BIOLOGY

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ONTO-MORPHOGENESIS OF THE SOLANUM DULCAMARA

ABSTRACT. This article contains characteristics of the biomorphology and taxonomy of the Solanum dulcamara L. The main living life-form of the plant is the lianoid subshrub with creeping rhizome. The authors single out 4 stages of the onto-morphogenesis of the S. dulcamara: 1) seed formation, 2) formation of the monaxonic plant, 3) bush formation, 4) rhizome formation; (in which 5 onto-biomorphs alternate (seed; monopodial growing vegetative plant with a taproot; sympodially growing upright standing semishrub with a taproot; sympodially growing upright standing subshrub with a taproot; sympodially growing subshrub with a mixed root system; sympodially growing subshrub with long rhizome). On the basis of the main life-form, under the influence of environmental conditions, formation of six ecobiomorphs is possible (dry land lianoid or prostrate subshrub; coastal water lianoid or prostrate subshrub; water prostrate grassy plant; weed forming prostrate); their characteristic is given. The ontogenesis type of the species is defined (G-type (G2-subtype) according to L.A. Zhukova). Stages of onto-morphogenesis are related to the ontogenetic periods and conditions of the plants. It is noted that the end of the ontogenesis is difficult to trace due to the rejuvenation capacity of the plant and its vegetative propagation.

KEY WORDS. Solanum dulcamara, onto-morphogenesis, onto-biomorph, ontomorphogenetic stage, ecobiomorph.

Introduction. In spite of the fact that the study of life-forms has quite a long history, the problem of the change of the exterior of plants in the ontogenesis of a separate species is still vital. So far there has been two approaches to the characteristic of the plants ontogenesis according to their morphological peculiarities: 1) specification and description of ontogenetic periods and conditions [1-3]; 2) description of morphogenetic phases [4-8].

Age-related changes of an organism are reflected in its outer appearance and result in the change of its habit. Such process is called ontomorphogenesis. It is often described according to the ideas of O.V. Smirnova et. al. [9], where each phase is characterized by a certain structure ("primary offshoot", "lax-stemmed shrub" etc.) which was formed as a result of specific transformations. Later [10] the phase of ontomorphogenesis was understood not only as a structure but also as a stage (a period of time) and process during which a certain habit of a plant is formed. This is how we approach ontomorphogenesis of plants. The habit which evolved in the course of such transformations and which corresponds to a certain ontogenetic condition [11] we define as an ontobiomorph. Therefore, describing transformations of the life-forms of a plant in its ontogenesis, following M.T. Mazurenko [11-12], we single out biomorphs which are different from one another morphologically, within ontomorphogenetic phases. In this case a phase is understood as a process of a habit restructuring and ontobiomorphs are discreet structures which are formed during this process.

Materials and methodology of the research. The subject of the research is Solanum dulcamara L. It is a summergreen, vegetative-mobile, polycarpic, creepingrhizomatous lianoid semi-shrub with sympodially growing during the whole vegetative season and to different extent lignifying stems from the series of monocarpic offshoots.

The species belongs to the Solanaceae Juss., subgenus Solanum, section Dulcamara (Dun.) Bitter. Its native habitat includes the whole of Europe and part of Western Siberia; as an imported species it can be met in Pre-Caucasian region, Central Asia and North America, where it naturalized in some places [13].

The research is based on the materials of our own gathering in Kirov (2009-2012), Yaroslavl (2010-2011) and Nizhny Novgorod (2010-2011) regions, analysis of the herbarium collections LE, MHA, SYKO, IBIW, TK, NS, NSK, MWV, MOSP and SYKT and the herbarium collection of the biological department of the Vyatka State University.

The life-form has been characterized with the help of the comparativemorphological method [4; 14] and synthetic approach and ideas of O.V. Smirnova [9]. The phases of ontomorphogenesis and ontobiomorph are described according to M.T. Mazurenko [11-12]. The type and peculiarities of the ontogenesis are defined in accordance with L.A. Zhukova's classification of the types of plant ontogenesis [3].

Research findings and discussion. In the ontomorphogenesis of S. dulcamara there have been singled out 4 phases and described 5 ontobiomorphs.

Phase I – seed formation: begins with development of the zygote and continues till seed sprouting; as a result the ontobiomorph is formed 1 – seed (Fig. 1). Its color ranges from yellow to light brown; its size is 2x3 mm. It is oval and flattened at the sides. The seed surface is rough. The seed lobes are smooth and opaline. The curved or spiral embryo is located in the center or periphery of the seed occupying $\frac{3}{4}$ of its volume [15]. Opinions concerning the endosperm structure are different: A.L. Takhtadjan [16] defines it as deep; G.Ya. Zhukova [17] points out that it comprises several layers of cells. Our research confirms G.Ya. Zhukova's findings.

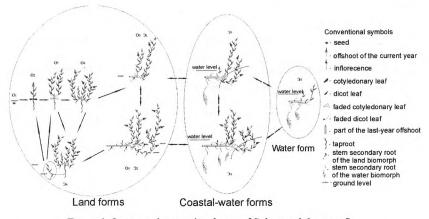


Figure 1. Ontomorphogenesis scheme of Solanum dulcamara L.:
O1-O2 — ontobiomorphs: O1 – seed; O2 – vegetative-non-motile taproot monopodially growing vegetative plant; O3 — vegetative-non-motile polycarpic sympodially growing upright semi-shrub; O4 — vegetative-weakly-motile polycarpic implicitly polycentric sympodially growing semi-shrub with a mixed root system; O5 — vegetative-motile polycarpic clearly polycentric long-rhizomatous sympodially growing semi-shrub;
O1-O2 — ecobiomorphs: O1 — land lianoid semi-shrub; O2 — land creeping semi-shrub; O3 — coastal-water lianoid semi-shrub; O4 — coastal-water creeping semi-shrub;
O5 — water creeping grassy plant; O5 — burr semi-shrub.

The seeds ripen in the fruits (berries) by the end of the vegetation season (September-October), fall to the ground surface and in the winter they remain under the fallen leaves and snow. In spring the seeds germinate. Our laboratory experiments showed that a number of conditions are necessary for germination: loose substrate, well warmed soil, moisture and no light. Such conditions are not always found in the places of the Solanum growing; maybe this is the reason why spermic species are rarely found. However in the summer of 2011 on the left bedrock coast of the river Vyatka (Kirov region) in the vicinity of the village Bolshaya Gora in the sand near the water line we found a numerous young population of the plant under study with a large number of seedlings. This phase of ontomorphogenesis corresponds to two periods of ontogenesis: embryonic and latent: the ontogenetic condition is dormant seeds.

Phase II – formation of a single-axis plant: lasts from the beginning of germination and till the end of the first vegetation season. During this time *ontobiomorph 2* is formed – a vegetative-immotile monocentric taproot monopodially growing vegetative plant (fig. 1). This phase corresponds to the pre-generative period of ontogenesis. It includes the stages of the seedling and immature plant. The immature ontogenetic condition is missing as the cotyledonary leaves remain almost till the end of the vegetation season. After the cotyledonary leaves typical leaves of median formation appear. By winter most of the offshoot dies apart from the basal piece with reproductive buds. This ontobiomorph corresponds to the primary offshoot according to O.V. Smirnova [9].

Phase III - bush formation: lasts from the replacement offshoots formation on the part of the last-year offshoot of the single-axis plant till the species separation. The phase can last for decades and be accompanied by consecutive change of the two ontobiomorphs in the ontogenesis. In the spring of the second year buds of the regular reproduction appear on the last-year offshoot and the development of ontobiomorph 3 begins - vegetative-immotile polycarpic monocentric sympodially growing upright semi-shrub (fig.1). This biomorph is formed due to the development of the sympodial axes from the series of monocarpic offshoots of the 3-4 order of branching. With blooming* of the primary offshoot apical domination terminates which stimulates development of the upper auxiliary bud (sometimes 2) which gives rise to a new offshoot of the next order of branching. Thus, a sympodial axis is formed from the series of sylleptic offshoots of the consecutive orders. The beginning of the plant development corresponds to the virginile ontogenetic condition of the pregenerative period as the generative organs are not formed in the buds in autumn. As the source offshoot blossoms, the plant becomes young generative. Such biomorph corresponds to the primary bush according to O.V. Smirnova [9].

By the 4-5th year *ontobiomorph 4* begins to develop: vegetative weakly motile polycarpic implicitly polycentric sympodially growing semi-shrub with a mixed root system due to the development of a stem secondary root on the basal parts of the offshoots, evolving from the reproductive buds (fig. 1). Appearance of this habit is connected with the development of the sympodial axes from 4-5 monocarpic offshoots under whose weight the source buds lie down in the basis and give roots. Due to the establishment of the new root centers, which are quite difficult to reveal, the plant acquires slight vegetative motility. Thus, this ontobiomorph of S. dulcamara is defined as weakly-motile. According to [9] it is a *lax-stemmed shrub*.

Phase IV — establishment of a rhizome plant: begins from the moment of particularization [term acc. to 18] of the species in its mature generative ontogenetic condition and lasts till the death of all its vegetative offspring. This phase can continue for decades. As a result of particularization ontobiomorph 5 develops - vegetative-motile polycarpic clearly polycentric long-rhizomatous sympodially growing semi-shrub (fig. 1). This ontobiomorph evolves due to formation of an epigeous rhizome which grows owing to the passive covering of the basal parts of the source offshoots with the ground. With such habit the plant exists during the whole period of its following ontogeny. The ontobiomorph corresponds to the shrub-forming particular according to [9].

The course of ontomorphogenesis of S. dulcamara is significantly influenced by the environmental conditions. The first four ontobiomorphs (seed, monopodial vegetative plant, sympodial upright taproot semi-shrub and sympodial semi-shrub with a mixed root system) are constant as the seeds germinate only on land. During

^{*} Source offshoots are the offshoots developing from the reproductive buds

the phase of the taproot plant formation development of the ontobiomorphs depends on the surrounding conditions. As a result several ecobiomorphs evolve [term acc. to 19] – ecologically dependent forms of the species in question:

1. On the land in the presence of some support as a result of nutation movements of the offshoots either a land lianoid semi-shrub is formed (ecobiomorph 1) or without a support a land creeping semi-shrub is formed – ecobiomorph 2 (fig. 1).

2. With periodical moistening depending on the presence of the support either a coastal-water lianoid (ecobiomorph 3) or creeping (ecobiomorph 4) semi-shrub evolves (fig. 1); these species unlike the land ones possess a number of peculiarities [20], including formation of stem secondary roots of over 30 cm long in the water, which branch a lot, contain chlorophyll and perform the functions of breathing and photosynthesis.

3. In the water a creeping plant with a live two-year-old part is formed, rooting in the year of offshoots formation, without blossoming or fruiting (inflorescence evolves only till the stage of flower-bud formation) – ecobiomorph 5. It can be considered a grassy one. Probably in such peculiar way (turion) the plant survives unfavorable environmental conditions developing according to its life strategy which is similar to non-plurannual plants of vegetative origin.

On the basis of the upright taproot semi-shrub, semi-shrub with a mixed root system and long-rhizomatous semi-shrub in the mobile substrate a burr-plant life form (*ecobiomorph 6*) may develop which provides rejuvenation of the species, often to the immature ontogenetic condition (fig. 1). As a result ontogenesis of *S. dulcamara* corresponds to G-type (G2-subtype) according to [3].

Conclusion. The main life form of *S. dulcamara* is a summergreen, vegetativemotile, polycarpic, long-rhizomatous land (coastal-water) lianoid (creeping) semishrub with sympodially growing during its vegetative season and to different extent lignifying stems from the series of monocarpic offshoots.

5 ontobiomorphs consecutively change each other in the ontomorphogenesis of S. dulcamara within the 4 phases, on the basis of which, depending on the environmental conditions, special ecobiomorphs develop: land lianoid or creeping semi-shrub, coastal-water lianoid or creeping semi-shrub, water creeping grassy plant and a creeping-rooted (burr) semi-shrub. The end of the ontogenesis of the plant is difficult to trace due to its ability of rejuvenation and vegetative reproduction. The ontogenesis of S. dulcamara belongs to G-type (G2-subtype) according to [3].

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