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The effect of changes in environmental conditions on the morphology of *Sparganium natans* L. (Typhaceae) in the taiga zone of European Russia

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Received: 26.03.2018
Accepted: 10.04.2018

DOI: 10.23859/estr-180326
UDC 581.4+581.5(470)
URL: http://www.ecosysttrans.com/publikatsii/detail_page.php?ID=55

ISSN 2619-094X Print
ISSN 2619-0931 Online

Translated by D.D. Pavlov

The study presents the results of the analysis of the morphology of vegetative and generative organs of *Sparganium natans* L., its seed production, ecology and phytocenology on the material collected in the wetland areas of the taiga zone of European Russia in 2006, 2011–2016. *S. natans* is a freshwater oligosaprobic species, found both in mesoeutrophic and in oligomezotrophic water bodies with an oscillating water level. The change in the depth of growth of *S. natans* leads to the formation of four ecological forms: terrestrial, emergent, submerged with leaves floating on the surface, completely submerged deep-water sterile. However, regardless of the formation of a particular ecological form, only one biomorph is characteristic of *S. natans*.

Key words: least bur-reed, distribution, ecological form, life form, vegetative and generative organs, seed productivity, ecological scale, community.

Belyakov, E.A., Philippov, D.A., 2018. The effect of changes in environmental conditions on the morphology of *Sparganium natans* L. (Typhaceae) in the taiga zone of European Russia. *Ecosystem Transformation* **1** (1), 29–41.

Introduction

The issues of biodiversity conservation involve not only the study of the causes leading to the changes of the habitats and the assessing of the vital state of the population, but also a comprehensive review of the species biology. Such complex studies are essential for the understanding of the functional role of different plant species, both in individual phytocenoses and in ecosystem processes. In the latter case, analysis and comparison of a wide range of features of morphology and ecology, leading to the awareness of the ways and characteristic features of species interaction among themselves within a single biological system are of a particular interest (Cheryomushkina and Astashenkov, 2014; Dehling et al., 2016; Garnier and Navas, 2012; Sulman et al., 2013; Tyllanakls et al., 2010). Such studies are not possible without long-term and time-consuming observations of natural populations (Kubentaev and Danilova, 2017).

Great interest in biological and ecological studies of water plants is associated with the study of the formation of various eco- and biomorphs (Belyakov and Lapirov, 2015a; Biancardi et al., 2012; Bobrov, 2017; Bobrov et al., 2017; Getmanets, 2010; Lebedeva et al., 2015; Lebedeva, 2016; Shabalkina and Savinykh, 2012; Thiebaut and Nino, 2009; Wood and Freeman, 2017; Zhuravleva and Savinykh, 2013; etc.) in changing environmental conditions.

Sparganium natans L. 1753, Sp. Pl. 971. (*S. minimum* Wallr. (1840), Erst., Beitr. Fl. Hercyn. 2: 297.) – least bur-reed. This species has a wide native range, being a pronounced polymorphous and extremely plastic taxon. It forms a number of ecological forms and / or variations (from typically terrestrial to aquatic), which creates certain difficulties in the study of its vegetative and generative organs. Disparate materials on the morphology and ecology of this species are contained in a number of works of Russian (Alekseev, 1979; Belyakov and Lapirov, 2015a; Rothert, 1910, 1913; Yuzepchuk, 1934) and foreign (Casper and Krausch, 1980; Cook and Nicholls, 1986; Crow and Hellquist, 1981; Dubyna et al., 1993; Gluck, 1924; Graebner, 1900; Molnar et al., 1997) researchers.

The aim of this work is to identify the morphological features of the vegetative and generative sphere of *S. natans* and their relationship to the environmental conditions of habitats, as well as to assess the role of this species in plant communities.

Material and methods

The work is based on materials of original research obtained in 2006, 2011–2016 on water bodies, watercourses and mires of the taiga zone of European Russia (Arkhangelsk, Vologda, Nizhny Novgorod, Tver and Yaroslavl regions). In this work we used live, fixed and herbarium material. We analyzed about 200 shoots of different ontogenetic states in total. The herbarium funds IBIW were also used for a more detailed study of *S. natans* biomorphology.

Ontogenetic and comparative-morphological (Savinykh and Cheryomushkina, 2015) methods of research that are used in the study of aquatic and littoral-aquatic plants were employed.

In order to identify seasonal changes in morphology field studies and collections in the Rostov area of Yaroslavl region (N 56°56'12", E 39°22'32"; a reclamation ditch on the southern shore of Lake Chashnickoe) were carried out once a month throughout the growing season of 2015–2016. The collected samples were cleaned from soil, put into polyethylene bags and delivered to the laboratory, where biometric analysis was performed. In the vegetative sphere, the length and the number of internodes of elevated shoots and rhizomes were counted in living plants (the number of investigated rhizomes of the terrestrial form of the least bur-reed was 17, in the immersed form with leaves floating on the surface of water – 83), the order of their branching, the capacities of terminal and lateral buds. Moreover, the number of leaves, their length and width were determined, the number of roots was counted and their maximum length was measured. In the generative sphere, the length of the flower stalk and its metamers was measured, the number of pistillate and staminate capitate inflorescences was counted (the number of investigated flower stalks was 19 in the terrestrial form of the least bur-reed, and 30 in the submerged form with leaves floating on the water's surface). The number of compound fruits and their diameter were counted in fructiferous plants. The number of small and large fruits was counted in each compound fruit. The length of the stem, column, and also the length of the fruit below and above the transverse contraction, as well as the diameter of the fruit, were measured. In the study of reproductive characteristics, the actual seed productivity (ASP) was determined, which includes all seeds on the shoot, according to Vaynagiy (1974). Reproductive characteristics were studied in 57 generative shoots (from the territory of Yaroslavl region – 39, Vologda region – 9, Tver region – 6) and 106 compound fruits. Herbarium specimens from SYKO, LE, MOSP, IBIW, NNSU, UDU herbaria were used to clarify the morphometric characteristics of the species.

The geobotanical description of the trial plots was carried out using traditional methodological approaches to the study of the vegetation cover of wetlands (Belavskaya, 1979; Katanskaya, 1981; Lobunicheva et al., 2013; Papchenkov, 2001; Philippov et al., 2017). When describing the plots, the type of a water body, the ecological features of the habitat (soil type, groundwater level/depth, and, if possible, flow velocity, temperature and water pH) were recorded; species that constitute the cenosis were listed noting their abundance and phenological phase.

The analysis of the ecological scales of Landolt, Ellenberg, and Tsyganov was carried out using the materials presented in the monograph by L.A. Zhukova and colleagues (2010).

All data were statistically processed and analyzed using Student's t-test (for p ≥0.05 the differences were considered significant, having previously checked the data for normality of distribution in Statistica 6.1 software package (StatSoft Inc., USA)). Numerical values in the text of the work and in the tables are represented as x±SD.

Results

General distribution

S. natans is a circumpolar boreal species widespread in the taiga zone of the northern hemisphere: frequent in the coniferous and coniferous-broadleaf forests (Shcherbakov, 2014), rare in the forest-steppe and Carpathians, very rare in the steppe zone (Dubyna et al., 1993). In the Volga basin the species occurs sporadically (Lisitsyna et al., 2009). R.E. Perlova (1930) points out that in the north the boundary of its range reaches 68°N, in the south – up to 21°N, in the west 99°W, in the east –160°E. The species is found in the Caucasus, Western (from the

Arctic Circle to the Altai), Central and East Siberia, the Far East (Kamchatka), Scandinavia, East, as well as Middle, and Atlantic Europe, North America (from Alaska and further south to Colorado and New Jersey) (Alekseev, 1979; Casper and Krausch, 1980; Dubyna et al., 1993; Yuzepchuk, 1934).

Despite the fairly wide distribution, *S. natans* is a subject to protection in a number of Russia's regions. In Tatarstan the species is considered rare (category 3), with stable abundance (Prokhorov, 2016); in Saratov region it is regarded as vulnerable species (category 2) (Sedova and Skvortsova, 2006); in Penza region and Moscow – is under threat of extinction (category 1) (Decree..., 2013; Ivanov, 2013); in Vologda region – included in the list of plants that need biological control (Resolution..., 2015). In Udmurtia and Samara region, the least bur-reed is presently not included in the protected species lists. Also, S. natans is protected in a number of regions of the Ukraine (Andrienko and Peregrym, 2012).

Ecological peculiarities

S. natans is a typical freshwater oligosaprobic species found in both mesoeutrophic and oligomesotrophlc water bodies with fluctuating water level (Casper and Krausch, 1980; Dubyna et al., 1993; Sviridenko et al., 2011).

The least but-reed grows in mire lakes and streams, along boggy shores of lakes and rivers, in the spaces between hummocks and hollows of lowland and transitional bogs, in technogenically transformed biotopes (watery sandy-gravel and peaty quarries/excavations and ditches, roadside belts) (Alekseev, 1979; Kantserova, 2012; Lisitsyna et al., 2009; Panarina and Papchenkov, 2005; Philippov, 2015; Seregin, 2012; Shcherbakov, 2014; Yuzepchuk, 1934). It prefers peaty, silt-peaty, silty-sandy, occasionally clay soils. It inhabits the depths from 5–20 to 70(100) cm (Casper and Krausch, 1980), and sometimes 1.5 m. The most favorable conditions for the development of the species are at water depths of up to 20–40 cm (Cook and Nicholls, 1986) as evidenced by our data as well. Temporary drying is being sustained in terrestrial ecological form (Casper and Krausch, 1980; Dubyna et al., 1993). It prefers a weakly acid reaction of the environment (Cook and Nicholls, 1986). According to Crow and Hellquist (1981), the taxon inhabits the water bodies in the north-eastern United States with pH of 6.5 to 8.5 (average – 7.3) and mineralization in the range of 3.5-69.5 mg/l. We have encountered the least bur-reed in biotopes with pH of 6.1–7.7 and mineralization of 50–150 mg/l. Cook and Nicholls (1986) noted that the species is able to tolerate water salinity to 0.22 ‰ and that it is not resistant to large wave effects.

The analysis of the ecological scales allowed establishing the following. On the thermoclimatic scale of H. Ellenberg and E. Landolt, *S. natans* refers to plants of the temperate-warm climate. On the scale of D.N. Tsyganov it is located in a wide range of ecological suites – from the subarctic to the nemoral. According to E. Landolt's climate continentality scale, the plant is a part of a group of widespread taxa that avoid extreme continental regions. This is also reflected in the scale of H. Ellenberg, where the species is referred to as an intermediate group, existing within the range from weakly oceanic to weakly subcontinental types of regimes. However, in accordance with D.N. Tsyganov's scale the species is still widespread in a wider range (from oceanic to ultracontinental type of regimes). On the aridity/humidity scale, *S. natans* is encountered in the range from subarid to humid/pergumide type of regimes; on a cryoclimatic scale – in a range of conditions from soft and warm to severe and very severe winters. The analysis of the soil moisture scales indicates the attribution of this species mainly to a group of mire and coastal-aquatic plants. According to the soil trophicity scales, the species grows either on poor (usually with a low content of nitrogen) or on rather humus-rich soil horizons. On the scales of soil acidity, the least bur-reed grows in a wide range of conditions: from acidic to neutral. In accordance with the data of different scales of illumination/shading, the species successfully develops in both open habitats and being slightly shaded.

A detailed study utilizing D.N. Tsyganov's ecological scales demonstrated that the potential ecological valence of *S. natans* varies from 0.13 to 0.87 (Table 1). Therefore, we consider *S. natans* to belong in the following valence fractions: *stenovalent* – according to the trophicity (Tr) and soil moisture (Hd) scales; *hemistenovalent* – according to aridity/humidity (Om) and illumination/shading (Lc) scales; *mesovalent* – according to the thermoclimatic scale (Tm) and soil acidity index (Rc); *hemi-euryvalent* – according to cryoclimatic scale (Cr) and nitrogen availability scale (Nt); *euryvalent* – according to the climate continentality scale (Kn). The coefficient of environmental efficiency is 81.8% on average. The lowest realization of *S. natans* potencies is according to the soil humidification scale (61.5%) (Table 1). Apparently, this is the main limiting factor. The coefficients of ecological efficiency of other scales are high – from 75.0 to 92.0%. We refer this species to the mesobiont group according to the general tolerance index.

The wide ecological valence, ensuring the existence of *S. natans* at different depths, was the reason to describe various ecological forms and variations of this taxon by a number of researchers. For example, K.F. Meinshausen (cited in: Yuzepchuk, 1934) distinguished four species close to *S. natans* - *S. ratis* Meinsh., *S. septentrionale* Meinsh., *S. flaccidum* Meinsh. and *S. perpusillum* Meinsh.,

Ecological scale		Scale value range	PEV	REV*	$K_{ec.\ eff.}$ %*	It according to scales	It_{total}*
Climatic scales	Tm	3–10	0.74 (MV)	0.41	87.2	0.58 (HEB)	0.47 (MB)
	Kn	3–15	0.87 (EV)	0.80	92.0		
	Om	7–12	0.40 (HSV)	0.33	85.5		
	Cr	2–10	0.60 (HEV)	0.53	88.3		
Soil scales	Hd	19–21	0.13 (SV)	0.08	61.5	0.39 (HSB)	
	Tr	3–7	0.26 (SV)	0.21	80.7		
	Nt	1–7	0.64 (HEV)	0.54	84.3		
	Rc	3–9	0.54 (MV)	0.46	85.2		
Scale of illuminance/ shadowing	Lc	1–4	0.44 (HSV)	0.33	75.0	0.44 (HSB)	

Table 1. Characteristics of potential (PEV) and realized (REV) ecological valences, tolerance index (It) and the coefficient of ecological effectiveness ($K_{ec.\ eff.}$) *Sparganium natans* in correspondence with D.N. Tsyganov's scale (from Zhukov et al., 2010, with additions). Note: * – authors' data. Species valence fractions: SV – stenovalent; HSV – hemistenovalent; MV – mesovalent; HEV – hemieuryvalent; EV – euryvalent. Species tolerance groups: HSB – hemistenobiont; HEB – hemieurybiont; MB – mesobiont.

while P. Graebner (1900) indicated five variants (var. *flaccidum* (Mainsh.) Aschers. et Graebner, var. *typicum* Aschers. et Graebner, var. *oligocarpum* (Angstrom) Aschers. et Graebner, var. *perpusillum* (Meinshausen) Aschers. et Graebner, var. *strictum* Luerssen in Schrift. var. *flaccidum*). W.A. Rothert (1910), in turn, noted only three ecological forms – aerial (*Luftformen*), transitional or partially submerged (*Obergangsformen*) and a form with floating leaves (*Schwimmformen*); H. Gluck (1924) has only distinguished the aquatic (*Wasserform*) and terrestrial (*Landform*) ecological forms.

We distinguish four ecological forms: 1) *terrestrial* (a form of periodically drying habitats); 2) *emergent* (habitually and morphologically similar to terrestrial, but growing in shallow water); 3) *submerged form with leaves floating on the water surface*; 4) *a completely submerged deep-water sterile form* (plants can have either completely submerged leaves or leaves floating on the surface of the water, depending on the depth of submersion) (Fig. 1).

Morphology

We have established that the sympodially growing shoot system of *S. natans* is represented by unevenly aged monopodially growing anchoring shoots of two- and three-year-old monocarpic medio-rosette anisotropic and one or two year vegetative rosette shoots. They are all connected by a system of hypogeogenic rhizomes. Formation of dicyclic monocarpic medio-rosette shoots occurs on the basis of tricyclic monocarpic medio-rosette shoots. We should point out that the rosette part of the tricyclic monocarpic shoot (in contrast to the dicyclic monocarpic shoot) is characterized by the presence of two rhythm shoots, terminology by Grudzinskaya (1960). The first (downstream) rhythm shoot (0.94±0.35 cm length, 0.30±0.05 cm diameter) is formed by 15–20 truncated metamers, the second (upstream) rhythm shoot (0.75±0.20 cm long, 0.30±0.05 cm in diameter) by 11–14. They are separated by a section (0.28±0.06 cm in length) of smaller diameter – up to 0.24±0.02 cm.

Acropetally developing buds are located in the axils of all the leaves of the rosette part of the shoots. However, their fate is different. 3–5(7) buds of the basal part of the shoot can form hypogeogenic rhizomes, the rest remain usually sleeping. It is worth noting that iterative branching[1] is characteristic for *S. natans*. Thus, a sympodial system of anisotropic monopodial anchoring shoots of third and fourth order of branching based on the primary shoot is formed by the end of the vegetative season.

Up to 3–5(7) hypogeogenic rhizomes of the n-th order (length 15.1±5.0 cm, diameter 0.07–0.12 cm), usually consisting of 6-7(8) metamers ending with rosellate shoots are formed on one plant. Rhizomes are formed extravaginally from axillary buds. The length of rhizome metamers of the least bur-reed changes along a unimodal curve, and the third and the fourth internodes (4.4±1.8 and 4.6±1.7 cm,

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[1] Iterative branching - continuous formation of several branching shoots following one another and forming a complex skeletal axis of the plant (term. Troll, 1964, from Zhmylev et al., 2005).

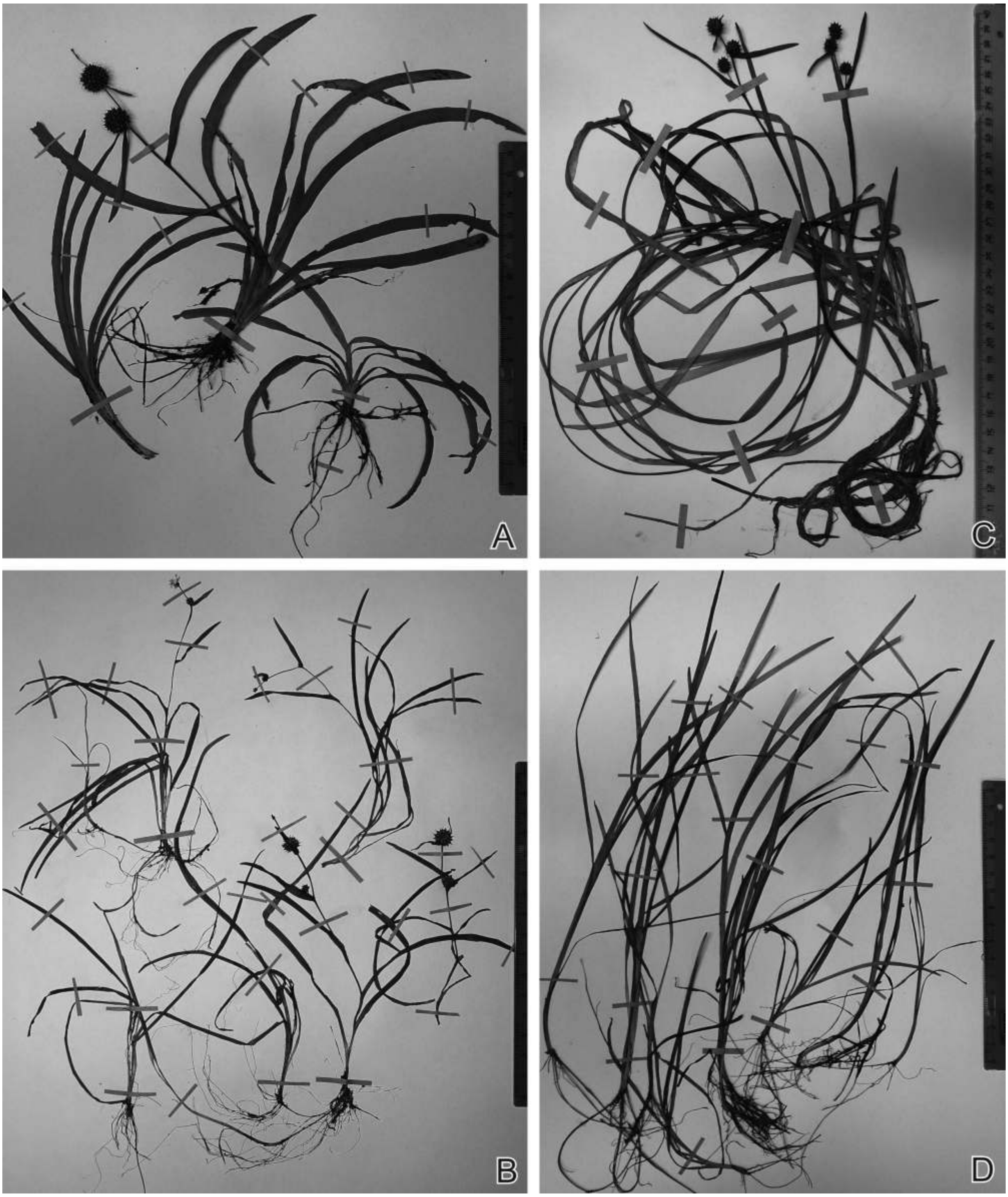

Figure 1. Ecological forms of *Sparganium natans*: **A** – terrestrial; **B** – semi-submerged; **C** – submerged with leaves floating on the surface of water; **D** – completely submerged, sterile.

correspondingly) are usually the longest. Thin, amplexicaule squamose leaves – cataphylls – grow from the nodes of the rhizomes. Buds are formed in their axils. Some of them provide branching of the shoot to n+1 order, while the other remain sleeping. Rhizomes of n+1 order (5.5±3.1 cm long) are represented by 5–6 metamers.

We have noticed that a significant change in the length of the rhizomes depends on the nature of the ecological form of the species. At the same time, the number of their constituent metamers remains the same. Thus, in the terrestrial and emergent ecological forms, the mean length of the rhizomes is 2.7 times less (5.5±2.0 cm) than that of the submerged form with leaves floating on the surface of the water (14.7±5.4 cm).

By autumn, shortened rhizomes (up to 2) up to 5 cm long, ending with terminal tuber-like structures, sometimes develop from the upper (1–3) axillary buds of the rosette sections. The terminal tuber-like structures are represented by two short metamers (length from 0.15 to 0.20 cm, diameter to 0.15 cm), slightly enlarged in diameter and an apical bud hidden by squamose leaves. The capacity of the apical bud of the tuber-like structure reaches 11–14 rudiments (primordial leaves) in the autumn, and these leaf rudiments already carry the "daughter" buds in the axils. Similar formations are formed in other *Sparganium* species.

Annual roots (branching endogenously to 2(3) order) which gradually break down during the whole growing season are formed in the nodes of the rosette vegetative part of the *S. natans* shoot. The length of the roots of the plant during the growing season reaches 30–35 cm, and their number is 39.45±10.66.

Heterophylly is characteristic for *S. natans* similar to all other bur-reeds. The whole totality of leaves located on the shoot can be attributed to four types of formations: *lower* (squamose, growing from the nodes of the rhizomes), *transitional type*, *middle* and *upper* (bractea). All the leaves on the shoots are arranged alternately in two rows; they are sessile, with initially closed leaf sheath without a ligule, with linear, solid, smooth-edged laminae closed at the base.

The leaves of the transitional type (3–4) are located in the basal part of the rosette shoot; representing a reduced leaf lamina (up to 5.5–6.0(7.0) cm long) having similar features to the leaves of the lower formation (cataphylls), namely the presence of a glumaceous leaf sheath of considerable size. The only difference from the leaves of the middle formation located above is the rudimentary leaf lamina, slightly pointed at the top. The similarity with the leaves of the middle formation is mainly related to their assimilating functions.

The leaves of the middle formation are thin, translucent, not possessing a keel, with well-defined longitudinal and transverse veins. The leaves of the middle formation can either float on the surface of the water, or rise above it depending on the depth of plants' growth. Aerial leaves of the middle formation are usually slightly convex from the underside, darker and denser compared to those floating on the water surface. The latter are light green, ribbon-like, flat on both sides.

The length of the leaves is up to 16.65±1.97 cm in terrestrial and emergent ecological forms and usually does not exceed the length of the flower stalk axis in vegetative-generative shoots. The leaf length for this form of the European plants is considerably less – 4.6–14.0 cm (Gluck, 1924). The leaves in such plants are often semilunar or arcuate-curved. In the submerged form with leaves floating on the water surface, which often grows at depths of up to 30 cm, the length of the leaves is 38.12±4.37 cm. Completely submerged deep-water sterile form dominates on greater depths (from 0.6–0.7 to 1.5 m). The length of leaves of such plants can reach up to 50–80 cm (Casper and Krausch, 1980). The width of leaves in various ecological forms of *S. natans* is up to 0.48±0.07 cm, in some cases – up to 0.70 cm.

During the winter period, the system of geophylous rhizomes with vegetative rosette shoots of the last year development is preserved in the ground, at the depth of 3–5 cm. Here, as is the case with *S. emersum* Rehm., terminal buds of vegetative rosette shoots with short live leaves (developing during the winter period) are hidden by the bases of the last year's dead leaves. Winter leaves of the middle formation are dense, green with reddish patches.

The pistillate and staminate capitate inflorescences are usually located in the axils of the leaves of the upper formation – the bractea. In the region of the pistillate inflorescence, the bractea are 3.0±1.0 to 1.5±0.5 cm long, up to 0.3±0.1 cm wide and possessing a wide glumaceous base. In the region of staminate inflorescences (usually, the lower one), they are mostly glumaceous, up to 0.3±0.2 cm long and a little more than 0.1 cm wide. The staminate inflorescence, crowning the vegetative-generative shoot, usually does not bear bractea.

The flower stalk axis is rounded in the lower and middle part and slightly flattened in the zone where pistillate and staminate capitate inflorescences are located. The length of the metamers of the flower stalk axis varies along a single-vertex curve (Table 2). We have noted that the number of metamers that make up the flower stalk axis often varies depending on the depth at which the plant grows. Thus, in terrestrial and emergent ecological forms, the number of metamers of the flower stalk axis is lower (Table 2) compared to plants growing at the depth of 30 cm or more. The length of the flower-bearing axis is 12.5±2.6 cm in the studied populations growing on dry ground and depths of up to 5–10 cm, while in the specimens encountered at depths 25 to 30 cm – 30.1±11.5 cm (average value being 28.1±11.3 cm). In terrestrial and emergent ecological forms, the flower-bearing axis can be anfractuose or (most often) almost upright. The ascending flower-bearing axes are characteristic of the immersed form with leaves floating on the surface of the water. They become lodging when the water level drops.

The part of the flower-bearing axis with elongated metamers (diameter 0.1 to 0.2 cm) carries typical leaves of the middle formation (their structure is described above). Moreover, axils of the first

□ of flower axis metamere (down-top)	Length of flower axis metamere (cm)		
	Depth 0 cm	Depth 25–30 cm	Average values across samples
1	0.3±0.1	0.3±0.2	0.4±0.3
2	0.5±0.2	2.3±1.6	2.2±1.5
3	1.1±0.4	5.3±1.7	4.3±2.2
4	2.0±1.0	6.4±2.7	5.1±2.5
5	2.1±0.5	6.0±2.7	5.0±2.4
6	2.7±0.3	4.4±2.3	4.0±1.6
7	2.5±0.4	2.8±1.5	3.1±1.3
8	2.0±0.3	2.1±0.4	2.1±1.0
9	—	2.3±0.4	2.4±0.1
10	—	1.2±0.2*	2.2±0.8*
Region with male inflorescences	1.2±0.2	1.3±0.3	1.4±0.3

Table 2. The change in flower stalk metamere length of *Sparganium natans* in relation to the depth of growth.
Note: "—" – data missing; * – value seen in single plants.

3–4(5) leaves (from below upwards) carry buds with capacity of 9–10 to 12–13 leaf rudiments, 6–7 of which are the rudiments of squamose leaves. We should point that by the autumn these buds are sometimes able to form shortened rhizomes (length – from 1.0 to 1.5 cm, diameter 0.08–0.09 cm), formed by 3–4 metamers with terminal tuberous structures at the ends. Non-developed rudimentary pistillate capitate inflorescences were found in axils of leaves positioned above (2–3(4)). Further up the shoot there are 1–2(3) realized pistillate head inflorescences which, similar to the staminate capitated inflorescences located above along the flower stalk axis, are located in the upper formation's leaves' axils – bractea. The pistillate and staminate capitate inflorescences are delimited from each other by a metamer, up to 1.7±0.5 cm in length.

All inflorescences are usually sessile on the main flower stalk axis. However, sometimes one pistillate head inflorescence (usually the lowest one) is located on a stem 0.5–1.3(2.0) cm long. Such plants sporadically occurred not only on the studied territory, but also in North America (Harms, 1973). According to Harms (1973), this symptom can be associated with the introgression of individual genes from *S. hyperboreum* Laest. to *S. natans*. In the upper part, the flower stalk axis ends with shortened internodes with sessile staminate capitate inflorescences (usually 1–2) located alternately at the nodes. It is worth noting that the concaulescence phenomenon was not observed in the zone of pistillate and staminate capitate inflorescences in this species (in contrast to *S. emersum* Rehm., *S. glomeratum* Laest., and morphologically close *S. hyperboreum* Laest.). Therefore, we determine the type of *S. natans* inflorescence as a frondose-bracteose-ebracteose, racemose with floral units – axillary capitate inflorescences of same-sex flowers.

Pistillate flowers bear oblong, expanded in the upper part, glumaceous and semi-translucent tepals (3–6). At the time of flowering, they are pale green in color. Ovary is oblong. The column is up to 0.1 cm long. The stigma is subuiate-lanceolate, obliquely attached to the column. Its length is usually 2–3 times the width. Staminate flowers carry three free filaments with anthers, up to 0.5–0.7 cm long. Anthers are oblong and small, up to 0.05–0.07 cm long.

The ripening of dense compound fruit occurs in the middle of August – beginning of September. Their number on the shoot varies from one to three. According to our data, in 24.6% of the cases there is only one compound fruit on the shoot, in 55.6% – two, and in 19.7% – three. It is interesting that in Arkhangelsk region the number of compound fruit on the plant usually does not exceed 1–2. In this case, often the ratio of vegetative-generative shoots (in one population) with one and two compound fruit is approximately equal. Obviously, the latter is dictated by more severe climate conditions.

The average diameter of the least bur-reed compound fruit is 1.01±0.12 cm, which coincides with data for North American plants (Harms, 1973). According to our data, the average number of fruits in the compound fruit reaches 41.0±9.0 (of which 30.2±0.3 are large, and 11.0±7.0 are small and usually underdeveloped). A similar number of fruits in the compound fruit was provided earlier by

Belavskaya (1984). The characteristics of the main parameters of *S. natans* compound fruits, located on the flower stalk axis (bottom-up) are given in Table 3.

The fruit of *S. natans* (as, indeed, in other *Sparganium* species) is a dry upper pseudomorphic drupe (Belyakov and Lapirov, 2015b). The length of the fruit is 0.33±0.02 cm. In the lower part it has a short stem (0.06±0.01 in length, sometimes up to 0.1 cm). The middle part of the fruit is elliptical or egg-shaped (0.30±0.06 cm in length, 0.17±0.02 cm in diameter), with a pronounced constriction in the lower part. In the upper part the fruit narrows and goes into a column (0.07±0.02 cm in length). Ripened fruits acquire a yellowish-brown or light-brown color, with a darker constriction. Tepals are transparent, light brown, with darker veins, spread out in the upper third. Comparison of the dimensional characteristics of *S. natans* fruits collected in Arkhangelsk, Vologda, Murmansk, Nizhny Novgorod, Tver and Yaroslavl regions did not reveal statistically significant differences.

In the conditions of the taiga zone of European Russia, the actual seed productivity of the vegetative-generative shoots of *S. natans* is 68.4±25.5 fruits (the minimum number of fruits is 23, the maximum number is 169). In monocarpic shoots with one single crop, it reaches 35.6±7.1 fruits, with two compound fruits – 82.8±16.7, with three – 135.0±34.0.

Thus, our data demonstrates that the life form of *S. natans* can be characterized as a herbaceous polycarpic; summer-winter-green, vegetatively mobile, obviously polycentric long-rhizome short-lived plant with a racemose root system, anisotropic medio-rosette di- and tricyclic vegetative-generative shoots and partially submerged or floating on the surface of the water; hemicryptophyte.

Complete normal specialized fragmentation is observed in the second–third year. In the second year, thin rhizomes are rotted, and by the end of the 2nd – the beginning of the 3rd year – are the dying off and the decomposition of the basal rosette sections of the shoots takes place.

Cenotic description

The least bur-reed has a wide ecological valence and therefore is able to grow in different types of wetlands, however its role and activity in phytocenoses in deep-water, shallow-water and drying conditions is not identical.

In wetland lakes with peat and peaty-silty soils at the depth of 0.5 to 1.5 m, the submerged and deep-water forms of the least bur-reed form pure thickets (ass. ***Sparganietum natantis***). In this case, the projective cover of the species varies widely from 25 to 95%. Occasionally single specimens of other macrophytes (*Nuphar lutea* (L.) Smith, *Potamogeton natans* L.) may be found in the communities of this association. The area of cenoses can vary from 3–4 to 300 m^2 (Panarina and Papchenkov, 2005). Along the periphery of relatively deep reclamation ditches and quarries (0.5–1.0 m) of developed peat bogs in the headland communities, can be found *Lemna minor* L., *Potamogeton berchtoldii* Fieb., *P. lacunatus* Hagstr.

Almost pure thickets of the same association are also formed in slowly running mire streams on peat soils, but their area rarely exceeds 0.5–1 m^2 and their composition may include (not more than 10–15% of the projective cover) aquatic bryophytes (*Fontinalis antipyretica* Hedw., *Chiloscyphus* spp.) and hygrogelophytes (*Comarum palustre* L., *Menyanthes trifoliata* L., *Naumburgia thyrsiflora* (L.) Reichb., *Calla palustris* L.). A similar tendency for the increase of hygrogelophyte and partly helophytes role (*Equisetum fluviatile* L.) is also evident in the shallow waters of marshy lakes and rivers. At the same time, the covering of the least bur-reed (it mostly refers to the emergent form) rarely exceeds 20–25%. Such communities can already be attributed to the ass. ***Heteroherboso-Sparganietum natantis***.

In fen and transitional bogs, *S. natans* usually forms small-contour (0.5–2 m^2) cenoses (ass. ***Utriculario-Sparganietum natantis***). Depending on the amount of water in the hollows, pools, spaces between hummocks, the projective covering of the least bur-reed (usually terrestrial and less often emergent form) varies from 30 to 70%. Two species *Utricularia intermedia* Hayne and/or *U. minor* L.

No. of infructescence (down-top)	Total number of fruits in the infructescence (pcs.)	Number of large fruits (pcs.)	Number of small fruits (pcs.)	Infructescence diameter (cm)
1	47.0±6.0*	26.5±1.5*	20.5±7.5*	1.0±0.1*
2	41.6±9.5	29.5±11.3	12.0±7.4	1.0±0.1
3	40.5±9.0	31.0±10.0	9.7±4.6	1.0±0.1

Table 3. The main parameters of *Sparganium natans* infructescence.
Note: * – value found in two plants out of 54.

(covering up to 30%) are the codominants in this association. Other species of bog herbs (*Carex lasiocarpa* Ehrh., *Equisetum fluviatile*, *Menyanthes trifoliata*, etc.) and sphagnum mosses *(Sphagnum* sect. *Subsecunda*, *S. fallax* (H. Klinggr.) H. Klinggr., etc.) are characteristic of these communities.

Marsh herbage is replaced by widely distributed helophytes (*Alisma plantago-aquatica* L., *Phragmites australis* (Cav.) Trin. ex Steud., etc.) on silted mineral soils (usually in anthropogenically transformed water bodies). In this case, *S. natans* (terrestrial, emergent forms, less often forms with leaves floating on the surface of water) are individually found in the grass communities of the associations ***Caricetum vesicariae-canescentis***, ***Scirpetum sylvatici***, ***Typhetum latifoliae*** (Kantserova, 2012), associations ***Phragmitetum australis*** and ***Charetum-Phragmitetum australis***.

Discussion

Biomorph can be considered as an integral characteristic of the whole set of internal and external properties of plant organisms, which is "... an ecological and morpho-adaptive phenomenon..." (Getmanets, 2015). At present, the study of life forms with a wide variety of morpho-adaptive mechanisms (formed during a long historical process) is the leading direction in considering the degree of plasticity of various plant species to specific environmental factors (Cheryomushkina and Astashenkov, 2014; Talovskaya, 2015).

We have shown that, despite the wide geographic distribution and differences in ecological valences, and also the similarity of habitat conditions, all the representatives of the genus *Sparganium* have only one life form: a vegetatively mobile, obviously polycentric, long-rhizome short-lived plant with a racemose root system. The structure of the *S. natans*, shoot system (as well as in a number of other species, for example, *S. emersum*, *S. gramineum* Georgi, *S. erectum* L., *S. microcarpum* (Neum.) Domin., etc.), is rigidly genetically determined and does not depend on the specific ecological form of the plant. An important feature is the presence of two types of monocarp shoots, different in the duration of their growth – di- and tricyclic. As the main adaptation mechanisms conditioned by specialization to various habitats great vegetative mobility and effective vegetative propagation should be mentioned, which are provided by iterative branching (the formation of shoots to n+3-4 orders of branching during the growing season) and can be considered as a variant of sylleptic[2], as well as complete normal specialized fragmentation.

The presence of pronounced ecological polymorphism in *S. natans* (the presence of four ecological forms and/or variations) leads, first of all (in the vegetative sphere) to a change in the length of the leaf blade and its density, as well as the total length of rhizomes (the number of metamers of their constituents does not change). In the generative sphere, the form with leaves floating on the surface of the water (in contrast to the terrestrial and emergent forms), not only has longer flower stalk axis, but also the number of its metamers increases (which, apparently, is due to the need for elevating the generative organs above the water surface). A similar phenomenon was noted also for *S. emersum* – a species with a wide ecological valence.

It is necessary to note that not all of the bur-reeds are characterized by a wide variety of ecological forms. For example, the relict species *S. gramineum* forms the only one ecological form, immersed with leaves floating on the surface of the water. Apparently, this is due to the narrow ecological amplitude of the species – its confinement to typical freshwater oligotrophic and mesotrophic water objects, mainly lakes with a stable level regime. Fairly widespread in the territory of European Russia *S. erectum* (found in the shallow estuarine areas of rivers, water reservoir bays, lakes, etc., prefers well-warmed waters) and *S. microcarpum* (confined to zones of free flow of rivers, prefers cool waters) are also usually noted in the form of emergent and terrestrial ecological forms, similar to each other morphologically (Belyakov, 2015). Sharp and significant fluctuations in the level regime can greatly weaken populations of these species, sometimes even up to their complete destruction.

The analysis of the ecological scales shows that *S. natans* is a typical freshwater oligosaprobic species found in a fairly wide range of wetland objects (from mesoeutrophic to oligomesotrophic) with fluctuating water levels. In the taiga zone of European Russia, it often grows in low- and slightly mineralized and slightly acidic/neutral/slightly alkaline waters. A specific set of abiotic conditions affects the activity of *S. natans* in phytocenoses. Thus depending on the depth of growth, it can act as an edificator (forming thickets with a high projective cover), or simply be an assectator and less often a codominant within aquatic, coastal-aquatic or wetland communities. Only *S. emersum* possesses a wider range of habitats in the territory of European Russia in comparison with *S. natans*. The other types of bur-reeds are more narrowly specialized to environmental factors.

Conclusions

The results of the conducted study showed that *S. natans* is characterized by the presence of a single

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[2] Sylleptic shoot – shoot developing from the bud without resting period and simultaneously with continuing growth of the maternal shoot (Grudzinskaya, 1960).

life form – a vegetatively mobile, obviously polycentric, long-rhizome short-lived plant with a racemose root system. With changing environmental conditions, the least bur-reed is able to form four ecological forms: terrestrial; emergent; submerged with floating leaves on the surface; completely submerged deep-water sterile. Ecologically, *S. natans* is a typical freshwater oligosaprobic species found in a fairly wide range of wetland water bodies (from mesoeutrophic to oligomesotrophic) with fluctuating water level. A specific set of abiotic conditions affects the activity of *S. natans* in phytocenoses.

Acknowledgements

Research by E.A. Belyakov was conducted within the framework of Project of the Russian Foundation for Basic Research (no. 18-34-00257\18 mol_a), part of the work by D.A. Philippov was conducted within the framework of the State Contract of the Federal Agency for Scientific Organization (no. AAAA-A18-118012690099-2). Authors are grateful to A.M. Chernova, E.V. Garin (IBIW RAS), O.V. Galanina (BIN RAS, SPSU) and A.B. Chkhobadze (VoSU) for help in the field, A.G. Lapirov (IBIW RAS) for discussion on the manuscript.

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