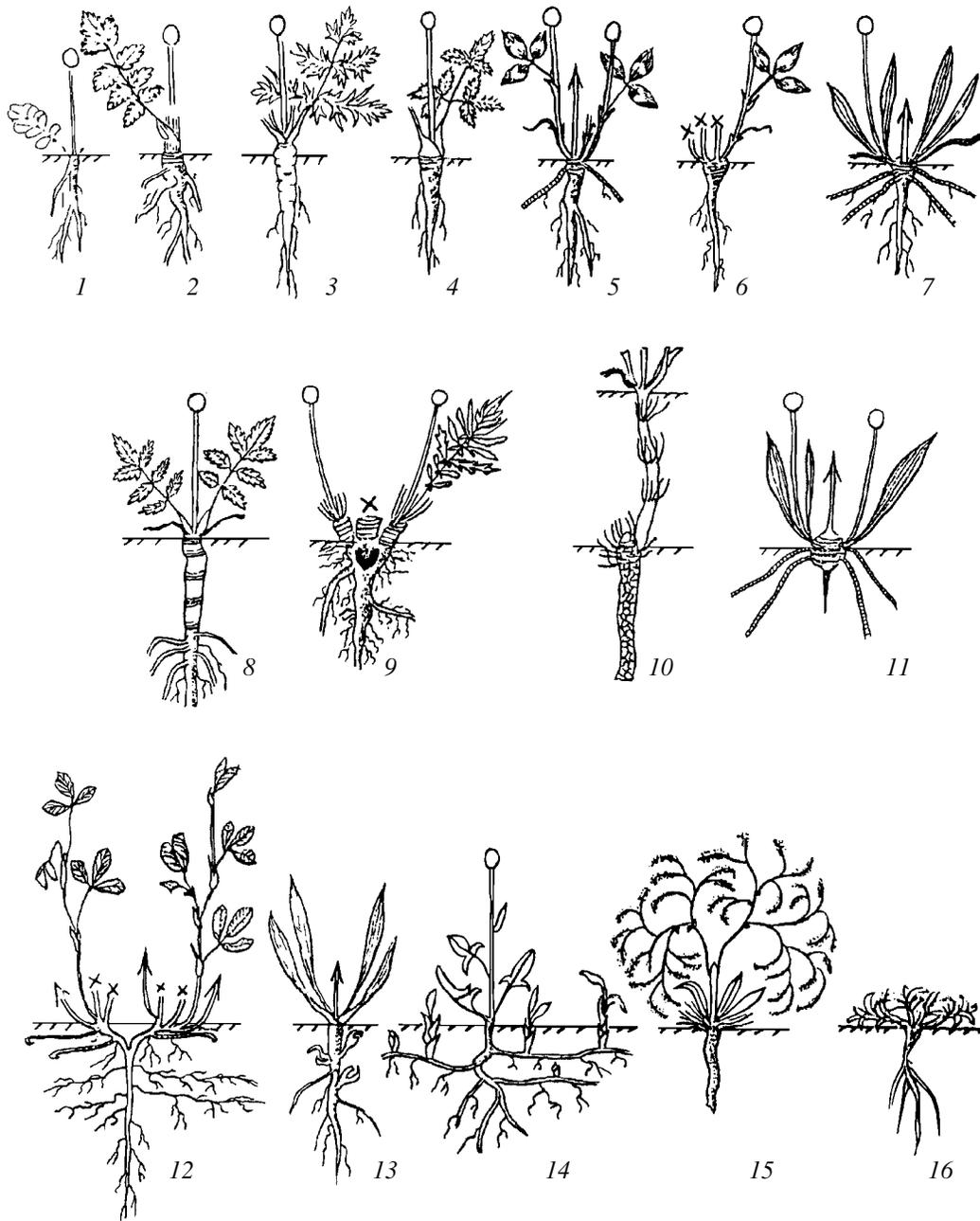


Fig. 1. Diversity of variants of the tap root biomorph of flower plants: (1) annual tap root biomorph, winter-ress *Barbarea vulgaris* R.Br.; (2) biannual or annual/biannual tap root biomorph, parsnip *Pastinaca sativa* L.; (3) biannual tap root biomorph with storing principal root, carrot *Daucus carota* L.; (4) perennial rhizomatous-tap-root biomorph with a compact zone of shortened internodes preserving the principal shoot and principal root until the end of ontogeny, wild parsley *Anthriscus sylvestris* L.; (5) "middle-leaved" rhizomatous-tap-root biomorph preserving the principal rosette shoot and forming generative shoots of the second and higher orders, red clover *Trifolium pratense* L.; (6) perennial tap root biomorph with a sympodial system of substituting shoots preserving the principal root, red clover *Trifolium pratense* L.; (7) perennial rhizomatous-raceme-tap-root biomorph with a mixed type of root system and preserving principal shoot, ribwort *Plantago lanceolata* L.; (8) perennial tap root biomorph with single-headed caudex, *Seseli libanotis* (L.) Koch.; (9) perennial tap root biomorph with multi-headed caudex, greater knapweed *Centaurea scabiosa* L.; (10) perennial tap root caudex biomorph with upper-rosette shoots, field eryngo *Eryngium campestre* L.; (11) perennial rhizomatous-raceme-tap biomorph with early dying principal root and preserving the principal shoot, ribwort "Plantago lanceolata" L.; (12) polycentric long-rhizomatous tap root biomorph, sickle medick *Medicago falcata* L.; (13) perennial tap root biomorph forming root offshoots on the principal root, ribwort *P. lanceolata* L.; (14) perennial polycentric tap root biomorph forming root offshoots on lateral roots, sheep's sorrel *Rumex acetosella* L.; (15) tap root biomorph "babies' breath," *Gypsophila paniculata* L.; (16) radial-flat pulvinate tap root biomorph, cushion pink *Silena acaulis* L.

lation. In this case, the morphogenetic processes take place during the life of an individual ramet.

Succession of life forms or appearance of different biomorphs in one or different plant populations is an extreme expression of morphological polyvariance. The life form, or biomorph, is an external appearance of the adult plant (Serebryakov, 1964), the biomorphs of the small-leaved lime *Tilia cordata* Mill. described by Chistyakova (1978) being a good example. Chistyakova distinguished single-trunk, few-trunk, multi-trunk, and grove-forming trees, tree-shrub, and facultative elfin wood.

Many examples of similar diversity in the populations of herbaceous plants have been described in both morphological and populational studies. The tap root herbaceous polycarpous plants were most extensively studied in this respect. We succeeded to describe 16 variants of this life form on the basis of our own materials and published data (Fig. 1).

The diversity of variants of the tap root biomorph of flower plants looks as follows.

Species	Biomorphs (see Fig. 1)
<i>Centaurea scabiosa</i>	4, 8, 9, 10
<i>Chelidonium majus</i>	2, 4
<i>Helichrysum arenarium</i>	1, 2, 6, 12
<i>Medicago falcata</i>	4, 6, 9, 10, 12
<i>Pastinaca sativa</i>	1, 2, 3, 6, 10
<i>Pimpinella saxifraga</i>	4, 5, 6, 9
<i>Plantago lanceolata</i>	4, 7, 11, 13, 14
<i>P. major</i>	5, 7, 9, 10, 11
<i>Rumex acetosella</i>	4, 6, 10, 13, 14
<i>Seseli libanotis</i>	4, 8, 10
<i>Scabiosa ochroleuca</i>	4, 6, 8, 9
<i>Taraxacum officinale</i>	4, 6, 8, 9, 10, 13, 14
<i>Trifolium montanum</i>	6, 8, 9, 11
<i>T. pratense</i>	1, 2, 4, 5, 6, 8, 9, 11

The minimal number of biomorphs (two) has been recorded in the greater celandine *Chelidonium majus* L. and the maximum one (eight), in the red clover *Trifolium pratense* L. The variants can be classified according to different characters:

- (1) length of ontogeny;
- (2) monocentric, implicitly or explicitly polycentric patterns;
- (3) duration of the primary shoot preservation;
- (4) time, methods of growth and decomposition of the primary root;
- (5) formation of adventitious roots and type of root system (allorhize, allhomorhize, or homorhize);
- (6) formation of long or short rhizomes;
- (7) presence of single- or many-headed caudexes;

(8) transfer of the tillering zone or caudex and formation of upper-rosette, upper-semirosette, or middle-rosette shoots;

(9) specific functions of shoot and root systems: storing root, formation of the shoot system as a "cushion" or "baby's breath."

Let us consider the red clover biomorphs under different climatic and ecological conditions in more detail (Pokrovskaya, 1976). The tap root biomorphs with the principal rosette shoot occur more frequently in meadow phytocoenoses of the southern taiga: perennial (Fig. 1, 4), annual/biennial (Fig. 1, 2), annual (Fig. 1, 1), and, less frequently, caudex (Fig. 1, 8 and 9) plants with additional second order rosette shoots. A perennial tap root biomorph with a sympodial system of substitute rosette of the consecutive orders (Fig. 1, 6) appears in swamp meadows as well as a perennial raceme-root biomorph (Fig. 1, 11), which can be considered as an extreme adaptation to soil swamping. In the steppe zone, a perennial tap root biomorph (Fig. 1, 5) with an extended pregenerative period and tomentous petioles in plants of all ontogenetic states and a steppe tap root annual/biennial (Fig. 1, 2) with early dying principal rosette shoot and elimination of some stages of the generative period. In the taiga zone, the role of adventitious roots increases and the principal root system weakens, as compared to those in the steppe zone, thus suggesting a more active rearrangement of morphostructures and realization of another developmental program. Therefore, the movement of the red clover in the northern parts of its range is less restricted than in the south. Thus, different biomorphs of the red clover can act as indicators of climatic conditions.

Comparative-morphological studies of the underground organs of the ribwort *Plantago lanceolata* L. in continental meadows in the subzone of coniferous-broad-leaved forests (Zhukova and Osmanova, 1999) have shown that this species may be represented by monocentric, implicitly polycentric, and polycentric biomorphs. The described biomorphs occurred under different edaphic conditions and constitute an adaptation-morphological sequence: tap root (on sand substrate) → short-rhizomatous-tap-root (on cobble) → single-rosette short-rhizomatous raceme-root (on dern soil) → many-rosette short-rhizomatous (on loamy sand) → polycentric root-shoot (on slope upon plant burial). This suggests a high variability of the species and confirms the exceptionally important significance of morphological polyvariance which ensures realization of different variants of the complete ontogeny of genets and incomplete ontogeny of ramets of the shoot and root origin.

Hence, appearance of a wide range of biomorphs is related to diverse changes in ecological situations, such as shading, flooding, burial in sand, ground compaction, etc. Therefore, the earlier idea that every species has one life form is true only in a few cases of extreme

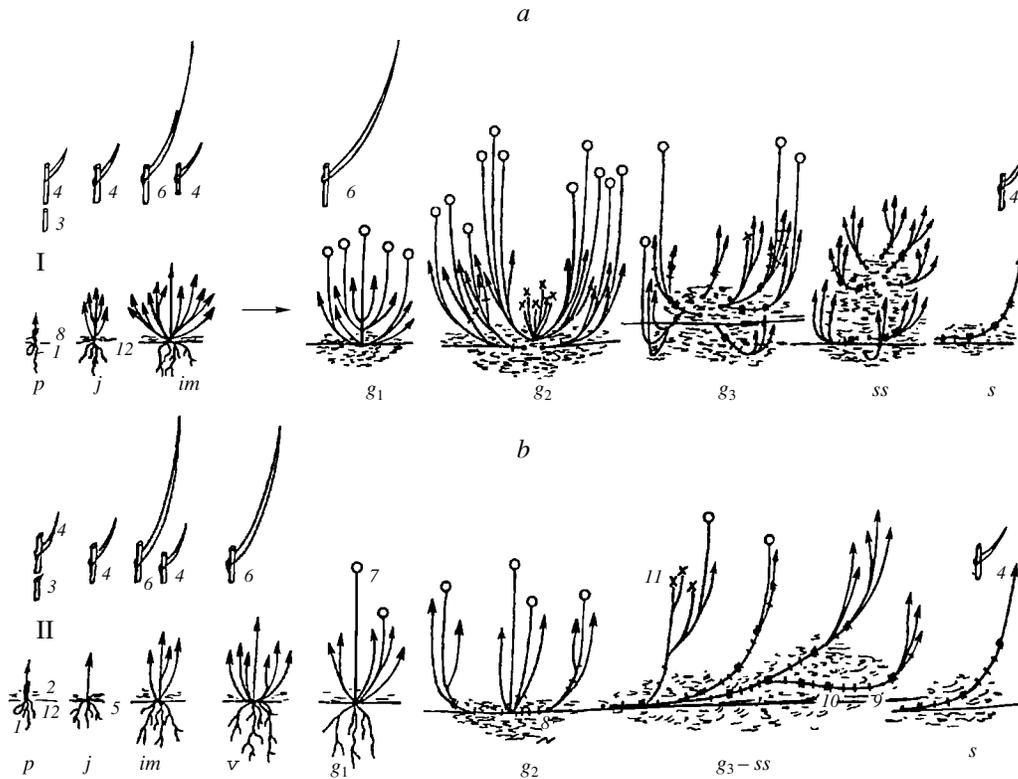


Fig. 2. Schematic diagram of age states of *Deschampsia flexuosa*: (a) monocentric or implicitly polycentric dense-cespitose biormorph; (b) polycentric stolon-dense-cespitose biormorph. (p) Plantlets, (j) juvenile, (im) immature, (v) virginil, (g₁) young generative, (g₂) mature generative, (g₃) old generative, (ss) subsenile, (s) senile. (1) Germinal root, (2) rosette shoot, (3) coleoptile, (4) leaf of juvenile type, (5) older leaf, (6) leaf of adult type, (7) generative shoot, (8) stolon-semirosette shoot, (9) stolon-rosette shoot, (10) old zones of tillering, (11) dead shoot.

specialization (“cushions” or “babies’-breath” of tap root herbage).

The diversity of life forms also determines that of ontogeny pathways, especially in the case of succession of biormorph types, when the monocentric biormorph becomes implicitly or explicitly polycentric. For example, two biormorphs were described for *Lerchenfeldia flexuosa* L. (Zhukova, 1979): monocentric or implicitly polycentric compact-cespitose on northern felled regions and polycentric stolon-compact-cespitose under the canopy of pine forests (Fig. 2). The plants of each biormorph realize their own ontogeny characterized both by duration and degree rejuvenation of ramets alternating in the population flow.

No less important consequences for the population life of plants are related to particulation at different stages of ontogeny. In cespitose grasses, cocksfoot *Dactylis glomerata* L., meadow fescue *Festuca pratensis* Huds. (Ermakova and Zhukova, 1985), and tufted hair-grass *Deschampsia caespitosa* P.B. (Zhukova, 1995), particulation proceeds in the old generative and subsenile states, as a rule, without rejuvenation of ramets. In some cases, however, reversions to the virginil state or, still more rarely, to the juvenile one are possible. Such a lability of the ramet behavior determines

the life span of coenopopulations and the rate of succession of its developmental stages.

Another aspect of morphological polyvariance is an increase in the number of shoots and dormant buds or laying down and development of adventitious buds on roots, rhizomes, or caudexes. This leads to the appearance of multi-rosette tap root, caudex, short-rhizomatous, and raceme-root plants and a number of transitional forms (Fig. 1) (Ontogeneticheskii atlas..., 1997, 2000), as well as to facultative root-shoot pattern: for example, in tap root polycarpous plants dandelion *Taraxacum officinale* L. (Ermakova, 1990), sickle medick *Medicago falcata* L. (Snagovskaya, 1965), and short rhizomatous herbage, including the ribwort (Zhukova and Osmanova, 1999).

The formation of stolons or creeping rhizomes in some grasses has a somewhat different morphological nature. For example, in *Lerchenfeldia flexuosa* and *Deschampsia caespitosa*, the first through third lower internodes of the rosette shoots could elongate and the latter could be transformed into upper-rosette or upper-semirosette shoots, thus leading to the appearance of stolon-tussock biormorph of the implicitly or explicitly polycentric type, which determines another method of assimilation and detention of the territory of a given

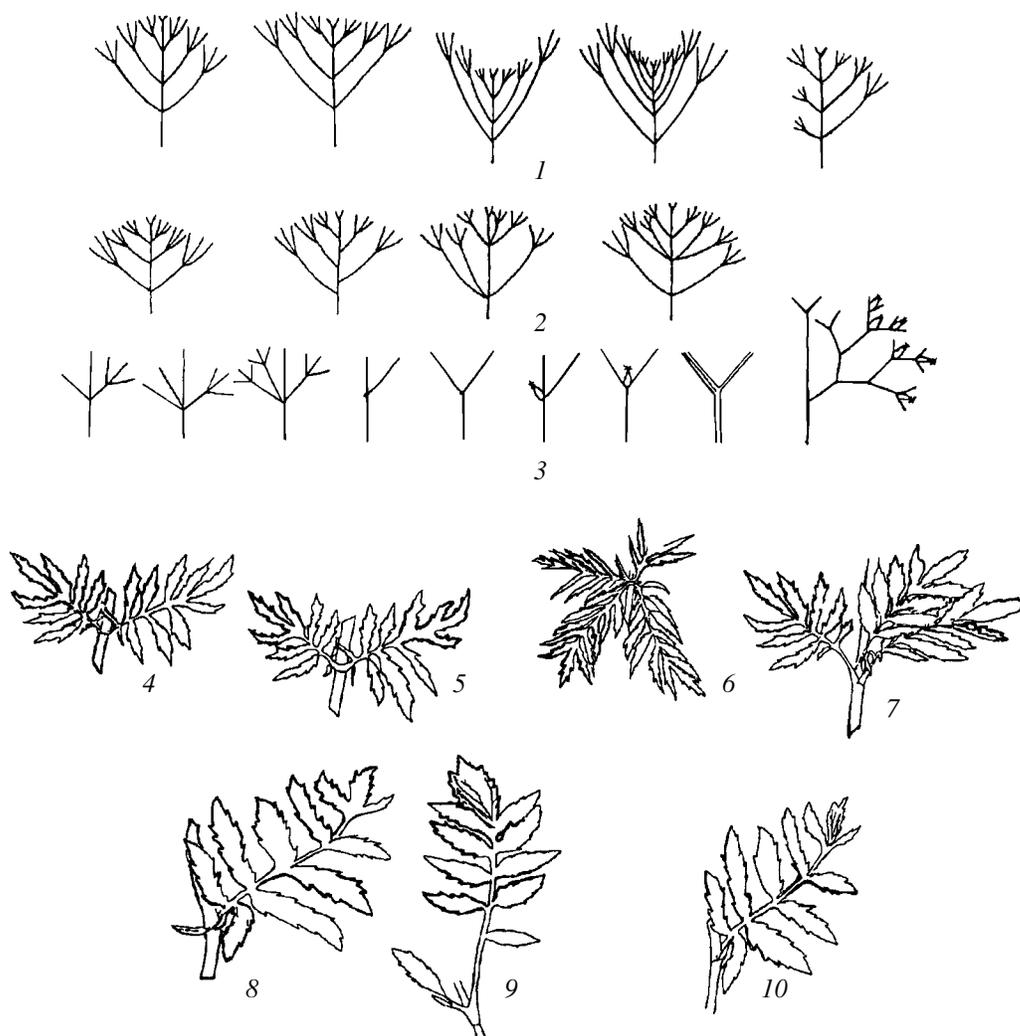


Fig. 3. Morphological polyvariance of *Valeriana officinalis* L.: (1) general appearance of inflorescence; (2) arrangement of first order paracladia; (3) arrangement of paracladia of the second and higher orders; (4) normal, opposite leaf arrangement; (5) opposite leaf arrangement, confluence of petioles; (6) shortened internode, whorl of four leaves; (7) whorl of three leaves; (8, 9) reduction of one leaf in opposite leaf arrangement; (10) alternate leaf arrangement.

coenopopulation. A similar picture could be observed in the greater plantain infected by powdery mildew, while its rosette shoots are transformed in middle- and upper-rosette shoots (Zhukova and Shestakova, 1995). Changes in the cyclicity of shoots have no less important consequences. After multiple hay-mowing on the Oka, Ugra, and Solotcha river meadows, the polycyclic shoots could be transformed into tri- or dicyclic shoots in the cocksfoot and fescue, while the duration of ontogeny was reduced.

At the same time, in loose-cespitose plants with mono- and dicyclic shoots, transition to polycyclic shoots is possible. This was recorded in sweet vernal grass *Anthoxanthum odoratum* L. (Zhukova, 1995) in Karelia and Irkutsk districts. The increase in shoot cyclicity leads, as a rule, to the longer life of ramets and slower development and turf degradation. This determines, in

turn, the time of particulation and formation of clones and their structure and dynamics.

Any deviations from the morphogenetic programs lead to morphological modifications and can be represented by changes in shape, edge, apex, base, and degree of segmentation of the leaf blade, pattern of leaf arrangement, increase in the number of elements of the generative organs, their confluence, elongation of the axial part of a flower or inflorescence, modification of the shape and color of flower elements, their reduction, etc. The scale of modifications is different: from variations in the leaf edge and coloration of petals to changes in the pattern of leaf arrangement, type of shoot, its cyclicity, transfer of the tillering zone, appearance of adventitious buds or roots, and metamorphosed vegetative organs.

If these modifications are preserved in the course of several ontogenetic stages, we deal with the morphological polyvariance of ontogeny. Those cases of morphological polyvariance that could change the population parameters are most significant for characterization of the populations. For example, the cases of appearance of whorl leaf arrangement on shoots of all-heal *Valeriana officinalis* L. instead of the typical opposite arrangement and reduction of inflorescence paraclydia are shown in Fig. 3. These modifications lead, in the first case, to an increased leaf surface and biomass and, in the second, to reduced seed productivity (Ilyushechkina, 1998).

Minute expressions of morphological variability in the vegetative and generative spheres occur in various herbaceous plants of most life forms. They were studied in detail for the all-heal, Greek valerian (Ilyushechkina, 1998), and trientale *Trientalis europaea* L. (Polyanskaya, 1999). The highest morphological biodiversity was recorded in the all-heal and trientale in the young generative state and the lowest at the old generative one. This may be related to the early death of individuals with morphological deviations, in agreement with the earlier data obtained for *Lysimachia vulgaris* L., *L. nummularia* L., and *Primula veris* L. (Primulaceae) (Zhukova, 1995). A positive correlation of phenotypic variability of the vegetative and generative in all ontogenetic groups of the generative period was shown for the all-heal.

The cumulative effect of different pollutants of the air basin and soil leads to a sharply increased (up to 80%) frequency of expressions of morphological polyvariance in the all-heal ontogeny. Unfavorable climatic conditions induce the same effect. At the same time, the morphological polyvariance of this species is fully absent or very rare in ecologically pure habitats or under optimal weather conditions. Hence, different expressions of ecological stress increase the level of intrapopulation diversity.

Further studies of morphological polyvariance will help solve some issues of the population biology of plants (Glotov and Zhukova, 1995):

(1) estimation of microgeographical distribution of biomorphs and morphogenetic disturbances within the territory occupied by a population, with special reference to heterogeneity of the habitat according to edaphic and phytocoenotic conditions, etc.;

(2) estimation of the degree and pattern of genetic determination of different biomorphs and morphogenetic disturbances; here, identification of the clones of vegetative-mobile species using protein and DNA markers can serve as a methodically important approach;

(3) estimation of the contribution of different biomorphs and morphogenetic disturbances in the next generation under different ecological conditions, i.e., determination of their role with respect to adaptation.

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