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Biology of *Halothamnus glaucus* (M. Bieb.) Botsch. (Chenopodiaceae)

Биология *Halothamnus glaucus* (M. Bieb.) Botsch. (Chenopodiaceae)

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Summary. This study examines the morphogenesis, shoot system, phenology, and reproductive biology of the xerophytic orthotropic subshrub *Halothamnus glaucus* (M. Bieb.) Botsch. (Chenopodiaceae) in the Ararat Valley of Armenia and under cultivation at the Yerevan Botanical Garden. Observations were conducted using bio-morphological and phenological methods. The aim of this study was to identify adaptive strategies that enable *H. glaucus* to survive under arid conditions, including annual partial shoot senescence characteristic of xerophytic subshrubs, maintenance of main green biomass, and efficient reproductive mechanisms. Structural and biological features of seed germination, seedling morphology, branching, flowering, pollination, the diurnal rhythm of flower opening, and fruiting were characterized. The results show that *H. glaucus* exhibits mesotonic sympodial branching, with a shoot system consisting of elongated and shortened vegetative shoots, as well as elongated generative shoots. Flowers are protandrous, and pollination occurs via a combination of anemophily and entomophily. Fruit dispersal occurs through anemo- and barochory, ensuring a stable soil seed bank. These mechanisms contribute to the successful regeneration of the species in its typical habitats. The complex morphological and biological adaptations of *H. glaucus* in vegetative and reproductive structures ensure species survival and maintain population viability under the extreme conditions of semi-desert ecosystems. The article is illustrated with original drawings.

Key words. *Halothamnus glaucus,* flowering biology, ontomorphogenesis, phenology, subshrub.

Реферат. В данном исследовании рассмотрены особенности морфогенеза, побеговой системы, фенологии и репродуктивной биологии ксерофитного ортотропного полукустарника *Halothamnus glaucus* (M. Bieb.) Botsch. (Chenopodiaceae) в условиях Араратской равнины Армении и при культивировании в Ереванском ботаническом саду. Наблюдения проводились с использованием стандартных биоморфологических и фенологических методов. Цель исследования – выявление адаптивных стратегий, обеспечивающих выживание вида в засушливых условиях, включая ежегодное отмирание части побегов, характерное для ксерофитных полукустарников, сохранение основной зеленой биомассы и эффективные репродуктивные механизмы. Выявлены структурные и биологические особенности прорастания семян и морфологии всходов, ветвления, цветения, опыления, суточного ритма и механизмов раскрытия цветка, плодоношения. Результаты показывают, что *H. glaucus* характеризуется мезотоническим симподиальным ветвлением, с побеговой системой, состоящей из удлиненных и укороченных вегетативных побегов, а также удлиненных генеративных побегов. Цветки протандрические, способы опыления сочетают анемофилию и энтомофилию. В способах распространения плодов отмечается анемо- и барохория, обеспечивающая стабильный почвенный банк семян и способствующая успешному возобновлению данного вида в его типичных местообитаниях. Комплексные морфологические и биологические адаптации *H. glaucus* в вегетативных и репродуктивных структурах обеспечивают выживание вида и поддержание жизнеспособности популяции в экстремальных условиях полупустынных экосистем. Статья иллюстрирована оригинальными рисунками.

Ключевые слова. Биология цветения, онтоморфогенез, полукустарник, фенология, *Halothamnus glaucus.*

Introduction. Subshrubs are a characteristic life form of desert habitats across all continents of both the Old and New Worlds (Prozorovsky, 1940; Serebryakov, 1954; Rachkovskaya, 1957; Golubev, 1960; Bespalova, 1965; Lavrenko, 1962; Mazurenko, Khokhryakov, 1977; Butnik et al., 2001).

The morphogenesis and structural features of desert subshrubs have been studied by Golubev (1960), Mulkidzhanyan (1965), Nikitin (1966), Serebryakov (1965), Rotov (1969), Nechaeva et al. (1973), Butnik et al. (2001), and others. In the flora of Armenia, this life form within the Chenopodiaceae family is represented

by xeromorphic orthotropic and plagiotropic subshrubs, including cushion-shaped, tussock-forming rhizomatous, and caudex-forming subshrubs and dwarf subshrubs (Akopian, 2013). A key diagnostic feature of this life form is the annual dieback of part of the current year's shoots, while their lignified basal portions persist. The structural description takes into account the ratio between renewal and senescence zones, as well as the spatial distribution of renewal buds along the basal metamers of elongated axial shoots. In xeromorphic subshrubs, the dieback zone corresponds to the reproductive portion of the shoot; however, it extends beyond the inflorescence to include the several underlying metamers. The annual shoot is regarded as the principal structural unit (Serebryakov, 1964; Bespalova, 1960; Rotov, 1969; Nechaeva et al., 1973; Vasiliev et al., 1978).

The Chenopodiaceae family includes, alongside morphologically and biologically specialized subshrubs and dwarf subshrubs (caudex-forming, vegetatively mobile rhizomatous, and cushion-shaped), a group of non-specialized subshrubs in which adaptation to arid conditions is expressed primarily at the level of individual xeromorphic traits rather than through overall plant architecture and shoot system organization. In the flora of Armenia, this group includes such species as *Atriplex cana* C. A. Mey., *A. turcomanica* (Moq.) Boiss., *Caroxylon ericoides* (M. Bieb.) Akhani et Roalson, *C. nodulosum* Moq., *Halothamnus glaucus* (M. Bieb.) Botsch., *Krasheninnikovia ceratoides* (L.) Gueldenst., and *Suaeda microphylla* Pall. (Akopian, 2013).

Halothamnus glaucus is widespread in Southwest, Middle and Central Asia, in the Caucasus it is found in Eastern and Southern Transcaucasia. In Armenia *H. glaucus* grows in dry solonchaks, on foothill slopes and saline depressions in the semi-desert zone in the Yerevan (everywhere), Darelegis and Meghri floristic regions. Despite its widespread distribution in Armenia, the bio-morphological characteristics of this subshrub have not been previously studied. The aim of the work is to identify patterns of ontomorphogenesis and reproductive biology of *H. glaucus* in the conditions of the semi-deserts of Armenia and under *ex situ* cultivation.

Materials and Methods. The material for the study consisted of plants growing in natural populations as well as under cultivation in the Yerevan Botanical Garden. Field observations were carried out on salt marshes, gypsum-bearing clay-gravel hills, and sandy areas of the Ararat Valley, in the Ararat, Armavir, and Kotayk provinces. In the Yerevan botanical garden, on the exhibition plot "Flora and Vegetation of Armenia," specimens of *H. glaucus* transplanted from natural habitats, as well as those grown from seeds on local soil or soil transferred from natural habitats, were observed. The morphology of seedlings was also studied under laboratory conditions. To identify the features of morphogenesis of the plant, the studies were conducted at all ontogenetic stages. Standard bio-morphological methods were used to investigate life form, ontogenetic and seasonal development. Phenological observations were carried out according to the scheme of Beideman (1974), taking into account the specific characteristics of the studied plant. The study of flowering biology was conducted in natural conditions and under cultivation following the methods of Ponomarev (1970), Golubev, and Volokitin (1976). The main stages of flower opening and their details were illustrated using an MBS-9 stereomicroscope.

Results and Discussion. *Halothamnus glaucus* is a xerophytic orthotropic subshrub 30–75 (–100) cm tall, with grayish branches, woody at the base. Shoots are glabrous and directed obliquely upward. Leaves are 3–10 to 15–50 mm long, alternate, sessile, subterete, flat above, acute, and mostly slightly curved upward. Seed germination in *H. glaucus*, as in all centrospermous plants, is epigeal. Cotyledons are green, pinkish at the base, glabrous, linear, rounded in cross section, tapering toward the apex, not distinctly pointed, 12 mm long and 1–1.5 mm wide (Fig. 1a). At the base, the cotyledons gradually transition into a slightly flattened, quadrangular hypocotyl, wine-red in color, 50–60 mm long, tapering into the root. The epicotyl and subsequent internodes of the primary shoot are undeveloped. The first two leaves are bright green, glabrous, linear-cylindrical, up to 8 mm long and 1 mm in diameter, flattened above and tapering to a soft apex. By mid-April, seedlings with a rosette form produce 5–6 additional leaves (0.1–1 mm) (Fig. 1b, c), and the apical bud is surrounded by 10 more leaf primordia.

On a first-year *H. glaucus* plant (Fig. 2A), about 23 lateral shoots develop, up to 20–22 cm long, forming the structure of the plant. Several leaves and shoots at the base of the main shoot dry up, and higher up the main shoot, leafy, unbranched, alternate second-order shoots develop. Then, starting from the sixth leaf, lateral shoots branch into third-order branches, which then outgrow the main shoot by 20–25 cm. Thus, this lateral branching in *H. glaucus* can be defined as mesotonic. In April-May, closed renewal buds are formed at the base of the main and lateral shoots, some of which become dormant. According to our observations at the Yerevan Botanical Garden, renewal buds of *H. glaucus* contain 12–15 bud elements in the summer, and up to 20 by the end of autumn. The maximum height of the main shoot in first-year plants reaches 30–35 cm. In

highly vigorous plants, single flower buds are formed on the main shoot, sequentially, in the axils of 7–9 alternately arranged bracts, and by the end of October, produce fruits with developed and rudimentary wings. Subsequently, the metameres of the upper and middle tiers of the first-order shoot undergo senescence (Fig. 2B, a), while the basal portion of the plant overwinters, bearing renewal buds from which sympodial shoots develop in the second year (Fig. 2B, b).

The annual dieback of current-year shoots, while retaining their lignified perennial bases, affects up to two-thirds of the shoot length. The shoot system of *H. glaucus* consists of elongated and shortened vegetative shoots, as well as elongated generative shoots, which together constitute the main green biomass of the mature subshrub.

The annual (seasonal) cycle of *H. glaucus* is extended with a spring-summer-autumn phenological rhythm. Budding occurs in (May) June-August, flowering in July-September. *H. glaucus* flowers are collected in spike-shaped inflorescences with an acropetal development order. An individual flower is protected by a bract and paired bracteoles (Fig. 3a). The bract with a wide base is equal to or usually longer than the perianth, the bracteoles are 3.5–18 mm long, usually broadly ovate below, membranous-bordered along the margin, tapering at the top. Anthers with thecae fused for slightly more than half their length. Stigmas are usually as long as the style, sometimes half as long or longer. The structural features of the flower are shown in Table 1. The *H. glaucus* flower functions for 52 (54) hours. On the first day, slight dehiscence of the tepals and slow anther exposure (Fig. 3b) begin, and protandry is observed. On the second day, anther exposure continues and is complete by 2:00 PM. The anthers emerge from the closed perianth to a quarter of their length, with the stigmas not exceeding the perianth, and the thecae dehisce introrse. Pollination begins after 1:00 PM, and on relatively cool days after 2:00–2:30 PM. At this stage (Fig. 3c), the flower is constantly visited by representatives of the Apidae family – *Halictus* sp., *Nomia* sp., and *Nomioides minutissimus*. The following attractants are noted: visual (androecium coloration), pollen, and nectar secretion from the hypogynous disc. On the third day, the flower's functioning ends, the empty anthers fall off, and subsequently the tepals, bracteoles, and bract close together. Active insect pollination of *H. glaucus* begins in the first ten days of August and continues throughout the month. At the beginning and end of the flowering period, insect pollination (the primary method) is combined with wind pollination. Wind pollination

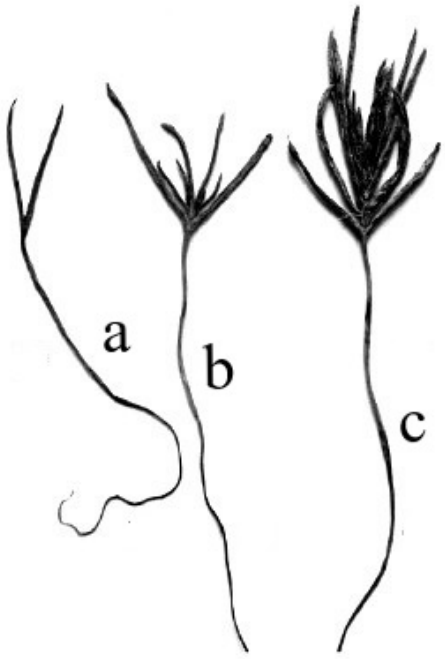

Fig. 1. *Halothamnus glaucus* seedlings at the cotyledon stage (a) and the first 6–12 leaves (b, c).

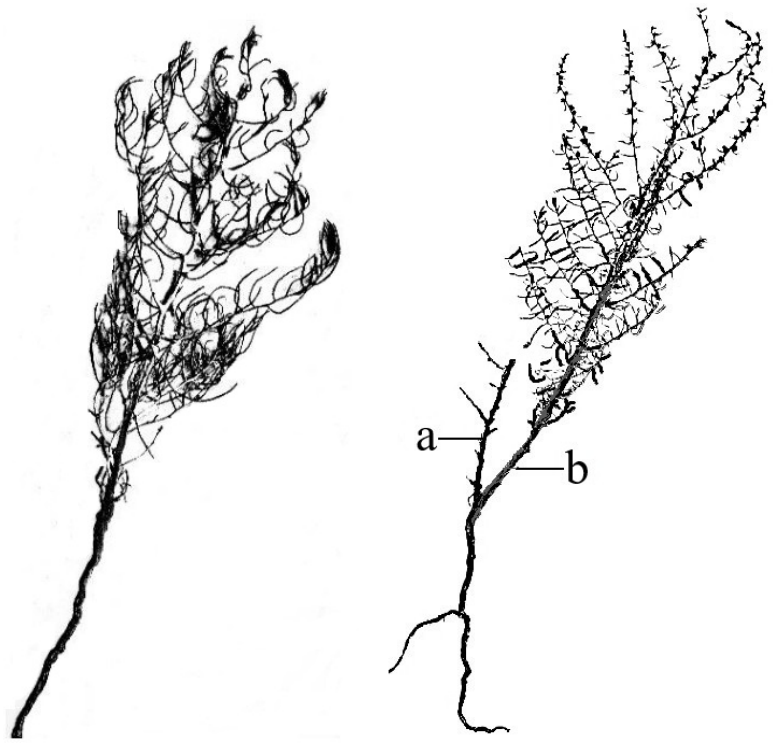

Fig. 2. A – *Halothamnus glaucus* plant in the first year of development; B – *H. glaucus* early generative plant in the second year of development: a – primary senescent shoot, b – sympodial shoot of the current year.

occurs as follows: in some flowers, the stamen filaments are slightly longer than the perianth, and the anthers, which are completely mobile, flip over, assuming a horizontal position and orienting themselves extroverted (Fig. 3d). Under the influence of gusts of wind, the pollen is released and dispersed. Some flowers were bagged during the flowering period; no evidence of autogamy was observed in *H. glaucus*.

Table 1. *Halothamnus glaucus* floral morphology

Structure	Length (mm)	Width (mm)	Shape	Color
Perianth segments (tepals)	3.5	1.8–2.0	triangular-lanceolate	with green triangular spot
Anthers	2.3	0.5–0.6	narrowly triangular	red
Connective	0.7	ca. 0.08	linear	pink
Filaments	3.4–3.6	0.5–0.6	flattened, broadened at base	dark crimson
Pistil	2.9	ca. 1 (diam.)	clavate	green
Stigmas	1.0	0.5	spathulate, flattened, apically dentate	dark red
Hypogynous disc	ca. 0.3 (height)	ca. 1.5 (diam.)	saucer-shaped, with semi-rounded lobes	bright green

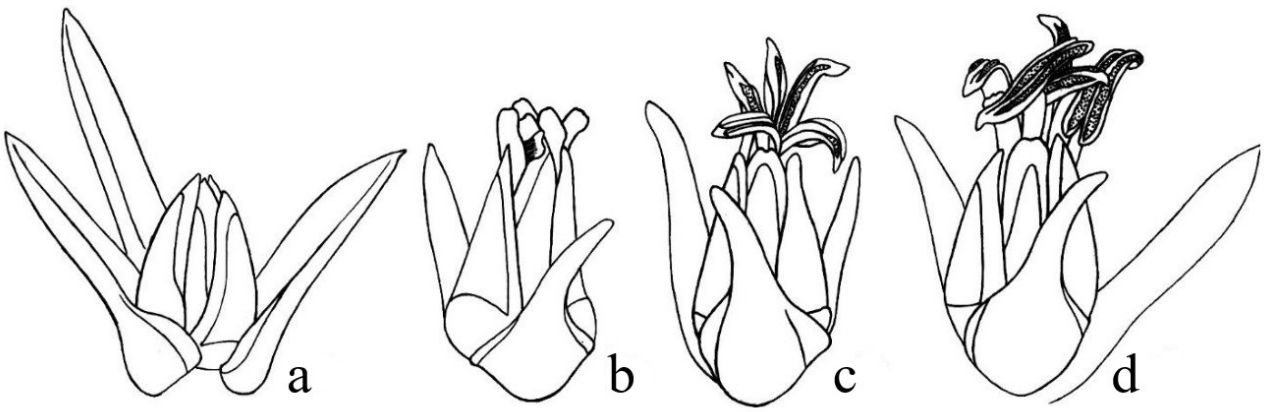

Fig. 3. Stages of *Halothamnus glaucus* flower opening.

Fruiting takes place from mid-September to early November. During this period, membranous, broadly obovate, overlapping wings, yellowish or pale pink in color, develop on the perianth lobes below their midpoint. The fruit, including these wing-like extensions, reaches a diameter of 10–12 mm, with the base measuring 4–5 mm. Above the wings, the perianth lobes converge to form a fairly compact, conical structure. The outer layers of the fruit comprise the persistent perianth, which serves an additional protective function, a dark brown pericarp, and the seed coat. The embryo contains chlorophyll, is spirally coiled, and clearly differentiated into cylindrical cotyledons, a hypocotyl, and a radicle. In the axils of the cotyledons, two true leaf primordia can be observed. Fruit dispersal occurs through a combination of barochory and anemochory. Some of the seeds are stored in the soil, forming a persistent seed bank. The combination of seed dormancy with barochory, which causes many seeds to germinate close to the parent plant, helps maintain the species under extreme conditions and ensures its establishment in characteristic habitats. Our results indicate that *H. glaucus* exhibits integrated morphological and biological adaptations in both vegetative and reproductive structures, enabling the species to persist and sustain population viability under the extreme conditions of desert and semi-desert ecosystems.

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