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Formation of Morphological Structure of the Alpine Cushion-Shaped Dwarf Semishrub *Gypsophila uralensis* Less. in the Course of Ontogenesis[1]

P. L. Gorchakovskii and A. V. Stepanova

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. 8 Marta 202, Ekaterinburg, 620144 Russia

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Abstract – Observations were made of the changes in the morphological structure in a long life cycle of an endemic plant, one of the most specific of the high mountains of the Ural region, and the peculiarities and adaptive features of the biomorph of the cushion-shaped caudex dwarf semishrub were revealed.

Gypsophila uralensis Less. is one of the most typical representatives of the Ural alpine endemics. It is common from the polar Ural up to the south Ural. It grows mainly in high mountains, in the mountain tundra belt ("goltsy") and "subgoltsy" belt, on rock fields, and in alpine tundras; it occurs more seldom on mountains of lower levels and, mainly, at limestone outcrops along banks of rivers (Gorchakovskii, 1969; 1975). High mountains are the primary places where this species grows; its emergence on the littoral outrops of rocks is the result of the latest migrations. Like other endemic plants of the Ural region, *Gypsophila uralensis* Less. belongs to a number of the most vulnerable components of the local flora. It is closely related to a specific type of substrate, distributed sporadically, and represented by a few isolated populations.

The elaboration of measures for the protection of *Gypsophila uralensis* Less. and the organization of the monitoring of its populations requires knowledge of the specific morphoecological features of this species, which are displayed, in particular, in the peculiarities of the biomorph and the stages of a long life cycle. The results of such an investigation are presented in this paper. The source material was collected in the north Ural, i.e., mountains of Semichelovechii Kamen' and Tretii Bugor (the District of Kos'vinsk Kamen'), and in the south Ural – in mountains of Big and Small Iremel'. Analogous investigations were conducted earlier with respect to other endemic plants (Gorchakovskii and Zueva, 1993; Gorchakovskii and Stepanova, 1994a; 1994b).

ONTOGENESIS

In the long life cycle of *Gypsophila uralensis* Less. (see figure), it is possible to distinguish the following age states: plantule (pl), juvenile (j), immature (im), young generative (g_1), middle age generative (g_2), old generative (g_3), and senile (s).

The *plantule* in the first year of life has an epigeal hypocotyl with two lanceolar cotyledons and a short hypocotyledonary shoot with several linear leaves. Soon after the emergence of the first leaves, cotyledons die off. At the end of the epicotyledonary shoot, a crown bud is formed, and in the axil of leaves axillary buds arise. The leaves function only one season and die off in autumn, but their remnants remain on a shoot for a long time. During the next 2 - 3 years the main shoot grows monopodially, and annually a crown bud is formed on it, giving rise to a shoot of the subsequent year. There are no formations of lateral shoots as yet, and axillary buds covered by the remnants of dead leaves are in a state of rest. The root of the plantule is a tap-root; it is very thin, and exceeds the above-ground portion in length by several times.

Juvenile individuals. Monopodial growth of the main shoot stops, as a rule, by the 4th - 5th year of life of the individual. By this time, the crown bud dies off, and from axillary buds located in the zone of the growth of recent years several lateral shoots arise. Not all the axillary buds stir to grow; a portion of them passes into a dormant state, maintaining vital activity for a long time. Lateral shoots (axes of the second order) grow for several years also monopodially; they are located radially and are curved and raised. Soon, the lateral shoots are levelled off with the main shoot and surpass it in length. The root becomes more branched.

In *immature individuals* there appear several new axes of the second order from the dormant buds located at the base of the leader shoot. In addition, at axes of the second order, from axillary buds shoots of the third order grow, which in their turn give rise to the shoots of the fourth order and so on. All the newly emerging shoots grow monopodially for 3 - 4 years. Then their apices die off, but the thickening and elongation of a perennial branch may proceed thanks to the emergence of shoots of a higher order. This is the way the gradual formation of a bush occurs. By this time, the base of a

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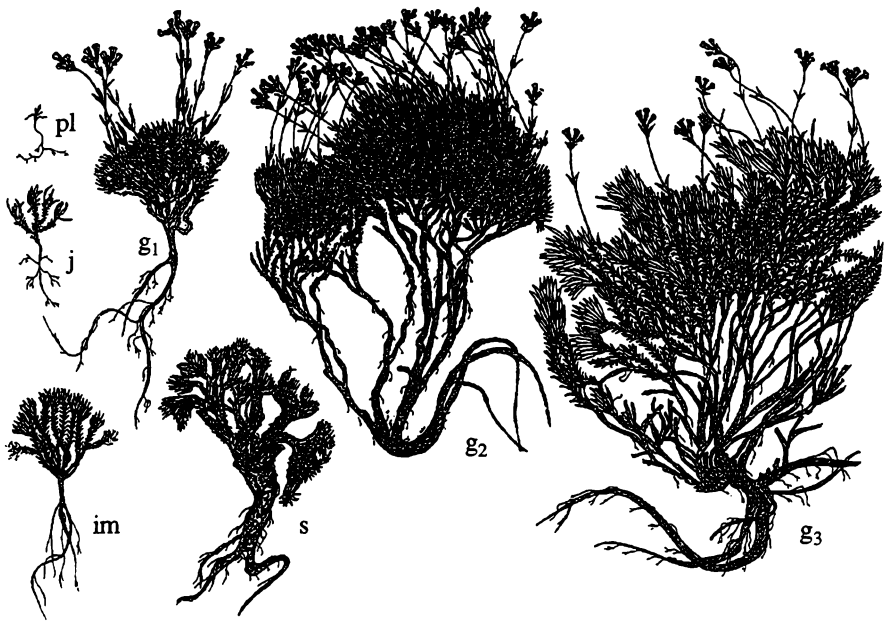

Age states of *Gypsophila uralensis* Less. (conventional symbols are explained in the text).

future cushion, consisting of 6 - 10 perennial branches, begins to show. The leading shoot, which formerly stopped its growth, is hardly discernible and is often shifted to the periphery of the bush. The root is well developed and sometimes has distinct lateral branches.

Young generative individuals. The aboveground part has a shape of a cushion with a diameter from 6 to 12 cm. Perennial branches, which are repeatedly branched off and carry numerous young shoots at their ends, are distinctly pronounced. Peripheral branches are located plagiotropically. The bases of perennial branches are submerged into a substrate. This is the result both of the root sucking-in activity, evidenced by cross wrinkles in its basal part, and the introduction and retaining by the cushion of the fine earth. Within the cushion, remnants of dead leaves and stems accumulate, and mosses settle. Defoliated parts of vegetative shoots and generative shoots raise upon the layer of fine earth, organic remnants, and mosses. The annual increment of vegetative shoots is in the range of 0.6 to 1.2 cm; the number of leaves at an annual shoot is from 6 to 12, the length of leaves being 1.6 - 3.0 cm. The number of generative shoots is in the range of 1 to 45, and their length is from 10 to 15 cm. The bottom parts of perennial branches are lignified. Already discernible is a many-headed stem-root-caudex. The root is moderately powerful, branched off, and deeply penetrates into the cracks between stony lumps and rubble.

Middle age generative individuals. Vegetative and generative spheres reach maximum growth. By this time, the particulation of the bush is clearly defined, i.e., several separate parts of the bush are formed, called particules, or skeletal branches. Particulation is the result of the repeated branching off and the increase in size of the portion of the remaining perennial branches, whereas other perennial branches die off. Skeletal branches carry upon them numerous vegetative and generative shoots. The orthotropous orientation of peripheral branches of the cushion is gradually changed by a plagiotropic one. The basal parts of skeletal branches become woody. They are submerged into a substrate and covered by deciduous leaves, remnants of stems, and moss. The bases of dead shoots of the second, third, and subsequent orders are noticeable.

The bush has a shape of a slightly convex, compact, moderately flat cushion with a diameter from 15 to 35 cm, and in the vertical projection it is oval, as a rule. The youngest vegetative shoots raise above the substrate and moss by 4 - 5 cm; it is precisely these shoots that form the cushion part visible externally. The annual increment of vegetative shoots is 0.7 - 2.0 cm, and the number of leaves per annual shoot is 10 - 16, length of the leaves being 2.2 - 4.5 cm. The number of generative shoots is from 25 to 100; in rare cases it reaches 350, their length being from 10 to 17 cm. After intensive fruit bearing, particular branches die off, and in their place appear shoots of subsequent orders. The caudex is well developed. The root is powerful, with developed lateral branches, deeply penetrating into the cracks of rocks.

In *old generative individuals* in the aboveground part, the processes of dying off gradually begin to dominate over the process of regeneration. A portion of particules dies off completely or almost completely. In their place, from the base of skeletal branches that retained vitality, or from their parts from the dormant buds, new, thinner perennial branches form. The particulation of the bush sometimes becomes less pronounced. At perennial branches one can see numerous bases of dead shoots of lower orders. The formation of new buds of regeneration reduces. As a result of dying

off of a portion of skeletal branches, the cushion becomes less dense, its integrity is disrupted, and in the vertical projection it loses its regular shape. Several peripheral branches of a higher order die off as well. All this leads to a decrease in the diameter of the cushion to 10 - 28 cm.

In the bush, young shoots that remained in a vegetative state prevail. The annual increment of vegetative shoots decreases and comprises 0.7 - 1.2 cm; the number of leaves at the annual shoot is 8 - 12, the length of leaves being 1.8 - 2.0 cm. Reduction in annual increment induces a decrease to 2.5 - 3 cm in the height of the aboveground portion of the cushion. The number of generative shoots significantly reduces (2 - 20); their length reduces likewise (7.5 - 9 cm). The caudex thickens, the root becomes more powerful and more branched off, and its particular branches are only slightly inferior to the stem part in thickness and length.

Senile individuals. Most of the particules have died off and separated from the plant. Only the bases of several branches and shoots of lower orders remain. As a rule, the bases of 1 - 2 skeletal branches alone stay viable; at them from the regeneration buds that rested for a long period or emerged 2 - 3 years earlier, there form few shoots that remain in a vegetative state. The magnitude of the annual increment decreases to 0.3 - 0.7 cm, the number of leaves at the annual shoot – to 6 - 10, and the leaves become smaller (0.8 - 1.7 cm). The total surface of leaves and the mass of vegetative organs strongly diminish. The cushion is almost completely destroyed. Its remaining part has a diameter no more than 7 to 10 cm, the shape of the cushion being irregular. The caudex and the root are usually contaminated with rot and are partially subjected to destruction.

THE STRUCTURE OF A CUSHION-SHAPED BUSH

The aboveground part of a cushion-shaped dwarf semishrub is most pronounced in middle age generative individuals. The structural base of the formed cushion is made of isolated perennial strongly branched off skeletal branches (particules), which represent a system of different aged shoots, connected by a joint base (Steshenko, 1960). In the course of ontogenesis, the formation of a perennial branch begins with the formation of a lateral shoot (the axis of the second order), branching off the leading shoot (the axis of the first order). When the apex of the lateral shoot dies off, from axillary buds on it the axes of the third order are formed, and on these axes – axes of the fourth order and so on.

At branches of the highest order young monocarpic leaf-bearing shoots located. A complete cycle of development of the monocarpic shoot includes a vegetative and a generative phase. It grows monopodially. At first, for one or two years, only its vegetative part grows (innovative shoot), which carries leaves with shortened internodes, and then the generative part (generative shoot). At the generative part of the monocarpic shoot at its base, there locate leaves with shortened internodes, then 2 - 3 (4) couples of accumbent leaves with extended internodes, and at the end – the inflorescence in the shape of an umbel-like panicle. After fruit bearing and dissemination, the apex of the monocarpic shoot dies off, and monopodial growth ceases, but from the buds located in the axils of leaves in its vegetative part, at the growth of the preceding years, new monocarpic shoots of the subsequent order appear. However, not all the monocarpic shoots undergo a complete developmental cycle. In the case of incomplete development, the monocarpic shoot functions only as a vegetative assimilating shoot, for 1 - 3 (4) years its vegetative part alone grows monopodially, then its apex dies off, and from the buds in axils of leaves, new shoots of a higher order sympodially arise.

At the skeletal branch, monocarpic shoots that underwent a complete or incomplete cycle of development are annually replaced by new shoots of a higher order, arising sympodially from axillary buds. Diversification of the branch and the complication of its structure usually take place until most shoots of higher orders reach the fruit bearing stage. Then, the skeletal branch dies off, but from dormant buds located at the base of skeletal branches new shoots usually emerge. Several of them may replace the atrophied perennial branch. Thus, in the lifespan of an individual, a replacement of a portion of perennial branches takes place. As the order of branching off of skeletal branches increases, the size and density of the cushion also increase.

The isolation of perennial individuals and the particulation of the bush begin in the young generative state and become most clearly manifested in the middle age generative state. The old generative state is characterized by the emergence of new perennial branches instead of dying off, and the senile one – by the mass dying off of perennial branches without their replacement by new ones.

BIOMORPH

Gypsophila uralensis Less. belongs to the biomorph of cushion-shaped dwarf semiherbs, which form caudex. Dwarf semiherbs were recently studied by many investigators, for the most part, in arid regions of central Kazakhstan (Bespalova, 1960; Rachkovskaya, 1957; *Biokompleksnaya Kharakteristika* ..., 1969). In the system of biomorphs, dwarf semishrubs are intermediate between dwarf shrubs and herbaceous plants. These are plants in which the bottom parts of perennial branches become woody to a certain degree, while the upper ones are herbaceous with annual shoots, which die off at the end of the first season of their growth and retain vitality for several years.

In *Gypsophila uralensis* Less. the aboveground part has a shape of a dense cushion with nonrooting shoots. A cushion shape of growth ensures the survival of this species under severe conditions of stony alpine tundras, rock streams, rock outcrops, residual rocks, and mounds.

In the cushion, a more favorable microclimate is created, temperature decreases, wide fluctuations in temperature level off in 24 hours, moisture is accumulated, and the strength of the wind decreases, enabling shoots to better withstand its dehydrating and freezing effect.

At the base of skeletal branches, fine earth washed away by snow melt and rainy waters along the slope accumulates, as well as a great amount of the stagnant organic matter, i.e., the remnants of dead leaves and stems. Often in the cushion mosses settle. Therefore, the bottom parts of perennial branches turn out to be well protected from freezing and other unfavorable environmental effects. It is precisely these regeneration buds, which are located in the basal part of perennial branches and are capable of prolonged resting, that make up the reserve, which provides for the replacement of dying branches by new perennial branches.

Above the layer of fine earth, vegetative remnants, and moss, only young shoots with leaves and inflorescences are exposed. Regeneration buds, located at these shoots, are protected from the dehydrating effect of wind and freezing by a dense spacing of shoots and coverage of buds by dead leaves, which do not fall off for several years. As the height of skeletal branches increases, their bottom parts increasingly bury into the layer of fine earth and vegetative remnants.

If the cushion dies off from the side, most subjected to wind exposure, then it intensively grows from the opposite side. This is why cushions in the vertical projection are oval, as a rule.

Retaining by the cushion of the products of erosion of rocks, washed out along the slope, as well as of organic matter, creates for the plant the most favorable local soil–ground conditions (accumulation of moisture, fine earth, and humus), this being very important for plants dwelling under extreme conditions at stony sites.

CONCLUSION

As an independent species, *Gypsophila uralensis* Less. is likely to form on the basis of an ancestor, similar to it and to *Gypsophila sambukii* Schischk., common in arctic Siberia at rock outcrops. From the phylogenetic point of view, the morphogenesis of *Gypsophila uralensis* Less. proceeded in high mountains of the Ural, in mountain tundras, and rock streams under conditions of a strongly reduced growth season, heat deficiency, low temperatures during the growth season, prolonged severe winter, low snow accumulation, and strong winds, which in summer cause dehydration of shoots and in winter contribute to their freezing, poorness, and low power of the soil.

These were the conditions to which corresponded the adaptive strategy of the initial form, which led to the formation of a stocky cushionlike dwarf semiherb with parts of young shoots that annually die off, a developed caudex, a root deeply penetrating into the cracks in rocks, numerous branches, which become woody at bases, are partially submerged into fine earth, and endure severe winter conditions under the cover of abscised leaves, mossy bog, and snow cover.

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