

Comparative study of ontomorphogenesis and anatomy of different ecotypes of *Clematis tangutica* (Maxim.) Korsh. (Ranunculaceae) based on the evo-devo concept

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Summary: Ontomorphogenesis, morphological and anatomical features of vegetative organs of high-mountain *Clematis tangutica* ecotype show vividly the cryophilic line of adaptogenesis in the *Clematis* genus. High-mountain *C. tangutica* ecotype is highly similar to *Clematis* species from *Atragene* section by a different set of adaptive features. The main mode of morphological evolution in this case is retardation, too.

Keywords: *Clematis tangutica*, Ranunculaceae, ontomorphogenesis, morphology, anatomy, secondary thickening, adaptation, retardation

Inhabiting different ecological conditions leads to a considerable biomorphological polymorphism of species. However, the existence of smooth transitions determines some conventions, while distinguishing discrete ecotypes. According to GREY-WILSON (1989), *Clematis pamiralaica* Grey-Wilson belongs to close relatives of *C. tangutica*. It is an endemic of Pamir with habitats on open stony plots at altitudes exceeding 3350 m a.s.l. In the opinion of this author, it originated from *C. tangutica* as ecotype which was isolated in high altitudes. GREY-WILSON (l.c.) analysed herbarium material and living plants grown from seeds gathered in the mountains of China. However, similar samples were found earlier northerly, in Kirgystan in Tian Shan Mountains and were brought to MSU Herbarium [MW] under the name *C. salessoviana*. Unfortunately, *C. salessoviana* is not included in the species list of the genus *Clematis*. So one has to use the 'terms' 'low-mountain' and 'high-mountain' (samples).

Materials and methods

Clematis tangutica (Maxim.) Korsh. grows in high-mountain regions of Central Asia, Eastern Pamir-Alay, Eastern Tian Shan, in Mongolia and north-western China on rocky and crushed stony slopes of river valleys, down by the riverside on screes (KRASHENINNIKOV 1937; SHIPCHINSKY 1954; USMANOV & KOSTELOVA 1974). It is remarkable because of a high-altitude variability which is expressed in morphology and anatomy of vegetative organs as well.

We investigated high-mountain samples of *C. tangutica* collected on the bank of Nichke-Djilga river (tributary of Murgab river) between Murgab and Dzhilandy in Tajikistan, Pamir 3600 m a.s.l., in the dry bed of Ak-Sai river, Tajikistan, Pamir, 3860 m a.s.l. as well as plants grown in Nikita Botanical Garden, Crimea, Yalta, 200 m a.s.l. and in the Botanical Garden of Lomonosov Moscow State University from seeds of Pamir which were sent by Donetsk Botanical Garden.

Morphological features of *C. tangutica* growing in subtropical and lukewarm regions of North America (REHDER 1949) were also taken into account.

Table 1. Morphometric peculiarities of embryo and endosperm in mature seeds of different ecotypes of *Clematis tangutica*, *C. orientalis* and *Atragene speciosa*.

Species	Length of embryo (mm)	Length of cotyledons (mm)	Cotyledons / embryo length ratio	Length of endosperm (mm)	Embryo / endosperm length ratio	Period of seed germination (days)
<i>C. tangutica</i> low-mountain	1.38	0.58	0.42	2.80	0.49	20–30
<i>C. tangutica</i> high-mountain	0.50	0.20	0.40	2.40	0.48	30
<i>C. orientalis</i>	1.08	0.45	0.42	2.58	0.42	15–30
<i>A. speciosa</i>	0.74	0.40	0.54	2.30	0.32	50–60

For comparison of ontomorphogenesis of ‘low-mountain’ and ‘high-mountain’ plants, we analysed the seeds, germinated and cultivated them in the nursery of MSU Botanical Garden.

In order to get comparable results, we analysed the morphology of vegetative organs, cross sections of leaves, annual and perennial stems of cultivated and natural samples of *C. tangutica*.

For comparison with other representatives of *Clematis*, we used the shoots of the close relative *C. orientalis* L. (section *Meclatis*) (TAMURA 1956), which were gathered on the bank of Issyk Kul lake near Darkhan settlement (Djety-Oguzskiy area, Issyk Kul region) (Kirgizstan, 1600 m a.s.l.) and the shoots of *Atragene speciosa* Weinmann, which were gathered in bush thickets on the slopes of natural boundary Sarcrama (Zailiyskiy Alatau), Kazakhstan (1690 m a.s.l.).

Anatomical analysis was carried out according to established methods (PROZINA 1960; BARYKINA et al. 2004). We used light microscopes Axioplan-2 Imaging and MBI-3. Images of the sections were taken with Axioplan-2 Imaging equipped with digital camera AxioCam MRc.

Histological analysis of xylem was studied using material macerated by concentrated nitric acid.

Measures of length and diameter of histological xylem elements were carried out with the aid of spiral eyepiece micrometer MOV-1, calibrated by objective micrometer OMP for different microscope magnifications. Arithmetical average from 30 measurements and coefficient of variation ($\pm k$) were counted using the express-method (KAPLAN 1970).

Results of morphological investigations

Ontomorphogenesis. In mature seeds of *C. tangutica*, the embryo is found on the micropylar pole. It is small, but well differentiated into cotyledons and axial part (Table 1) with a wide (5–6 cells) and flat apex. Germination is hypocotylar. Developed plantlet has two short-petioled (1–5 mm in length) oblong (8–11 mm / 3–4 mm) cotyledons, a long (up to 20 mm) hypocotyle and a main root with numerous adsorbing root hairs.

During the first season a well-leaved, epigeal semi-rosette shoot develops.

First, 2–4 leaves are alternate, short-petioled (petiole is 3.5–13 mm in length) with lanceolar (5–30 mm / 5–10 mm) leaf blades. Formation of metamers of the main shoot occurs during its growth.

In low-mountain samples up to 10 metamers with a full length of about 10 cm are formed. During growth, phyllotaxy changes from alternate to opposite. Leaf series is replenished by leaves



Figure 1. *Clematis tangutica* (Yalta, Nikita Botanical Garden), annual shoots: vs – elongated vegetative shoots; pgs – proleptic generative shoots; c – cataphylls; fl – foliage leaf.

with dissected and compound leaf blades. Buds form in the axils of all leaves, a part of them develops into shortened enrichment shoots with 1–2 small entire leaves.

In high-mountain samples, length of the main shoot does not exceed 7 cm, leaf series includes 2 alternate and 3 pairs of opposite leaves with entire-kind (up to 10 mm in length) or ternate (up to 20 mm in length) leaf blades. Buds stay resting and do not form enrichment shoots.

At the lower borderline of high-altitude distribution and in cultivation, in particular in the botanical gardens of Moscow and Yalta, adult plants of *C. tangutica* reproduce at 4–10 year. Generative specimens have the habit of geoxyl shrubs with lianoid vegetative shoots up to 3 m in length. Shoots include up to 20 metamers with large unpaired, pinnately compound leaves (leaflets are up to 50 mm in length and 30 mm in width).

Obvious features of lianoid habit are characteristic of them: great length and small diameter, rapid growth, inhibition of expansion of upper leaf blades until shoots are strengthened by means of the petiole support. Axillary buds on the vegetative shoot form vegetative and non-specialized generative shoots in the same year after a short dormant period. Generative shoots are rather short. They develop following the model of proleptic shoots and form 3–4 pairs of cataphylls with the rudiments of leaf blades in their base, one pair of foliage leaves and single, yellow, rather large flowers on the long (8–15 cm) flower stalks (Figs 1; 2). Sometimes, sylleptic short generative shoots of second order without cataphylls in the base develop in the axils of leaves of generative shoots.

Length of continuing shoots, number of their metamers and size of leaf blades decrease noticeably with increasing altitude. At an altitude of more than 2000 m, the vegetative shoots of *C. tangutica* shorten gradually up to 50–30 cm. Lianoid habit, which is characteristic of samples from lower zones, reveals itself only in the inability to support the vertical growth. Because of the absence of support, they sprawl out substrate and are often uncovered by soil. Following the model of proleptic shoots, they take a vertical position and form a tuft of rather long (mainly due to the flower stalks) shoots with 3–4 pairs of cataphylls and 2–3 pairs of foliage leaves (Fig. 2).

High-mountain samples from Pamir and Tian Shan gathered at the altitude above 2500 m (Fig. 3) have annual shoots along with flower stalks, which do not exceed 30 cm. Shoots are



Figure 2. *Clematis tangutica* (China, province Sichuan, up to 2700 m a.s.l.). Photo: M. Mikhailova.

thin, have few metamers, 3–4 pairs of scale-like leaves at the base and 2 pairs of foliage leaves on approaching nodes. Leaf blades of foliage leaves (as well as of low-mountain samples) are unpaired compound pinnate, but leaflets are small, 20–30 mm in length and 8–10 mm in width. Vegetative shoots are short (up to 30 cm), too, and have a little number of metamers. Leaves with simple lobed, pinnatifid and pinnately compound leaf blades appear after the formation of scale-like leaves. Generative shoots develop, as a rule, from basal buds.

In nature, plants grow under conditions of movable substrate – in the floodplain of mountain rivers, beds of temporary watercourses or on crushed stony slopes or sand dunes – and have a tillering zone which is usually buried subsurface. In this case, the nodes arranged near the substrate surface take over their function. Semishrubs form gradually from underground dormant buds. However, the system of main root remains. The branching of tillering shoots is basitonous, because of approximate nodes in the base; at the same time, generative shoots form on the shoots of the last year. Owing to annual dieback of shoot tips, their relative small length, their active tillering and branching, the plant looks like a semishrub or false cushion plant. Plants attain to their maximum development at the age of 60–80 years and are a system of partial shrubs at this time (STESHENKO 1965, 1977).

So, life-form of *C. tangutica* changes noticeably with the increase of altitude. In the alpine zone, geoxyl shrubs with long, lianoid (leaf-climbing) shoots and a tap root system form low-growing semishrubs or false cushion plants with a strongly marked dimorphism of annual shoots.

While attempting to graft high-mountain plants in the transplant nursery of MSU Botanical Garden from seeds, the plants grew with short vegetative shoots, small leaves and a long flower stalk, typical of high-mountain samples. Life cycle of seedlings decreased strongly. After a single

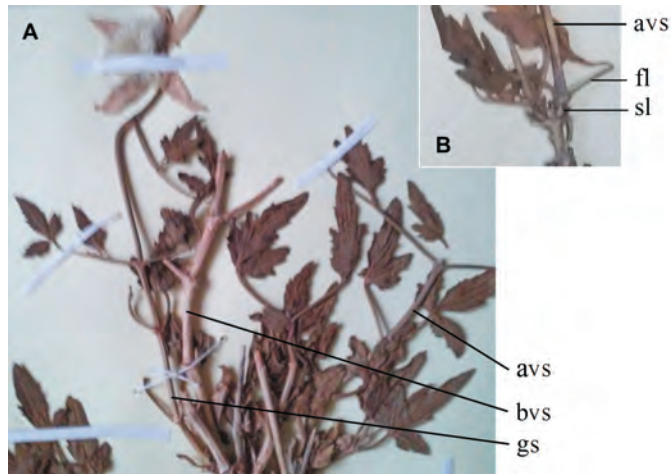


Figure 3. *Clematis tangutica* (Pamir, dry bed of Ak-Sai river; leg. Ikonnikov). A – dimorphism of annual shoots: avs – annual vegetative shoot, bvs – biennial vegetative shoot, gs – annual generative shoot; B – the bases of vegetative and generative shoots: sl – scale leaves, fl – foliage leaf.

flowering, 3-year old plants died off which gives evidence of the high level of specialization of high-mountain samples.

Results of anatomical investigations

The singularity of the high-mountain ecotype *C. tangutica* is clearly demonstrated by the anatomical structure of vegetative organs, in particular by the structure of definitive leaf and shoot. The leaf blade of high-mountain samples is noticeably thicker than in low-mountain ones (430 μm vs. 300 μm), mainly due to a greater number of palisade cell layers (3 vs. 1) and to the outgrowth of lacinate cells of spongy mesophyll (Fig. 4A, B). Rich supply of leaf veins (up to 1000 mm/cm^2 vs. 600 mm/cm^2 in low-mountain samples) is embedded in the mesophyll. Leaves of *C. tangutica* are amphistomatic (upper and lower epidermis include numerous stomata). Stomatal density in high-mountain samples measures up to 270/ mm^2 vs. 190/ mm^2 in low-mountain samples. Epidermis is covered by a thick cuticle and by a layer of wax.

Epidermal cells are small, polyangular with nearly straight anticlinal cell walls. Histological composition of the xylem in annual and perennial stems as well as special features of its separate elements may be an essential supplement to the anatomical characteristics of *C. tangutica*.

Annual stems of low-mountain samples have 12 primary vascular bundles separated by narrow (2–3 rows) medullary rays which lignify only at the level of the primary xylem. Secondary xylem includes vessels, vascular and fibrous tracheids and fibres. In perennial stems, the secondary xylem is ring-porous. Annual growth of xylem does not exceed more than 7 layers (inspite of 20 layers in *C. orientalis*).

In the perennial as well as in the annual stem, vessel members have simple perforations on horizontal or inclined walls. Small-pored vessels as well as vascular tracheids have bordered pores and tertiary spiral thickenings on the lateral walls.

Walls of fibrous tracheids are thick with poorly bordered pores. Fibres have simple pores, quite often septate, frequently performing storage function when replacing the xylem parenchyma.

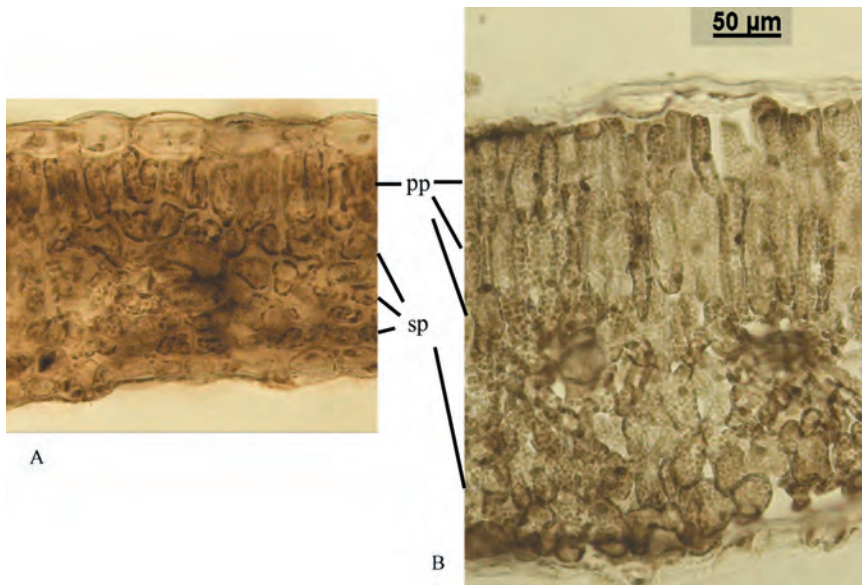


Figure 4. Anatomical structure of leaf blades of low-mountain (A) and high-mountain (B) samples of *Clematis tangutica*: pp – palisade and sp – spongy parenchyma.

Together with the formation of additional secondary vascular bundles by the interfascicular cambium, the primary rays split into narrower, 5–9-rowed segments. Ray parenchyma cells grow in radial direction and become orthogonal. In vascular bundles, secondary 3–5-rowed parenchymal rays are formed. Secondary thickening can be classified as *Tilia*-type (ESAU 1953; STRASBURGER et al. 1962); the same applies to *C. orientalis* (Fig. 5C). Below the mechanical ring, which is formed by protophloem and lignified parenchym, phellogen and periderm form. Periderm consists of 1 layer of phelloderm and 2 layers of phellem (in spite of 5-layered phellem in *C. orientalis*). Subsequent periderms form in deeper layers of the phloem, cutting off the non-conducting part of the phloem. Numerous periderms (up to 10 layers) alternate with died-off phloem and form thick cork which cracks, when time passes by.

High-mountain specimens of *C. tangutica* have very thin annual stems with only 6 procambium bundles and correspondingly 6 primary vascular bundles. They are separated by wide, 10–15-rowed parenchymal rays like in *A. speciosa*. Annual growth of the secondary xyleme is very small even though it consists of 6–7 layers. It is formed by longer vessel members and tracheids of considerably small diameter compared to low-mountain samples. In high-mountain samples fibres have not been found (Table 2).

The first periderm appears below protophloem fibres and consists of 1 layer of phelloderm, phellogen and 2 layers of phellem.

Perennial stems of high-mountain samples of *C. tangutica* as well as low-mountain samples have a poor growth of secondary vascular elements (7–9 layers). The annual growth of the xylem is very thin, because of the small diameter of the majority of vessel elements.

Walls of small-pored vessels and vascular tracheids have bordered pores and tertiary spiral thickenings. Beside vessel members and vascular tracheids, the xylem of the perennial stem includes fibrous tracheids and fibres. All histological elements of the xylem in the perennial

Table 2. Quantitative characteristics of xylem elements of annual stems of different ecotypes of *Clematis tangutica*, *C. orientalis* and *Atragene speciosa* (µm).

Species	Length of vessel members	Diameter of vessel members	Length of vascular tracheids	Diameter of vascular tracheids	Length of fibrous tracheids	Diameter of fibrous tracheids	Length of fibres	Diameter of fibres
<i>C. tangutica</i> low-mountain	318±81	31±7.9	268±41	12±3	294±40	14±9.4	294±17	12±1.8
<i>C. tangutica</i> high-mountain	375±90	24±8.3	352±86	9±2	343±45	16±1	–	–
<i>C. orientalis</i>	214±39	41±21	234±17	8.5±2	253±31	18±2.6	219±50	18±3.8
<i>A. speciosa</i>	343±89	30±15	289±81	14±4	316±46	6±2	–	–

stem of high-mountain ecotype are considerably shorter and narrower (Table 3) than analogous elements in the stems of low-mountain samples.

Separate vascular bundles are typical of perennial stems of high-mountain samples (Fig. 5B). Parenchyma of 8–10-rowed rays does not lignify. Cells of interfascicular cambium rarely undergo division. The cell situated in medial plane is divided two times and separates one by one the daughter cells in the direction of xylem and phloem. The cells near the bundles undergo divisions more often and form up to 3–4 layers of parenchymal cells annually. But even this process does not compensate the annual growth of the xylem, because of the ray cells which are not able to stretch in radial direction and so retain rounded outlines. This leads to the formation of schizogene air cavities. Secondary rays do not form. Secondary thickening may be characterized as simplified *Aristolochia*-type (STRASBURGER et al. 1962) or *Atragene*-type (CHUBATOVA & TIMONIN 2015). Cork includes up to 5 periderms and died layers of secondary phloem.

Discussion

It is difficult to give a definite evolutionary appreciation of the absolute size of embryos and their parts. However, formation of large, well developed seeds with differentiated embryos gives evidence for favourable life conditions of the plant. The development of relatively small

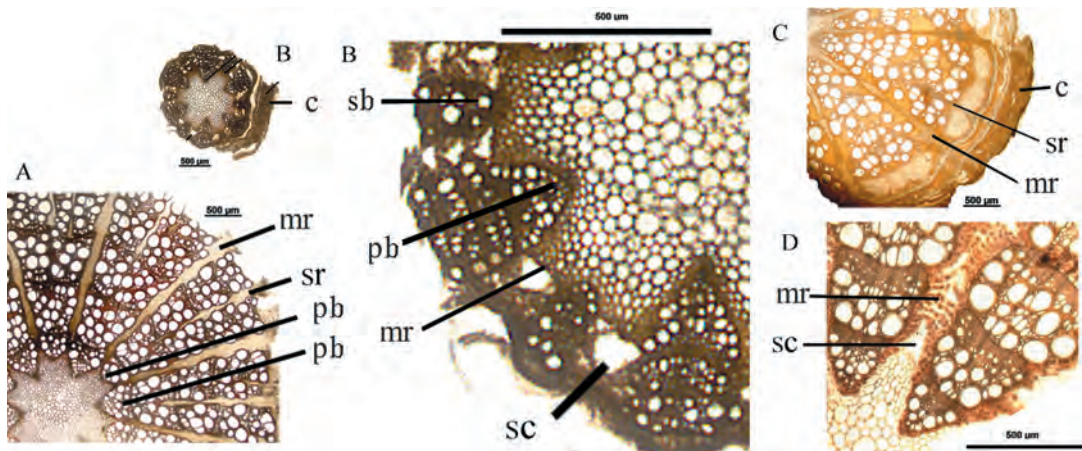


Figure 5. Anatomical structure of perennial stem of low-mountain (A) and high-mountain (B) samples of *Clematis tangutica*, (C) *C. orientalis* and (D) *Atragene speciosa*. c – cork; mr – medullary ray; sc – schizogene cavities; pb – primary bundle; sb – secondary bundle; sr – secondary ray.

Table 3. Quantitative characteristics of xylem elements of perennial stems of different ecotypes of *Clematis tangutica*, *C. orientalis* and *Atragene speciosa* (μm).

	Length of vessel members	Diameter of vessel members	Length of vascular tracheids	Diameter of vascular tracheids	Length of fibrous tracheids	Diameter of fibrous tracheids	Length of fibres	Diameter of fibres
<i>C. tangutica</i> low-mountain	200 \pm 54	115 \pm 31	246.7 \pm 77	33.3 \pm 10.4	283.3 \pm 80	16.6 \pm 3	450 \pm 120	18 \pm 3
<i>C. tangutica</i> high-mountain	172 \pm 58	36 \pm 16	198 \pm 37	13 \pm 2.4	179 \pm 24	15 \pm 2	200 \pm 33	11 \pm 3,8
<i>C. orientalis</i>	214 \pm 30	72 \pm 56	247 \pm 35	22 \pm 3.8	302 \pm 52	21 \pm 3.3	447 \pm 58	11 \pm 3.2
<i>A. speciosa</i>	245 \pm 44	31 \pm 13	280 \pm 59	14 \pm 3.2	257 \pm 42	10 \pm 3.6	225 \pm 35	7 \pm 2.8

carpelled seeds with small embryos as we can see in high-mountain samples of *C. tangutica* quietly corresponds with severe conditions of their environment.

With increase in altitude, vegetative shoots noticeably grow shorter, lose lianoid features and creep on the substrate. The zone of formation of proleptic generative shoots is shifted into the basal part of vegetative shoots. Length of generative shoots increases with altitude, but mainly at the expense of flower stalks. When approaching the upper borderline of distribution area, proleptic buds are replaced by winter buds, from which generative shoots develop during next spring. The extension of the period of generative shoot formation over two growing seasons promotes seeds ripening in conditions of short growing season. However, mature nutlets with well-developed embryos appear infrequently in high-mountain samples. As a rule, they are smaller than in low-mountain samples and have smaller embryos (Table 1). Harsh conditions also do not promote their germination, therefore seed propagation occurs rarely.

Growing at such high altitudes under intense insolation with a higher UV-radiation requires predominantly an adaptation of the whole photosynthetic apparatus. A greater extent of palisade mesophyll in high-mountain species should be considered as adaptation feature. An arrangement of chloroplasts along the vertical walls of palisade cells protects them from solar radiation influence. Formation of large cavities in the mesophyll improves frost-resistance of foliage leaves.

Sudden changes of weather invariably cause stress reactions which are revealed in the decrease of functional activity. Like in other alpine plants, cell activity decreases as a result of energetic resource mobilization to overcome the effects of unfavourable factors.

Inhibition of growth hormone synthesis and increase of inhibitor formation are very common. They cause a slowing down of plant growth by means of reduction of cell divisions and growth rates (POLEVOY 1986). Energetic and synthetic processes in plants are suppressed noticeably under stress, too (POLEVOY 2001). All changes occur as cascade processes and allow to mobilize all reserves for rapid general response to the influence of cold.

Nanism is considered to be an obvious morphological display of influence of cold on plants. In *C. tangutica*, it reveals itself in shortening of shoots, formation of small leaves and decrease of secondary thickening intensity in the stem (change of the manner of secondary thickening from *Tilia*-type to modified *Aristolochia*-type). Poor soil conditions, as the result of suppression of microflora activity by cold, and inhibition of photosynthesis due to low temperatures play a

prominent role in the formation of dwarf forms. At the same time and regardless of the cause of its formation, dwarfing gives plants a certain advantage at low temperatures. Growing in subsoil layer, they mostly warm up in summer and are protected by snow in winter. They often grow as cushion plants (Polsterpflanzen), as the result of intensive branching and slowed down growth of shoots. All of these features ensure a small supply of warmth from soil and its preservation inside the shrub.

In low doses, repeated stress facilitate the conditioning of the plant. Low temperatures cause crystallization of water in tissues. During long-term influence of frost, crystals grow up to significant size and may squeeze cell cytoplasm and damage the plasmalemma. The process of ice formation depends on water-holding capacity of tissues and on the rate of temperature decrease. If winterkill proceeds slowly, the water has time to leak from cells to intercellular space. In this case, ice crystals form outside the cells. When melting, cells stay alive. A small diameter of vascular elements, which decrease considerably the water-holding capacity of the stem, and availability of large intercellular ducts in primary rays of stem and in leaf mesophyll of *C. tangutica* increase frost-resistance of plant.

In high-altitude environments, where physiological processes are reduced and the vegetative period is short, the slowed down differentiation of cambium and its derivatives leads to the xylem of annual stem mainly consisting of primary elements. High values of average length, small diameter of vessel members and tracheids, a small amount of fibrous tracheids and a general lack of fibres indicate that fact.

Because of weak cambium activity (7–8 layers) and small diameter of its derivatives, the width of the annual ring in perennial stems remains small. In the perennial stem, unlike annual, the composition of secondary xylem is enriched with fibres. However, small length and small diameter of all elements testify to a relatively high level of xylem specialization, what corresponds with extreme environmental conditions of high-mountain ecotopes.

According to the mode of its formation, periderm of the stem of high-mountain samples resembles periderm of *Atragene*. So, the secondary thickening of stem in *C. tangutica* high-mountain ecotype may be attributed to simplified *Aristolochia*-type, but it would be better to classify it as an *Atragene*-type.

As a result, morphological and anatomical features of *C. tangutica* high-mountain ecotype display cryophilic direction of adaptogenesis in *Clematis*. Finally, it should be emphasized that the character of adaptation of *C. tangutica* to high-mountain conditions is rather similar to *Atragene*, in particular with *A. speciosa* (CHUBATOVA 2015; CHUBATOVA & CHURIKOVA 2016). In this case, the main mode of morphological evolution is retardation, too.

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