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Diversity of architectural units of *Thymus* (Lamiaceae) dwarf shrubs

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Abstract. Dwarf shrub structure was studied in the context of the modular organization of plants. The objects of study were 11 *Thymus* species of the dwarf shrub life form growing in Siberia. The architectural units representing a multi-year, monopodially-sympodially accreting compound skeletal axis and shoots of various types were distinguished in the structure of adult individuals. A monopodially accreting, branched formation shoot is an axis basis. Three variants of architectural units – orthotropic, orthotropic-plagiotropic and plagiotropic are described. It is found that dwarf shrubs may be structured on the basis of separate architectural units or their combination. An individual structure of most of studied shrub species is formed by a combination of orthotropic-plagiotropic and plagiotropic units. Diversity of formation shoots which differ in structure and length, duration of monopodial accretion and character of root development is shown. It is established that polyvariation of plagiotropic formation shoots is responsible for implicitly or obviously polycentric dwarf shrub.

Key words: architectural unit, dwarf shrub, compound skeletal axis, ecotope, *Thymus*.

Introduction

Study of plants of various life forms is very important in the context of the concept of architectural models. One of the key stages of the approach is identification of architectural units. An architectural unit (AU) is the main structural-functional unit of a concrete species containing a full range of all hierarchically subdominant structures and repetitive in the general plant architecture (Barthélémy et al. 1989, Barthelemy & Caraglio 2007). It is characterized by a certain set of features: direction of growth, arrangement of reproductive structures, pattern of accretion, arrangement of regeneration buds, the number of units of the lower level (metamer, elementary shoot, module), length and others. The characters of AU in each plant species are stable and change quantitatively according to growth conditions (Caraglio & Edelin 1990). They are currently studied mainly in trees, shrubs (Caraglio & Edelin 1990, Tortosa et al. 1996, Sabatier & Barthélémy 1999, Charles-Dominique et al. 2010, Antonova & Sharovkina 2012, Antonova & Gnilovskaya 2013, Getmanets 2015, Kostina et al. 2015, Nedoseko & Viktorov 2016, Gambino et al. 2016 and others) and partly in herbs (Notov & Kuznetzova 2004, Tumidajowicz 2005, Bartušková & Klimešová 2010, Astashenkov & Cheryomushkina 2016, Cheryomushkina & Guseva 2017, and others.). Dwarf shrubs in the context of plant modular organization have been poorly studied (Gogina 1990, Berko & Koziy 1993, Mazurenko 2008, Navarro et al. 2009, Götmark et al. 2016); we have studied this issue concerning some species of the family Lamiaceae (Kolegova 2014, Kolegova & Cheryomushkina 2012, Cheryomushkina & Guseva 2015, Talovskaya (Kolegova) 2015 and others).

Dwarf shrub life form is characteristic of *Thymus* L. species growing in hard conditions of North Asia. Their habitats are diverse and restricted to the communities of montane and plain steppes, forest-steppe, forests and tundra. Typical habitats for most of species are petrophyte, rich in herbs communities of middle or upper parts of cobble slopes and levelled hill tops. Some species (*T. jenisseensis* Iljin, *T. mongolicus* (Ronn.) Ronn. and others) elevate to the alpine belt, enter into the composition of petrophyte meadows along rocky outcrops of mountain ranges, as well as into the composition of alpine meadows in the plain sites. Study of *Thymus* species in the context of the architectural approach will permit determining a set of structural-functional units ensuring their growth in diverse ecotopes of North Asia. The aim of the work is identification of AUs in *Thymus* species of the dwarf shrub life form.

Materials and Methods

The objects of study were 11 *Thymus* species – dwarf shrubs growing in Siberia: *T. altaicus* Klok. et Schost., *T. baicalensis* Serg., *T. elegans* Serg., *T. iljinii* Klok. et Schost., *T. jenisseensis, T. minussinensis* Serg., *T. mongolicus*, *T. petraeus* Serg., *T. proximus* Serg., *T. schischkinii*, *T. sibiricus* (Serg.) Klok.). Identification of AUs was carried out in adult individuals using currently available approach to the study of plant structure (Barthélémy et al., 1989, Caraglio & Edelin 1990, Notov & Kuznetzova 2004, Barthélémy & Caraglio 2007). A module was used as a unit of the lower level repetitive in the dwarf shrub structure. The module was considered as a result of apical meristem activity since its emergence to dying off. The activity of one shoot apical meristem may continue for several years in dwarf shrub thymes. As a result, a perennial monopodially accreting shoot is formed. Here we use the shoot classification of Mazurenko and Khokhryakov (1977) based on the role of shoots in the bush structure.

According to phytocoenotic classification of Smirnova (1987) based on the pattern of spatial arrangement of shoots, regeneration buds and plant roots, a biomorph type (monocentric, implicitly polycentric and obviously polycentric) was earlier established for all model species (Talovskaya & Cheryomushkina 2017). When describing shoots the following terms are used: rosetted, rosetteless, semirosular shoots (Serebryakov 1959); formation shoot, compound skeletal axis (Mazurenko & Khokhryakov 1977); top rosetted shoot (Nukhimovskiy 1997); rosetted-top rosetted shoot (the first growth is rosetted, the next ones are top rosetted, Kolegova & Cheryomushkina 2012). Rosetted shoots of dwarf shrubs correspond to the shoots described by Serebryakov (1952), which have true leaves on the metamers with shortened internodes.

Results

The AU of *T. altaicus*, *T. baicalensis, T. elegans, T. iljinii, T. jenisseensis*, *T. minussinensis*, *T. mongolicus*, *T. petraeus*, *T.*

proximus, *T. schischkinii*, *T. sibiricus* adult individuals represents a hierarchically subordinate system consisting of a multi-year monopodially-sympodially accreting compound skeletal axis and shoots of various types. A formation shoot is perennial, it performs the function of rejuvenation of the bush shoot system and capture of a new place; serves as a basis for development of skeletal axes. It develops from a dormant or wintering bud. A branching shoot is perennial, it is intended for increase in assimilative organs (leaves, green shoots) and seed productivity. It develops mainly from wintering buds. An ephemerous shoot is annual, it performs the role of bush enrichment in assimilative and reproductive organs, does not participate in construction of a multi-year shoot system. It develops sylleptically or proleptically. Totality of formation shoots (modules) as a result of sympodial accretion represents a multi-year branched monopodially-sympodially accreting, compound skeletal axis.

Three variants of AUs distinguished by direction of growth are described (Fig. 1). AUs of thymes are characterized by the following features: direction of growth, composition; structure, length and duration of monopodial accretion of the compound skeletal axis, and rooting character. The results are presented as a table as it was recommended by Edelin (1990) (Table 1.).

Architectural unit I. The basis of AU I is orthotropic monopodially-sympodially accreting, compound skeletal axis, in which each of substituting formation shoots continues orthotropic direction of growth of the maternal shoot (Fig. 1). Formation shoots may be biennial-triennial branched rosetted, vegetative or generative (Fig. 2a). In the middle part of the axis, from dormant buds develop branched formation shoots of order n+1. They accrete monopodially for 2-3 years and match the formation shoots of the compound skeletal axis by structure and nature of branching. A distinctive feature of formation shoots of order n+1 is that they do not become the basis for axis forma- tion. Their long existence in

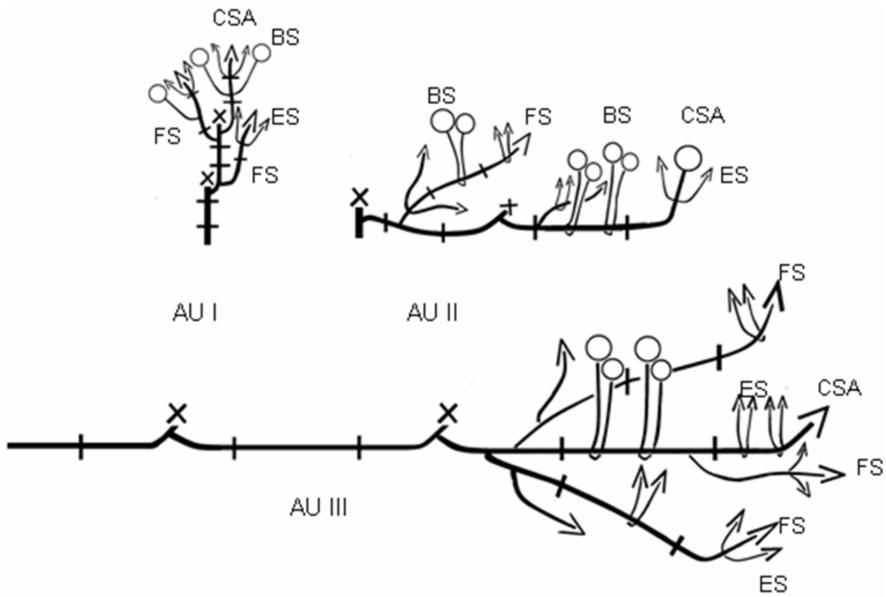

Figure 1. Aus in *Thymus* species of the dwarf shrub life form (AU – architectural unit; AU I – orthotropic, AU II – orthotropic-plagiotropic, AU III – plagiotropic; CSA – monopodially-sympodially accreting compound skeletal axis, FS – branched formation shoot of order n+1, BS – branching shoot, ES – ephemerous shoot, ✖ dead of the terminal bud of the shoot, ✚ the border of annual growth, ↑ a vegetative shoot, ♀ a generative shoot).

Table 1. Characteristic of formation shoots depending on habitat conditions

Features	Petrophyte steppes on montane tops	Steppe communities at the foot and along gentle slopes of the mountains		Steppe communities of the plains and steep montane slopes, high-mountain meadow steppes		Steppe communities on mobile substrate	
Variants AU	AU I	AU I	AU III	AU II	AU III	AU II	AU III
The number of formation shoots in the compound skeletal axis, it	2-5	2	3	3	3	3-4	3-4
Structure of formation shoots	rosetted	rosetted	top rosetted, rosetted-top rosetted	the first one – rosetted, the rest – top rosetted	top rosetted, rosetted-top rosetted	the first one – rosetted, the rest – top rosetted	top rosetted
Duration of monopodial accretion of formation shoot, yr	2-3	2-3	5	3	3	4	4
Length of formation shoots, cm	up to 2,5	2,0	up to 10	up to 6	up to 8	up to 11	up to 18

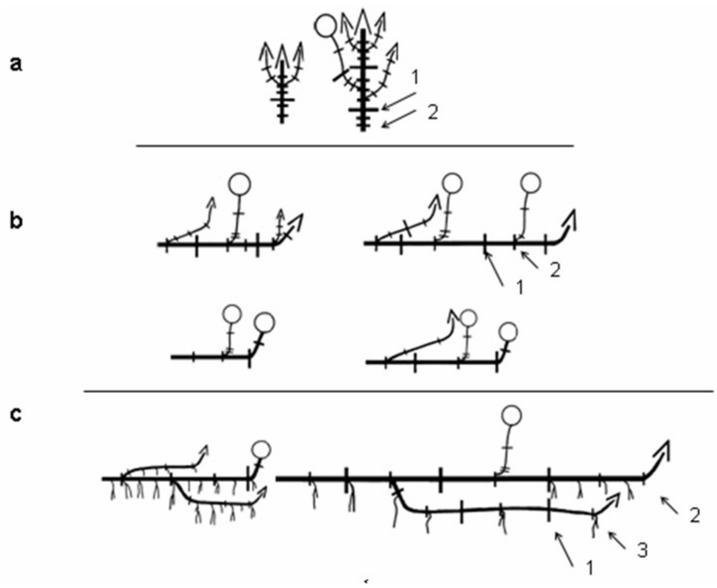

Figure 2. Diversity in formation shoots in the structure of *Thymus* AUs (1 – the border of annual growth, 2 – node, 3 – an adventitious root; a, b, c – explanation in the text, the rest of notes like in Fig. 1).

the bush structure provides a stock of regeneration buds, leads to increase in density and bush formation. An additional characteristic of formation shoots is given in the Table 1. Generative branching shoots are also a part of AU. They develop on the compound skeletal axis or on formation shoots of order n+1. By structure generative shoots can be rosetted or semirosular. One more shoot type-ephemerous shoots develop in the apical part of the compound skeletal axis and formation shoots of order n+1. A rosetted structure is usually characteristic of them. Ephemerous shoots die off together with the terminal bud of the maternal shoot in winter.

For full identification of peculiarities of AU I, we studied its development pattern in individual ontogenesis. It is established that the basis for the main compound skeletal axis becomes a primary rosetted shoot consisting of three annual growths. A change from monopodial accretion to sympodial one takes place by the 4th year as a result of dying off of the terminal bud of the primary shoot. From the lateral bud close to the point of dying off develops a substituting formation shoot which copies the maternal one. At the same time develop lateral formation shoots of order n+1. By the 5th year of development in the axis structure may appear lateral semirosular generative branching shoots. The accretion of the compound skeletal axis stops by the 7th year when its structure is formed by three shoots. The axis length may reach 10 cm. In succeeding 2th-3th years lateral ephemerous shoots develop from retained dormant buds, they die off subsequently together with the compound skeletal axis. Progressive drying of the axis takes place from the apical to the basal part by the 9th year.

Architectural unit II. The basis of AU II is a monopodially-sympodially accreting compound skeletal axis with orthotropic- plagiotropic direction of growth. A basal formation shoot has an orthotropic position on the axis, and all subsequent substitution shoots – a plagiotropic one (Fig. 1). Formation shoots are diverse in structure. The orthotropic formation shoot corresponds to formation shoots of the axis described above (Fig. 2a). Plagiotropic formation shoots are branchy, 3, 4 years old, vegetative, every annual growth is top rosular (Fig. 2b). There is also di-, tricyclic generative shoots.

Their vegetative growths occupy a horizontal position, and an annual generative shoot – a vertical one. The first in structure can be top rosular or rosetted- top rosular, the latter – rosetteless. Often in the metamer nodes at the boundary of annual growths in vegetative and generative formation shoots appear adventitious roots. In this case they represent a rooting skeletal axis. Also included in AU II are branched formation shoots of order n+1. They are settled plagiotropically, accrete monopodially for 2-3 years and unlike formation shoots of order n+1, which are a part of AU I, perform the function of capture and retention of a new territory. Generative branching shoots and ephemerous ones are identical to those described above.

AU II formation takes place on the base of a primary rosetted shoot of orthotropic direction of growth, which accretes monopodially for 3-4 years. A change of accretion occurs by the 4th-5th years. From a lateral bud the nearest to the point of dying emerges a substitution shoot which lodges at once. It accretes monopodially for 3-4 years. The following substitution shoot repeats the previous one. It is so formed the main orthotropic-plagiotropic compound skeletal axis. Lateral formation shoots of order n+1 and semirosular generative branching shoots appear in the axis structure by the 4th year. By the 7th year the compound skeletal axis attains its full development. The axis length may reach 40 cm.

Architectural unit III. The basis of AU III is a plagiotropic monopodially-sympodially accreting compound skeletal axis in which each of substituting formation shoots continues plagiotropic direction of growth of the maternal shoot (Fig. 1). Formation shoots correspond structurally to plagiotropic formation shoots of AU II (Fig. 2b). Plagiotropic shoots with longer monopodial accretion up to 5 years,

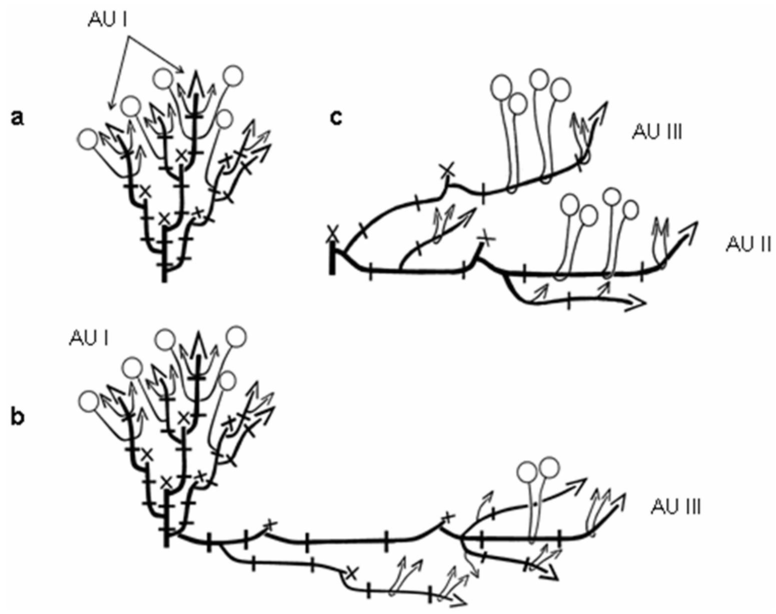

Figure 3. Combination of AUs in *Thymus* species of dwarf shrub life form (a, b, c – explanation in the text, the rest of notes like in Fig. 1).

increase in length (up to 70 cm), weak branching, intensive rooting are also revealed (Fig. 2c). Formation shoots of order n+1, generative branching shoots and ephemerous shoots are identical to those of AU II. The difference is that all diversity of AU III shoots is concentrated in the apical part of the compound skeletal axis.

In the structure of an adult individual, formation of AU III begins with development of the compound skeletal axis the basis of which is a lateral plagiotropic vegetative formation shoot. A change of monopodial accretion of the formation shoot occurs by the 3th-5th years. A substituting shoot develops like the maternal one. The plagiotropic compound skeletal axis attains its full growth by the 9th-15th years, when it represents three shoots.

Discussion

As our research shows, in different conditions of southern Siberia the individual structure of *Thymus* of the dwarf shrub life form can be formed by both separate AUs and combination of them. The individual structure of *T. baicalensis*, growing in petrophyte steppes on hill tops in moisture stress and high wind conditions, is formed by only orthotropic AUs I (Fig. 3a). An adult individual represents a monocentric aeroxylic dwarf shrub. The same type of biomorph is typical of *T. baicalensis* individuals in the steppe communities located at the foot and along gentle montane slopes. In these conditions takes place the complication of the shoot structure due to combination of AU I and AU III (Fig. 3b). A dwarf shrub assumes a trailing shape. An adult individual represents a loose shrub comprising a primary and partial bushes. The main compound skeletal axis is orthotropic and consistent with AU I. The orthotropic axes of n-order provide a basis for partial bush formation. The plagiotropic compound skeletal axes are the basis for formation of AU III. They develop from dormant buds in the basal part of the initial shoot or orthotropic compound skeletal axis of n-order. The analysis of formation shoots in the structure of AUs shows that orthotropic shoots are identical to those developing in the structure of individuals in the petrophyte steppes on hill tops. Plagiotropic formation shoots are characterized by weak rooting, mainly in the basal part, and prolonged monopodial accretion (Table 1). As a rule the individuals do not spread out vegetatively and form one center of fixation.

The combination of AUs II and III (Fig. 3c) forms the structure of most of studied species: *T. altaicus*, *T. elegans, T. iljinii, T. minussinensis, T. mongolicus*, *T. petraeus*, *T. proximus*, *T. sibiricus, T. schischkinii* growing in different ecological-coenotic conditions of southern Siberia: petrophyte variants of the steppe and meadow communities along the montane slopes, sandy steppes on deflation flat surfaces, groupings of vegetation in rock crevices; on static and mobile substrates; at 100% grassing. The adult individual represents a clump comprising a primary and partial bushes. The main compound skeletal axis is the basis for formation of AU II and the axes of n-order - for that of AU III. The analysis of formation shoots has made it possible to determine a wide range of their polyvariation which manifests itself in various habitat conditions (Table 1). So, in the steppe communities of the plains and steep montane slopes, high-mountain meadow steppes, in vegetation groupings in rock crevices, plagiotropic formation shoots branch out intensively and adventitious roots develop in the nodes at the boundary of annual growths. Weak vegetative spread and vegetative mobility are typical of the individuals. An indistinct polycentric biomorph is formed (*T. altaicus*, *T. elegans, T. iljinii, T. mongolicus*, *T. petraeus, T. proximus*, *T. schischkinii*, *T. sibiricus*). In the steppe communities, on the mobile substrate or in strong competition, the intensity of branching in plagiotropic formation shoots decreases, adventitious roots develop along the entire length both in the nodes and on the internodes. Individuals spread significantly, seize intensively a territory and correspond to a distinct polycentric biomorph (*T. iljinii,* *T. minussinensis*).

The analysis of the results obtained shows that the structure of *Thymus* dwarf shrubs growing in southern Siberia is formed by diverse AUs distinct in growth direction: orthotropic, orthotropic-plagiotropic and plagiotropic. It is established that the basis of each of them represents a monopodially-sympodially accreting compound skeletal axis consisting of the combination of monopodially accreting branched formation shoots. Besides the compound skeletal axis, various shoot types distinct in structure, duration of monopodial accretion and functional significance are identified in the composition of AUs.

Transformation of dwarf shrub architecture in southern Siberia is conditioned by dissimilar combination of AUs. In the petrophyte steppes on hill tops in moisture stress and high wind conditions, the individual structure is formed by only AU I. In the steppe communities located at the foot and along gentle montane slopes, the individual structure is formed by AUs I and III. In most of habitats: petrophyte variants of the steppe and meadow communities along the montane slopes, sandy steppes on deflation flat surfaces, groupings of vegetation in rock crevices; on static and mobile substrates; at different degree of grassing, the individual structure is formed by the combination of AUs II and III. The latter combination is typical of most of studied species.

The mechanism of morphological adaptation to the change of conditions of *Thymus* dwarf shrubs is polyvariation of formation shoot development manifesting itself in the structure and length, duration of monopodial accretion, and character of root development, which leads to emergence of monocentric, implicitly polycentric and obviously polycentric dwarf shrubs.

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