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Seasonal and spatial dynamics of *Stratiotes aloides* (Hydrocharitaceae) plants

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ABSTRACT: A study of the peculiarities of the spatial dynamics of *Stratiotes aloides* L. plants in different seasons is discussed. The mechanism of the immersion and buoyancy of *S. aloides* plant, established by phylogenetical factors, helps them to survive the unfavorable winter period in the water bodies of the temperate climatic zone of the North Eurasia. It was found that the mechanism of immersion in the fall and emergence in spring is based on several factors. The main contribution comes from seasonal variation of the structural "weight" of the leaves, while the seasonal dynamics of starch and mineral (ash) content is less important.

Key words: *Stratiotes aloides,* seasonal spatial dynamics of specimens, structural "weight" of leaves, starch content, ash content

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INTRODUCTION

Stratiotes aloides L. is a vegetative polycarpic plant with a long-growing cymose anisotropic system of shoots which is completely renewed within 2 to 3 years (Cook & Urmi-König 1983). An apical growth of monopodial rosette shoots can last indefinitely along with their gradual die-off in the basal zone (Efremov & Sviridenko 2008).

Adaptation of *Stratiotes aloides* plants to the seasonal climate results in significant ecological and morphological modifications of the plants. Perennial rosette shoots and the submissive-order shoots formed on them submerge in water in the fall, and winter in a rootless state. These rosette shoots and turions survive the winter season in the near-bottom water under the ice, at a depth of 0.7–1.0 m in water bodies of the West Siberian Plain. In the winter period, the leaves together with the stem perform a storage function keeping starch in their parenchyma cells. The lower leaves of the rosette shoots have a geotropic curvature and support the stem preventing the apex and accessory buds from submerging in the bottom mud.

Hibernating, temporarily rootless rosette shoots and turions rise toward the water surface in spring and remain near the surface throughout the summer vegetation period. With a new vegetation season, accessory buds activate, resulting in the formation by every plant of a complex system of branching shoots in early summer. In the beginning of vegetation, the hibernating rosette shoots produce new additional roots as they rise toward the surface, which by the beginning of summer get rooted in the bud and fix the rosette shoots within certain water area (Efremov & Sviridenko 2008).

The change in the position of *S. aloides* relative to the water/atmosphere interface has interested researchers for a long time. Several mechanisms of the seasonal spatial dynamics of *S. aloides* plants have been suggested. However, experimental data in the literature are scarce and contradictory (Cook & Urmi-König 1983; Kornatowski 1985; Prins & Deguia 1986). This study aims to clarify these contradictions.

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MATERIALS AND METHODS

Material for studying the seasonal dynamics of the *Stratiotes aloides* shoot system was collected by the stationary method in floodplain water reservoirs of the Irtysh river in the Omsk Region, Russia (forest-steppe climatic natural zone) in 2007–2008. Various populations of *S. aloides* were studied in different seasons (including winter). To establish the seasonal dynamics of starch content, generative plants were collected every 10 to 15 d at stationary sites. The overall weight of a raw sample was 1 kg or above. In laboratory conditions, preliminary sample preparation was performed (material washing, segmentation into organs, drying to air-dry and absolutely dry condition). Absolutely dry material was ground, and an average sample was prepared by the envelope technique, from which triple 3 g samples were taken for analysis. After sample preparation, 4 aliquots were taken for titration analysis. Starch level was determined by the Kh. Pochinok volume technique (Ermakov 1952). To determine the final titration point, 1 % aqueous starch solution was used. In total, 132 average samples were analyzed.

Study of the starch localization patterns in *S. aloides* tissues was performed on native and fixed material (O'Brien & McCully 1981; Barykina 2004). Mounts were examined using the transmission microscopy technique with a Mikmed-2-1600 microscope (Russia). The main preservative solutions were 70 % aqueous ethyl alcohol and FAA fixative (formalin – 70 % ethanol – acetic acid).

For further specification of the cell wall and protoplast compartments, special staining systems were used. As background staining agents, methylene blue and neutral red were used. Histochemical starch determination was performed using the iodine reaction (Prozina 1960; Pausheva 1988; Barykina 2004).

To determine the structural "weight" of individual organs, samples of generative *Stratiotes aloides* plants were taken. Excessive water was removed with blotting paper, and each plant was divided into separate organs and weighed. The structural "weight" was estimated as a percent relation of an individual organ's weigh to the weight of the entire plant:

$$Wc = A/C \times 100\%,$$

where Wc is the structural "weight"; A is raw weight of the entire separate organ; C is raw weight of the entire plant.

Descriptive statistics, linear regression analysis and Student t-test were done using Statistica 6.1 software.

RESULTS AND DISCUSSION

Montesantos (1913, cited in Cook & Urmi-König 1983), Davie (1913, cited in Cook & Urmi-König, 1983) and Arber (1963) suggest that the submersion of *Stratiotes aloides* at the end of the vegetation period should be connected with the accumulation of calcium carbonate in the leaves, while their emerging in spring should be caused by the development of new leaves which are not incrusted and thus lighter. However, the Montesantos–Davie concept does not account for the emergence and immersion of *S. aloides* in low-calcium waters. Our study of the seasonal dynamics of ash content (Fig. 1) suggests that there is a medium positive correlation between the ash content and the degree of immersion ($r = 0.47$, $p \leq 0.05$), therefore the Montesantos–Davie hypothesis is only partially true.

The maximum content of mineral substances in the tissues of *S. aloides* is observed in October, when the rosette plants are fully immersed in water with green leaves on the sediment surface. The minimum ash content is found in mid-February and March (Fig. 2) when *S. aloides* plants are still immersed. The maximum and the minimum ash contents differ more than two-fold. The sharp decrease of ash content in spring can be associated with an active consumption of mineral substances by vegetation under the ice.

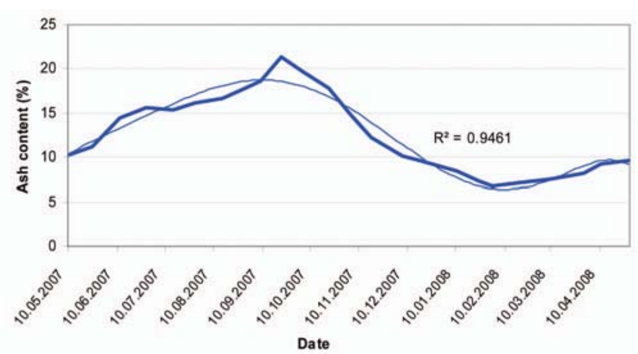

Fig. 1. Seasonal variation of ash content in dry *Stratiotes aloides* material.

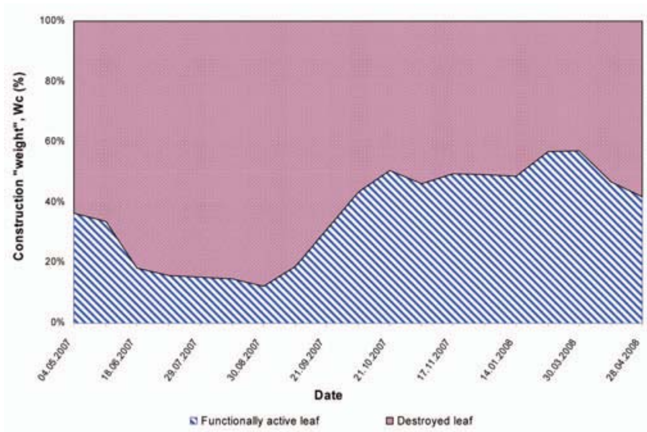

Fig. 2. Seasonal dynamics of the structural "weight" of *Stratiotes aloides* leaves.

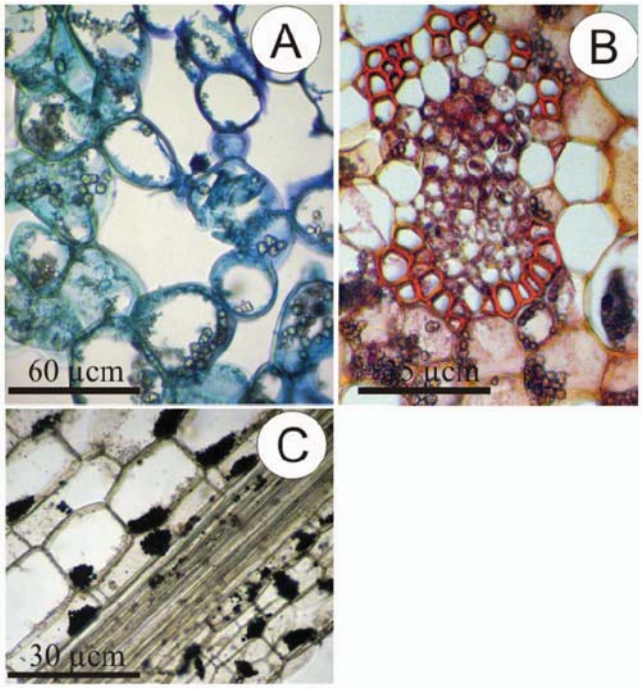

Fig. 3. The localization of starch kernels in *Stratiotes aloides* tissues: A — main stem parenchyma stained with methylene blue; B — lateral conducting bundle of the leaf (cross-section) stained with neutral red; C — sheath of a median conductive bundle of a stolon (longitudinal section) stained with iodine.

Sculthorpe (1967) suggested a different explanation of the seasonal emergence/submergence cycle of *S. aloides* plants. It is based on variation of the ratio between the overall volume of gas-filled intercellular spaces and the volume of functionally active tissue, which changes the specific weight of the plants. Typically, the plants become buoyant in spring following increased photosynthetic gas production and the formation of new leaves. This explanation is supported by experimental works by Cook & Urmi-König (1983) and Kornatowski (1985). At the end of summer, the water content in dead leaves, which reach their maximum structural "weight" (*Wc*) in this period, increases because the intercellular spaces are filled with water, and the leaves become partially immersed. By the end of the vegetative season the number of partially immersed leaves on each shoot increases, while no new leaves appear. As a result, the specific weight of such shoots grows, and the plants sink in water. In spring, after the decomposition of dead leaves, and the formation of new leaves with intercellular spaces that are filled with air, the plants emerge at the surface due to a lower specific weight.

Our data on the seasonal dynamics of the structural "weight" of the functionally active and degraded leaves support the suggestions by Sculthorpe (1967). The maximum structural "weight" of the functionally inactive

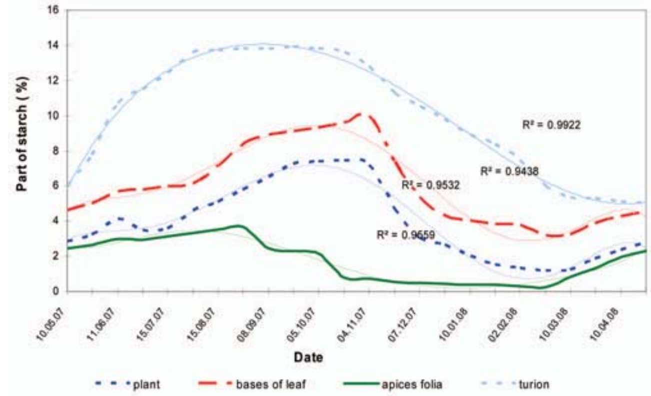

Fig. 4. Seasonal starch level profile in the dry material of different parts of *Stratiotes aloides* plants.

leaves of *S. aloides* is observed in October and November (the immersion period), and the minimum from July through August (the emerged period) (Fig. 2). The structural "weight" of degraded leaves and the immersion degree are connected by a strong positive correlation ($r = 0.86$, $p \leq 0.05$). Thus, the increase in structural "weight" of the degraded leaves seems likely to be one of the main factors determining the immersion of *S. aloides* plants at the end of the vegetation period.

The substantial decrease of the specific weight of *S. aloides* at the beginning of the vegetation period is connected with a high aerenchyma level in the young leaf tissues. According to calculations by Antipov (1968), for 1 g of raw leaf material of *Stratiotes aloides* there is 0.22–0.36 mL of air in the intercellular spaces.

Vereshchagin (1925, cited in Bykov, 1962) suggests that the immersion of *S. aloides* should be connected with the development of a strong root system and branching of the shoot system in the fall. However, this opinion has to be rejected because the root system is completely destroyed by the end of the vegetation season, and thus the contractile properties of *S. aloides* roots cannot be active.

Another concept of the position of the rosette shoot of *Stratiotes aloides* relative to water surface is connected with the variation of starch content in tissues (Zhdanov, 1987). A study of the seasonal dynamics of starch content in *S. aloides* tissues revealed phenological trends. The maximum starch content was observed at the beginning of winter, when *S. aloides* plants become fully immersed. In this case, starch granules act as statoliths. Numerous small starch granules often fill more than half the cell volume. Topographically, starch granules are localized in the first order parenchyma, in the stolons, in the flower-bearing stems, in the conducting bundle sheaths or, more rarely, in the subepidermal parenchyma (Fig. 3). The most rich in starch are the stem, the basal areas of the leaves and especially the turions.

During winter, a gradual decrease in starch level is observed, with the minimum concentration at the beginning of the spring emergence of rosette shoots (Fig. 4).

By the mid-summer, as the overall starch level increases, in the distal parts of leaves there is an efflux of assimilates to the proximal area and the stem. The differences between the minimum and the maximum starch levels within the vegetation period in various organs reached a factor of 2.1–4.4. Starch level in the *S. aloides* tissues and the degree of immersion were strongly positively correlated ($r = 0.81$, $p \leq 0.05$).

CONCLUSION

The mechanism of immersion and buoyancy of *S. aloides* plants due to variations of specific weight is caused by several factors. It is connected, to a large extent, with the change of ratio between decaying and functionally active tissues of the leaves. Another major factor is the seasonal starch profile in the tissues. The seasonal variation of ash content has a weaker effect.

Phylogenetically, the immersion and emergence mechanism developed by *S. aloides* plants is a way of adaptation which helps them survive the unfavorable (winter) season. This mechanism provides a relatively wide distribution range in the water bodies of the temperate climatic zone. However, this mechanism of seasonal spatial dynamics of *S. aloides* plants prevents the formation of stable phytocenoses in shallow or running water habitats as well as in the conditions of considerable seasonal variations of water level.

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REZIME

Sezonska i prostorna dinamika vodene biljke *Stratiotes aloides* (Hydrocharitaceae)

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U ovom radu se diskutuju osobenosti prostorne dinamike vodene biljke *Stratiotes aloides* tokom različitih sezona. Mehanizam uronjenosti i plovljivosti *S. aloides* uspostavlja se filogenetski tako što se favorizuju biljke koje preživljavaju nepovoljni zimski period u vodenoj sredini umerene klimatske zone severne Evroazije. Mahanizmi tonjenja u jesen i izronjavanja u proleće zavise od nekoliko faktora. Osnovni razlog je sezonsko variranje strukturne težine listova, dok je sezonska dinamika odlaganja skroba i sadržaja minerala (pepela) manje značajna.

Ključne reči: *Stratiotes aloides,* sezonsko-prostorna dinamika, struktura listova, sadržaj skroba, pepeo