

Structural organization of semi-rosette hygrophelophytes

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Summary: The composition of shoot systems of *Caltha palustris*, *Cicuta virosa*, *Oenanthe aquatica*, *Sium latifolium* and *Rorippa amphibia* is described by the use of comparative morphological and biomorphological methods and three module categories. 13 variants of elementary modules are distinguished. They differ in shoot location, internode length, presence or absence of leaves and leaf type, buds and their derivatives. The universal module is presented by a monocarpic shoot divided into structural-functional zones: the lower and the middle zones of inhibition, regeneration, enrichment and the main inflorescence. Its structure and development determine the diversity of biomorphs of the semi-rosette hygrophelophytes and the presence of a phenobiomorph, a salient-polycentric, vegetative mobile¹ short-lived plant. One can differentiate four main directions of changes in formation of their appearance which are determined by different levels of irrigation. The basal module of most semi-rosette hygrophelophytes is formed during the process of monopodial growth of the monocarpic shoot due to its branching.

Keywords: hygrophelophytes, *Caltha palustris*, *Cicuta virosa*, *Oenanthe aquatica*, *Sium latifolium*, *Rorippa amphibia*, shoot, shoot system, structural-functional zone, module, biomorph

Approaches to describe the plant body have broadened lately, including the peculiarities of morphogenesis showing its fitness to environment. This was inspired by defining plants as modular organisms (BEGON et al. 1990), by differentiating three module categories in the shoot structure (SAVINYKH 2003, 2006, 2015; SAVINYKH & MALTSEVA 2008), by the complementarity approach to characterize plant life-forms from the point of view of multiple synthetic classification (MEYEN 1978; SHORINA 1994) and by differentiating the directions of morphological changes, refrains according to MEYEN (1978), which happen in organisms of different taxonomic groups in similar environmental conditions (NOTOV 2005). Most researches in biomorphology of plants (KHOKHRYAKOV 1981) are devoted to dry land plants. The analysis of the structural organization of helophytic plants has not been made since the last century. Currently, it is being made mostly by Russian scientists by use of methods and approaches worked out in Serebryakov's school of thought (SAVINYKH & CHERYOMUSHKINA 2015). At the same time, ideas and approaches to phytocology of water plants of streams as well as of adjoining places under same environmental conditions have broadened (PAPCHENKOV 1985, 2001). Alongside with the already existing groups of water plants and helophytes such as hydrophytes, hygrophytes and helophytes, a special group of hygrophelophytes was distinguished by PAPCHENKOV (1985). They are typical of low levels of the flood shoreland, marginal associations of lakes, floating mats and shoal borders with the depth up to 20–40 cm. They inhabit damp, water-logged, slightly watered and water-covered grounds. Plants often approach the water surface rooting in marshy shores. There are different forms of hygrophelophytes, including semi-rosette grasses.

¹ Vegetative mobile are plants which have special organs (rhizomes, stolons, contractile roots) for spreading. They also include couch grass and plants of creeping habit.

Materials and methods

Semi-rosette hygrophelophytes of three families belonging to the class Magnoliopsida are investigated: *Caltha palustris* L. (Ranunculaceae), *Cicuta virosa* L., *Oenanthe aquatica* L., *Sium latifolium* L. (Umbelliferae) and *Rorippa amphibia* (L.) Bess. (Cruciferae).

The samples were collected in Kirov, Chelyabinsk and Yaroslavl regions of the Russian Federation. Additionally, we analyzed the structure of samples and shoots of dried specimens of the herbaria SYCO, LE, MOSP and IBIW.

The main research methods were comparative-morphological (Serebryakov 1964) and biomorphological (Khokhryakov 1981). The description of biomorphs was made according to the principle of complementarity (Begon et al. 1990) of contemporary botany (Shorina 1994; Cheryomushkina 2004; Savinykh 2006). The following characteristics were taken into account:

- the structure of subterranean organs (Serebryakov 1952);
- the number of centres of influence of the plant sample on the environment: salient-polycentric², non-salient-polycentric³, monocentric (Smirnova et al. 1976) and acentric (Shorina 1981) plants;
- life span of the plants (Vysotskiy 1915): perennial plants, short-lived plants and pseudoannuals;
- the number of bloomings and fruitings in a lifetime: monocarpic, oligocarpic and polycarpic;
- the stage (full and non-full), the type (specialized and non-specialized) and time (early, normal, late) of the morphological disintegration in the ontogenesis of the plant (Smirnova et al. 1976; Nukhimovskiy 1997).

The structural organization of plants was characterized and compared as to the main biomorph, i.e. the structure of the samples in the mature generative ontogenetic state. Due to appearance plasticity and relatively early morphological disintegration during the ontogenesis of the plants under research, we took into account the habit at a definite ontogenetic stage, i.e. its ontobiomorph (Khokhryakov 1978) and a definite phenological phase, i.e. its phenobiomorph (Khokhryakov & Mazurenko 2008).

The structure of shoot systems was described by use of three module categories (Savinykh 2003, 2015; Savinykh & Maltseva 2008): the **elementary shoot** that is formed during one plastochrone at the lower part of the shoot and represented by the lower internode, node, leaf, accessory bud or the sylleptic shoot formed by the bud; the **universal shoot** which is a monaxonic shoot formed as a result of activity of one apical system; the **basal shoot** which is a spatial-temporal structure formed on the basis of a whole universal module or its part and which is repeated in the structure of mature generative units. The elementary module is the less repeated part of the shoot, the universal module is the less repeated part of the shoot system and the basal module is the less repeated part of the plant.

The universal module of the investigated plants is a monocarpic shoot in the sense of Serebryakov (1952) and Troll (1964), as well as that of most dryland perennial grasses. It blooms once,

² Salient-polycentric plants are plants with several centers of influence on the environment. They are connected to each other by means of rhizome, stolons or other organs.

³ Non-salient-polycentric plants are plants with several centers influencing the environment, but these centers are not clearly discernible.

and it is divided into structural-functional zones (MALTSEVA & SAVINYKH 2008; SAVINYKH & VISHNITSKAYA 2008; SHABALKINA & SAVINYKH 2012) which are differentiated in accordance with the approaches of TROLL (1964), BORISOVA & POPOVA (1990). The phases of shoot development were characterized according to SEREBRYAKOV (1959) and SEREBRYAKOVA (1971).

Results

Hygrohelophytes under research seem to grow in similar conditions. In fact, it is not at all so, as they grow in different ecotypic conditions. The difference is connected with the degree of submersion, periodicity and the flood of the substrate. The usual habitats of *C. virosa* are water-filled squashy grounds between tufts in forest swamps, sedge tussocks bases, banks approaching constantly and being directly exposed to water and shallow waters 30–40 cm deep. *S. latifolium* grows on overgrown shallow waters and swamps, in ditches and drains with stagnant or lagging water. *O. aquatica* prefers flood-free higher spots of the micro-relief, the upper parts of sedge tussocks and it is rare in shallow waters. *C. palustris* grows on periodically long-time flooded territories and in less damp sites. *R. amphibibia* grows in waterbodies with changing water level, up to its complete disappearing, in the site of the water line and at a stationary water level at depth.

Generative units of all model species have a root system consisting of stem-developed secondary roots. Their growth strategy and formation of specific appearances are determined by the peculiarities of their development and the structure of monocarpic shoots which are universal modules. Those of monocentric biomorphs can be winter-annual (*R. amphibibia*), dicyclic (monocarpic *O. aquatica*, mature generative plants *C. palustris* and *R. amphibibia*), oligocyclic (mature generative plants *C. palustris* which develop with a pause in blooming), polycyclic (*C. virosa*, the first blooming plants *C. palustris* and *O. aquatica*).

The phases of development of a monocarpic shoot are represented by the phases of a bud, a vegetative assimilating shoot, budding, blooming, fruiting and secondary activity (of perennial and short-lived plants). The shoot of *O. aquatica* can have an intermediary phase, a stolon (PETROVA 2016). In *R. amphibibia*, a segment with long internodes and an upper-rosette part can be developed in the vegetative assimilating shoot phase. In both cases a monocarpic shoot becomes a semi-rosette one after forming the second prolonged section. Such shoots were not found in investigated species of Ranunculaceae. Shoot-formation of *Ranunculus repens* L. is similar to the previously described one. Evidently, development of semi-rosette monocarpic shoots in deep grass is one of the possible ways of plant's spreading.

Monocarpic shoots of mature generative units of semi-rosette hygrohelophytes are usually dicyclic. They are differentiated into structural-functional zones: the lower and the middle zones of inhibition, regeneration, enrichment and the main inflorescence (Fig. 1A). Each of them consists of its own elementary modules. The **lower inhibition zone** of orthotropic shoots of all investigated species is represented by a basal part of the shoot with numerous secondary roots. It includes 4(5)–8(10) elementary modules of a short internode, a node with a dead leaf of mid-formation and a dormant bud. Its main function is fixing the plant in the ground. Depending on the length of development proceeding the phase of blooming, the lower inhibition zone may be developed by annual accretions differing in number. The lower inhibition zone of semi-rosette shoots of *O. aquatica* also includes modules consisting of a long internode, a node with a mid-formation leaf and a bud (Fig. 1B).

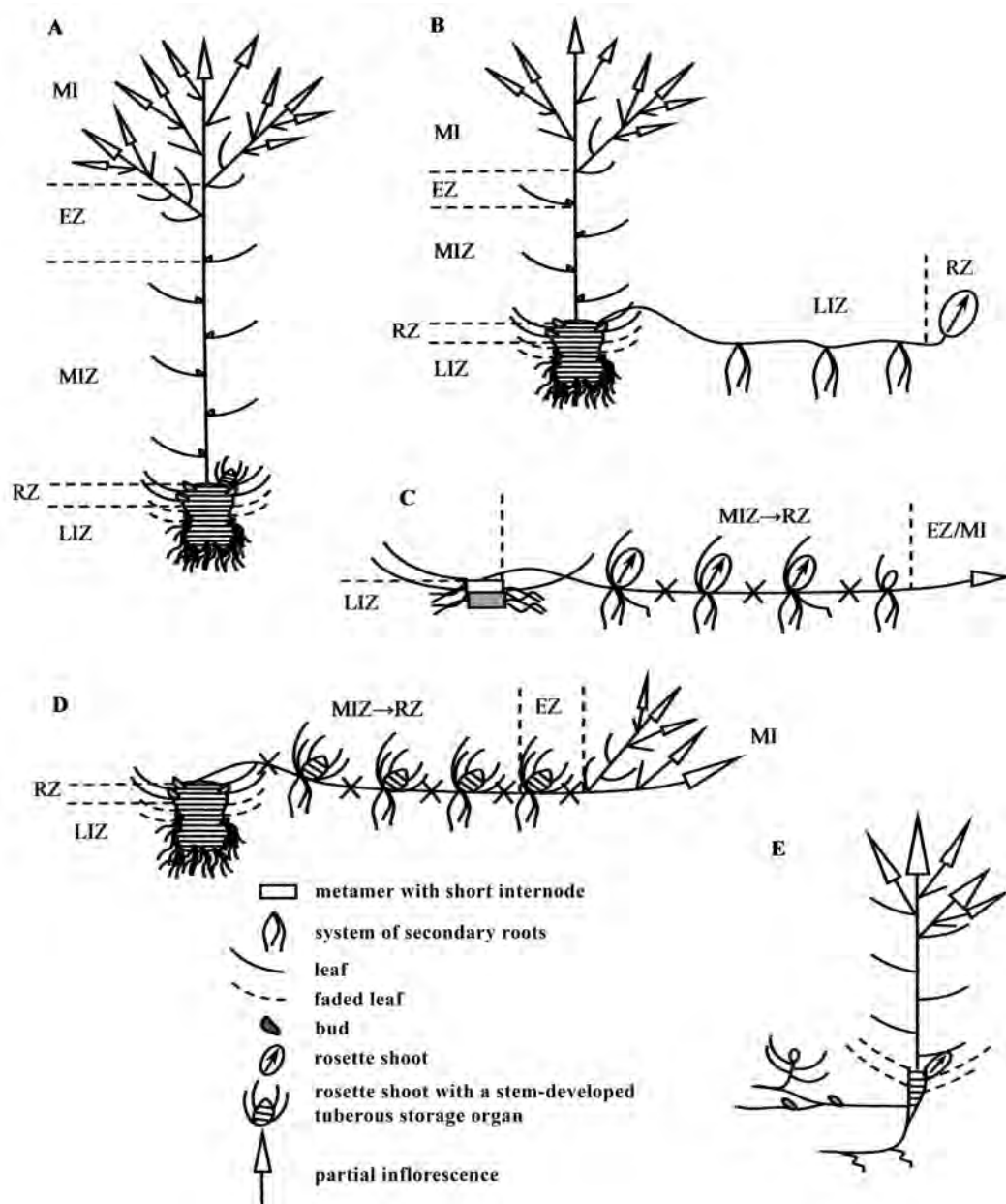


Figure 1. Schemes of monocarpic shoots and biomorphs. LIZ – lower inhibition zone; MIZ – middle inhibition zone; RZ – regeneration zone; EZ – enrichment zone; MI – main inflorescence.

In the **regeneration zone** (the upper metamers of a basal rosette) from 1–2 to 4–6 buds appear yearly. Substitution shoots are formed by them during blooming and fruiting of the original shoot. This zone consists of two variants of elementary modules: a short internode, a node with a mid-formation leaf and a vegetative rosette substitution shoot or a bud (if the substitution shoot is not developing). Dormant accessory buds in the regeneration zone are characteristic of many helophytic and water plants of different biomorphs (SAVINYKH et al. 2015).

The **middle inhibition zone** consists of 1(3)–15(25) elementary modules with a long internode, a node with a mid-formation leaf and a latent bud.

The **enrichment zone** and the **main inflorescence** form a synflorescence (a floral zone) of paracladia and partial inflorescences with numerous variants of elementary modules (MALTSEVA & SAVINYKH 2008; SHABALKINA 2010). The enrichment zone consists of 1–6 metamers with paracladia which vary in structure and in leaf formation. The basal inflorescence is complex botryose (double to multiple, Umbelliferae and Cruciferae) and cymose with a different degree of branching (*C. palustris*).

The variety of structural-functional zones and the degree of their intensity in the studied species differ depending on the conditions of growing. This is very typical of the enrichment zones and the middle inhibition zone. In habitats with decreasing water level, orthotropic semi-rosette shoots of *C. palustris* and *O. aquatica* lodge and root during the vegetation season. Vegetative rosette shoots are formed from buds of middle inhibition zone. In this case, the elementary modules consist of a long internode, a node with a mid-formation leaf and an accessory vegetative rosette shoot or a bud (Fig. 1C). A monocentric plant turns into a salient-polycentric one. Such development is also typical of shoots of *R. amphibibia* (Fig. 1D). During thickening the axis of the rosette part it forms a stem-developing storage organ of the kind of a tuber (Fig. 2). It provides early efflorescence for the plant in question as well as for the plants of other species from the habitats considered (SHABALKINA & SAVINYKH 2012; SAVINYKH & SHABALKINA 2017). Not all of the buds of this zone start to grow at the same time in *O. aquatica*. After morphological disintegration, a part of them develop turions in the form of a part of the stem with an accessory bud. According to SARYCHEVA (2002), they can stay dormant for 1–2 years.

Because salient-polycentric plants die off during the last third of their vegetation period, this appearance is characterized as phenobiomorph. Daughter plants, which developed in conditions of decaying internodes of the middle inhibition zone and morphological disintegration of the parent plant in autumn, pass winter as rooted rosette shoots. They form a turion. That's why the middle inhibition zone has not got an assimilating function like orthotropic shoots, but also provides additional regeneration, propagation and dispersal of the plant (Fig. 1C, D). After separation of the original salient-polycentric plant, a clone is developed with a diffuse spacial structure, a 'diffuse clone' (SMIRNOVA 1987). The phases of monocentric plant, salient-polycentric

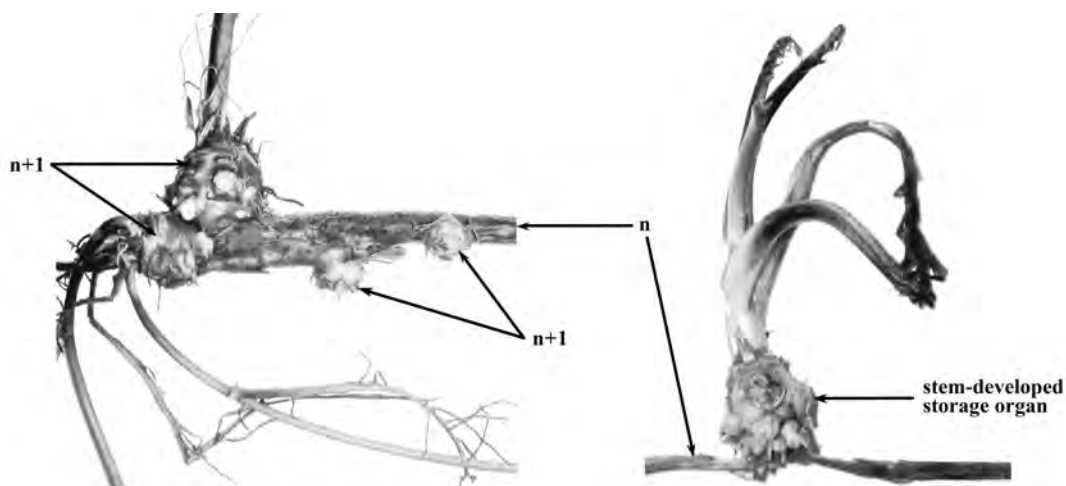


Figure 2. Shoot system of *Rorippa amphibibia* with diaspores which passed the winter (26.05.2010); secondary roots are removed). n, n+1 – shoots of sequential bifurcation.

plant, diffuse clone of monocentric plants, salient-polycentric plant, etc. successively change during plant ontogenesis. The plant exists in the form of monocarpic ramets which successfully change, it remains polycarpic and actually it becomes 'immortal' as many hydrophytes like *Hydrocharis morsus-ranae* L. and others.

Plants with orthotropic monocarpic shoots (*C. palustris*, *C. virosa*, *S. latifolium*) form a compact clone after morphological disintegration. Evident monocentricity of the plant is provided by interlacement of secondary roots which appear regularly and yearly. Usually, one bud unfolds in the zone of regeneration of such plants. Separate ramets appearing due to morphological disintegration do not live longer than two years. Therefore, such plants are called substituting perennial or biennial depending on time of shoot developing to blooming.

Depending on the peculiarities of monocarpic shoot development and the plant, the type of the structure on the basis of the universal module is changed into the basal module. It is represented by a shoot system formed during monopodial growth due to its branching. Besides, due to a pause in blooming, mature generative plants of *C. virosa* exist as a system of vegetative rosette shoots of the $(n+1)^{st}$ branching order as mono-, di- and polychasium with further development of a compact clone.

In permanent conditions of nearshore areas of lakes and ponds, ratoons are developed from subsidiary buds of *R. amphibibia*. The plant becomes a salient-polycentric short-lived ratoon with early full morphological disintegration. Ramets which appeared in this way under such conditions can hardly restock the population to a considerable degree. The land ecobiomorph of *S. latifolium* intensively develops ratoons in the generative period, the number and the degree of their development increase in case of injury of the main shoot (PETROVA 2016). Relatively deep ascending daughter shoots of ratoons have a prolonged part growing in the earth which quickly rots through. Obligatory developing of ratoons is characteristic of *Rorippa × anceps* (Wahlenb.) Reichenb. in sand beaches, wet meadows, in agrocoenoses and at roadsides (SHABALKINA & SAVINYKH 2013).

Taking into account the main biomorphs ontobiomorphs and phenobiomorphs, we have picked out 15 variants of semi-rosette hygrophelophytes (Table 1).

Ontomorphogenesis as a process of biomorph development at early stages is similar to all model species in the phase of a primary shoot (vegetative rosette → vegetative-generative semi-rosette). Further ontogenesis continues in several directions: 1) monocentric plant → non-salient-polycentric plant → compact clone (*C. palustris*, *C. virosa*, *S. latifolium*); 2) monocentric plant → salient-polycentric plant → diffuse clone from secondary monocentric ramets → salient-polycentric plant, etc. (*R. amphibibia*, *C. palustris*, *O. aquatica*, *S. latifolium*); 3) monocentric plant during its whole life (*O. aquatica*).

Discussion

The analysis of structure and formation of shoot systems has shown the following possible directions (refrains) of changes in appearance of semi-rosette hygrophelophytes determined by different levels (variation degrees) of biotope watering. In non-flooded zones of the relief, monocarpic therophytes are formed (*O. aquatica*). Turions of *R. amphibibia* are capable of living during winter and surviving spring watering. They can bloom and finish their life-cycle as typical monocarpic therophytes.

Table 1. Biomorphs of model species.

No.	Biomorph	<i>Rorippa amphibia</i>	<i>Cicuta virosa</i>	<i>Caltha palustris</i>	<i>Oenanthe aquatica</i>	<i>Sium latifolium</i>
Main biomorph						
1	Monocentric reserve perennial		+			
2	Monocentric reserve short-lived plant	+				
3	Monocentric reserve biennial			+		
4	Monocentric biennial of vegetative origin				+	
5	Non-salient polycentric reserve perennial		+			
6	Non-salient polycentric reserve short-lived plant					+
7	Non-salient polycentric biennial			+		
8	Short-lived plant of vegetative origin	+				
9	Monocentric monocarpic biennial	+			+	
10	Ratoon short-lived plant	+				+
Ontobiomorph						
1	Monocentric perennial		+	+		
2	Monocentric short-lived plant				+	
3	Non-salient-polycentric perennial		+			
Phenobiomorph						
1	Salient-polycentric short-lived plant with a lodging semi-rosette monocarpic shoot	+		+	+	
2	Salient-polycentric stolon-developing short-lived plant				+	

Together with increase of watering degree and restriction of basitonic branching the appearance changes this way: monocentric perennial (*C. virosa*) → reserve perennial (*C. virosa*) → reserve short-lived plant (*R. amphibia*, *S. latifolium*) → reserve biennial (*C. palustris*).

During the vegetative season in waterbodies with changing water-level, a special phenobiomorph appears, a salient-polycentric plant (optionally *C. palustris* and *O. aquatica*, obligatory *R. amphibia*) with formation of a diffuse clone from monocentric ramets. In waterlogged soil, a tendency to vegetative growth appears (stolons of *O. aquatica* and an upper-rosette shoot of *R. amphibia*).

Thus, the main trend in morphological adaptation of semi-rosette hygrophelophytes is monocarpic progeny. Sites with sudden seasonal changes of humidity (beaches, bank lands, slopes, tufts in damp meadows and swamps) are the places where typical monocarpic therophytes with highly effective seed propagation appear. In habitats with relatively stable increased moistening, annuals of vegetative origin like monocarpic ramets appear which substitute perennials and biennials.

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