Architectural modifications that allowed *Thymus marschallianus* to spread widely in Central and North Asia

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ABSTRACT: In the conditions of climate change, when some plant species are completely disappearing, and others are forced to adapt quickly, it becomes extremely important to find the main architectural characteristics that allow plants to spread to new territories. This study demonstrated the modifications of the architecture of *Thymus marschallianus* and its relationship with the environmental conditions of Central Asia (Kazakhstan and Kyrgyzstan) and North Asia (Russia). For the first time, we tried to combine architectural and eco-morphological approaches to studying plants, which allowed us to obtain the most complete information about the morphological mechanisms of plant adaptation. The diversity of shoots and categories of axes (monopodial system of shoots and sympodial axis) were identified. The variability of monopodial system of shoots and sympodial axis modify the architecture of *T. marschallianus*. We characterized three modifications of this architecture and established their relationship with specific habitats. We found out that the basitonic branching of the monopodial system of shoots determines life form (dwarf subshrub), and the growth direction of the sympodial axes determines growth form (prostate or erect). The differences in architecture, growth forms and quantitative characteristics of sympodial axes are related to environmental conditions, particularly the cover of herbaceous plants, dead grass, and stones, as well as topography. We propose that the morphological variability of *T. marschallianus* allowed this species to spread widely in the plains and mountains of Central and North Asia.

KEY WORDS: Asia, life form, plant architecture, steppe habitat, *Thymus marschallianus*.

INTRODUCTION

Plant architecture characteristics are an important tool of functional ecology, since they demonstrate stability, spatial arrangement of plants, growth and reproduction features (Klimešova *et al*., 2019). These data will allow to determine the response of species to the main environmental gradients and their ecological strategy (Grime, 2001; Klimešova *et al*., 2018). Despite this, a number of key articles have shown that functional ecology is largely underrepresented by architectural features (Laliberté, 2017; Klimešova *et al*., 2018; Astashenkov *et al*., 2022). This is especially true for plant species with a wide range and the diverse habitat conditions, when a number of signs demonstrating the plasticity of the structure remain unexplained. When faced with this problem, the works that consider the architecture of plants depending on habitats become especially valuable (Charles-Dominique *et al*., 2012; Abdusalam and Li, 2018; Das *et al*., 2020; Irl *et al*., 2020; Talovskaya *et al*., 2020; Adji *et al*., 2021).

The architectural characteristics for some plants have already been determined and are considered to be potential indicators of phytoclimatic conditions of the ecosystem (Serebryakov, 1964; Charles-Dominique, *et al*., 2010; Millan *et al*., 2019; Subedi *et al*., 2019; Das *et al*., 2020; Talovskaya and Cheryomushkina, 2022). For example, Serebryakov (1964) proposed the growth units of shoots as one of these characteristics. In the species - *Solidago virgaurea* L., *Carex limosa* L., *Carex aquatilis*

Wahlenb., *Carex inflata* Suter, *Festuca ovina* L., *Alopecurus pratensis* L. - the number of growth units of shoots increases as plants move from the desert zone to the tundra zone - from monocyclic (when the growth cycle of shoots last one year) to bicyclic (when the growth cycle of shoots last two years). Charles-Dominique *et al*. (2010) showed that *Cornus sericea* L. characteristics, such as the growth direction and the size of the modules (monopodia, which bear short shoots and twigs laterally disposed in an acrotonic position on their growth units), and the speed of their time course changes, and their branching and flowering can be used as indicators of the light environment. By the module, the authors mean the monopodium, which bears short shoots and twigs laterally disposed in an acrotonic position on their growth units. In *Thymus vulgaris* L., Millan *et al*. (2019) described a branched complex and showed that the location of the branched complex (basitonic, mesotonic and acrotonic) depends on the habitats. In such habitats, where access to light is limited, *T. vulgaris* has acrotonic and mesotonic architecture. In habitats with large fractions of open space, thyme has a basitonic architecture. According to Das *et al*. (2020), the life form (sensu Raunkiaer, 1934) of plants can be used as an indicator of altitude in the mountains of the Western Himalayas (India). They found that the average altitude zone (1500–3000 m) favors different life forms; phanerophytes and therophytes are indicators of low altitudes, while hemicryptophytes and cryptophytes are indicators of high altitudes. Studying the architecture of

Table 1. Environmental characteristics of **Thymus marschallianus** populations.

№ Location	Topography	Cover (%)				Slope steepness	Altitude (m a.s.l.)
		herbaceous plants	dead grass	stones	bare soil		
1 Russia, Altai region, Kulunda plain, near the village of Kapustinka (53.31126 N, 80.9648 W), bunch grass steppe	flat hill top	95	58	0	0	0	122
2 Russia, Altai region, Kulunda plain, Southern shore of Lake Kuchukskoe (52.701813 N, 79.777844 W), bunch grass steppe	plain	60	30	0	10	0	98
3 Russia, Altai region, foot of Kolyvan mountain, near the village of Kharlovo, (51.71133 N, 82.81072 W), meadow steppe	flat hill top	100	25	0	0	0	265
4 Russia, Altai region, Kulunda plain, near the village of Melnikovo (53.14128 N, 79.89628 W), meadow steppe	plain	70	5	0	25	0	116
5 Russia, Altai region, Kulunda plain, valley of river Ploskaya (50.82958 N, 82.19167 W), bunch grass steppe	plain	50	20	0	30	0	381
6 Kazakhstan, Jetısu region, foot of the South slope of Dzungarian Alatau (44.41128 N, 78.21308 W), bunch grass steppe	intermountain plain	80	0	0	20	0	969
7 Kazakhstan, Jetısu region, plumes of the Southern slope of the Toksanbai ridge (44.52389 N, 79.94108 W), petrofitic bunch grass steppe	flat mountain top	40	0	40	20	0	1888
8 Kazakhstan, East Kazakhstan region, Northeast slope of Ulba ridge (50.62762 N, 81.9167 W), petrofitic meadow steppe	slope	50	10	40	0	[10–15]	254
9 Kazakhstan, East Kazakhstan region, south slope Narym ridge (48.85356 N, 83.85611 W), petrofitic bunch grass steppe	intermountain plain	50	0	45	5	0	980
10 Kyrgyzstan, Chui region, the right shore of the Kara-Balta River, the Northern slope of the Kyrgyz ridge (42.63786 N, 79.89767 W), bunch grass steppe	slope	70	0	5	25	[30–35]	1187

Note. № – number of populations; topography (flat mountain top, flat hill top, slope, intermountain plain, and plain); steepness of slope – 0°, 10° to 15° and 30° to 35°; altitude (m a.s.l.). Visual estimation of cover: herbaceous, dead grass; stones (2 mm to > 20 cm); bare soil (> 1 cm) (%).

T. diminutus Klokov, *T. dmitrieva* Gamajun, *T. karatavicus* Dmitrieva, and *T. seravschanicus* Klokov in the Tien Shan mountains (Central Asia) allowed us to determine that the branching of plants can be used as an indicator of a specific vegetation belt in the Tien Shan mountains to predict the spread of other species with similar architecture (Talovskaya and Cheryomushkina, 2022).

In this study, the dwarf subshrub (chamaephyte sensu Raunkiaer (1934)) *T. marschallianus* Willd. (Lamiaceae) was selected because it is widely distributed in Europe, Western Siberia (North Asia) and Central Asia in different habitats: steppe and forest-steppe zonas and in the steppe belt of mountains (Klokov, 1954; Jalas, 1972). For 20 years (from 2002 to 2022), we observed the development of *T. marschallianus* in different habitats in Central and North Asia. This species is characterized by a high morphological diversity. In this article, we consider the diversity of shoots, monopodial systems of shoots and sympodial axis and determine the environmental factors that lead to their changes. We hypothesize that: (*i*) basally branched (basitonic) architecture determines the type of life form, and the

growth direction of the sympodial axes determines the growth form, the (*ii*) high diversity of shoots, monopodial systems of shoots and sympodial axes may be associated with certain habitats, which may allow *T. marschallianus* to become widely distributed in Central and North Asia.

MATERIALS AND METHODS

Sampling sites

The study was carried out in Central Asia (Kazakhstan, Kyrgyzstan) and North Asia (Russia). Material was collected in the plains and mountain steppes. A total of 10 populations were studied (Table 1). We selected 25 plants in mature generative states in each population. The mature generation state was defined according to Rabotnov (1950) and Uranov (1975), and was based on previously published ontogenetic data of *T. marschallianus* (Kolegova *et al*., 2013). The plants were dug up and placed in cardboard boxes, observing the peculiarities of the axis growth direction (orthotropic, plagiotropic). The architecture was analyzed in the laboratory. The following characteristics are given for

each population: topography (flat mountain top, flat hill top, slope, intermountain plain, and plain), steepness of the slope, cover, and altitude above sea level. The cover was visually estimated (as a percentage) based on the cover of herbaceous plants, dead grass, stones, and bare soil. The altitude above sea level was determined using a global positioning system (eTrex 10, Garmin).

Life form and biomorph type

In this study, 250 plants in mature generative state (25 in each population) were analyzed. The most commonly used classification of life forms worldwide is the Raunkiaer (1934) classification, which is based on the location of hibernating buds relative to the soil. However, the Raunkiaer classification is limited when the plant life form differs in different environmental conditions (Lavorel and Garnier, 2002; Burns, 2019). In this study, the life form of the species was described in accordance with the eco-morphological approach developed by Warming (1909) and Serebryakov (1962). According to this approach, the life form is the general appearance (habitus) of a certain group of plants (including their aboveground and underground organs (shoots and root systems)). This habitus historically occurs in these soil and climatic conditions as an expression of the adaptability of plants to these conditions. The life form reflects the features of the environment, such as climate or soil through the specifics of plant growth and development in the prevailing soil-climatic and cenotic conditions. We also used the category of growth form. The growth form (structural category) such as prostatic or erect is determined by the direction of growth of the axes (Serebryakov, 1962; Vareschi, 1970).

Additionally, we used the phytocenotic approach developed by Smirnova *et al*. (2002) to characterize the spatial structure of a plant or biomorph. According to this approach, a mature plant of any life form can have one or more locations (growth centers) where the formation of shoots, roots, and renewal buds is the most active and where biomass accumulates. Three types of biomorphs have been identified. In mature plants of monocentric biomorph, the roots, shoots, and renewal buds are concentrated in a single center: the center of growth. Mature plants of explicitly polycentric biomorph are characterized by the presence of several distinct centers of concentration of the roots, shoots, and renewal buds, which are interconnected via hypogeogenic rhizomes and stolons. They act as centers of growth and are autonomous. Mature plants of implicitly polycentric biomorph have several growth centers; however, these centers develop close to each other and are difficult to distinguish.

Identification of the axis

In temperate climate, *T. marschallianus* has one growth cycle (the period between two winters), i.e., the

Table 2. Main characteristics of the axes.

Characteristics	Categories of axes		
	S	**MS**	**SA**
Development	monopodial	monopodial	sympodial
Branching	–	+	+
Growth cycle	mono-, bi- or polycyclic	mono-, bi- or polycyclic	polycyclic
Age (years)	from 1 to 3	from 1 to 3	from 2 to 8

Note. S – shoots; MS – monopodial system of shoots; SA – sympodial axis. Development: monopodial or sympodial. Branching: «+» presence or «-» absence. Growth cycle: monocyclic, the growth cycle of shoots last one year; bicyclic, the growth cycle of shoots last two years; polycyclic, the growth cycle of shoots lasts three years. Age: age of shoot, monopodial system of shoot, or sympodial axis (year).

annual shoots represent growth units (Barthélémy and Caraglio, 2007). The growth units differ in the length of the internodes. They may have either short or long internodes in the distal part, with short internodes in the form of a rosette or inflorescence. The shoots can undergo several growth cycles and contain several growth units. The border between the growth units on the axis comprises short internodes.

The identification of axes requires the observation of several characteristics: growth cycle (monocyclic: the growth cycle of shoots last one year; bicyclic: the growth cycle of shoots last two years; polycyclic: the growth cycle of shoots last three years), development (monopodial or sympodial), branching (presence or absence) and age (Serebryakov, 1959; Barthélémy and Caraglio, 2007). Shoots (S), a monopodial system of shoots (MS) and sympodial axis in the architecture of *T. marschallianus* were identified (Figure 1, Table 2). Shoots consist of a main stem and orthotropic growth direction. Reproductive shoots end distally with an inflorescence and vegetative shoots never flower and ends with a vegetative bud. The monopodial system of shoots consists of a main stem, branches and a monopodial system of shoots of the n+2 order that develops along the entire main stem. The main stem ends distally with an inflorescence or vegetative bud. After fruiting (or the death of the terminal bud), one of the monopodial systems of shoots of the n+2 order develops the most. The sympodial axis is formed as a result of the basitonic branching of the monopodial system of shoots. The sympodial axis branches and includes all categories of axes: sympodial axes of the n+2 order, monopodial systems of shoots and single shoots. Sympodial axes have adventitious roots.

To characterize the quantitative indicators of sympodial axes of the n + 1 order in 25 individuals of mature generative state in each population, one axis was selected according to the following criteria: 1) the axis develops from the lateral bud of the primary shoot; by the onset of the mature generative state, the sympodial axis
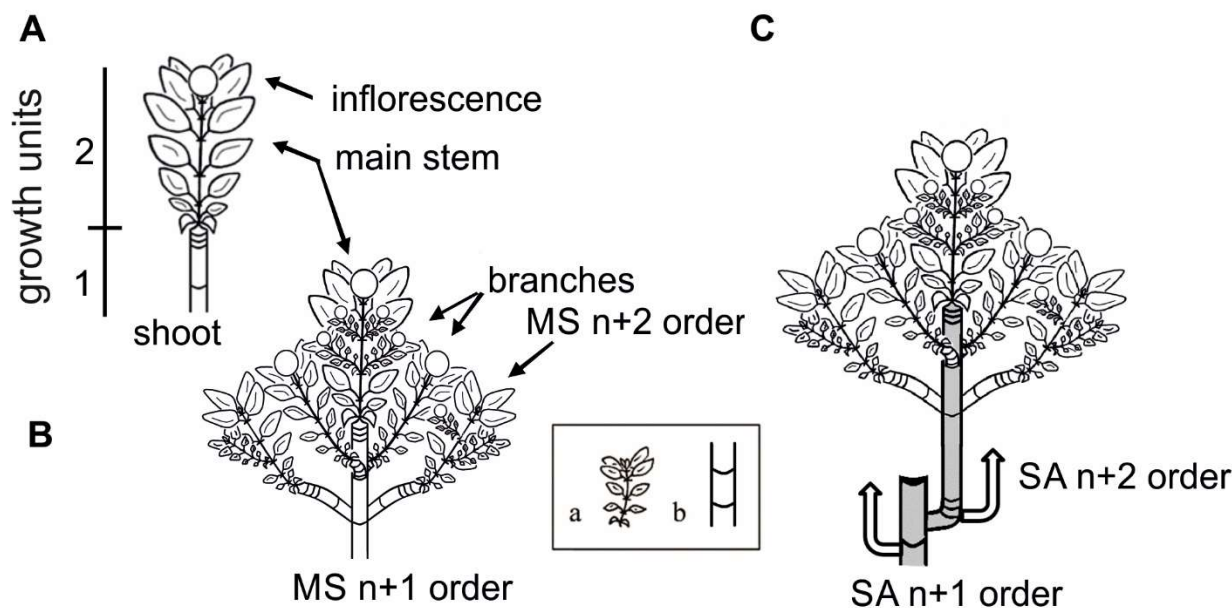
Fig. 1. Axes of *Thymus marschallianus*. Shoots consist of a main stem **A**. Monopodial system of shoots (MS n + 1 order) consists of a main stem, branches, and monopodial system of shoots of the n + 2 order (MS n + 2 order) **B**. The sympodial axis (SA n + 1 order) consists of all axis categories: shoots, monopodial system of shoots of the n+2 order, and sympodial axes of the n + 2 order (SA n + 2 order, arrow). **a**, Herbaceous part of the shoot; **b**, lignified perennial part of the shoot or axis; dark color, sympodium.

carries all categories of axes. 2) The axis has a plagiotropic direction of growth, since this axis persists for a long time in the bush structure and is involved in the formation of the biomorphs (spatial structure) of plants.

The quantitative characteristics of the sympodial axes were characterized in populations 1–6 and 10. In populations 7–9, there were no plagiotropic sympodial axes in individuals. The following quantitative characteristics were selected: length and age, number of SAs n + 2 order and adventitious roots. When measuring the length of the sympodial axis, the plagiotropic lignified sympodial part and the annual orthotropic herbaceous shoot were taken into account. The age of the sympodial axis was determined by annual rings (Esau, 1977) using a Carl Zeiss SteREO Discovery V12 stereomicroscope with an AxioCam HRc camera (Germany).

Statistical analysis

The similarity habitats of populations were assessed using the following criteria: type of steppe; herbaceous cover, dead grass, stones, and bare soil; and topography, and steepness of the slope. The analysis was carried out via clustering (Ward's method). Using the Statistics 10 software package, a dendrogram of habitat similarity was constructed. Based on big data collected for different Asian *Thymus*, we found that climatic factors such as temperature, precipitation and relative humidity do not correlate with their morphological characteristics of *Thymus* (Talovskaya and Cheryomushkina, 2022), therefore, these parameters were not considered for the analysis of the species.

The average values and a confidence interval of all quantitative characteristics (length and age, number of SAs n + 2 order and adventitious roots) of 25 plagiotropic sympodial axes in populations 1–6 and 10 (n = 7) were calculated. We used one-way ANOVA to find out what environmental factors (topography, slope steepness, cover (herbaceous, dead grass, stones, bare soil), height above sea level) in populations 2, 4–6 and 10 (n = 5) were associated with characteristics of the plagiotropic sympodial axes (the P value for the *F* coefficient was less than 0.05) (Glantz, 1998).

RESULTS

Variations of shoots

Three types of shoots were found that differed in the number and structure of growth units, growth direction and features of flowering (some of them never flowering). The growth cycle of shoots can last one (monocyclic), two (bicyclic) or three (polycyclic) years (Figure 2).

S1. Monocyclic vegetative and reproductive shoots had one growth unit and an orthotropic growth direction. Vegetative shoots were short or long (Figure 2 a, b). Reproductive shoots ended in inflorescence (Figure 2 c). Shoots developed syllepsis in the apical parts of the main stem. Monocyclic vegetative and reproductive shoots are ephemeral shoots found in herbaceous plants that completely die off in winter.

S2. Bicyclic vegetative or reproductive shoots had an orthotropic growth direction, consisting of two growth units. The first growth unit was a short or long, it lignified
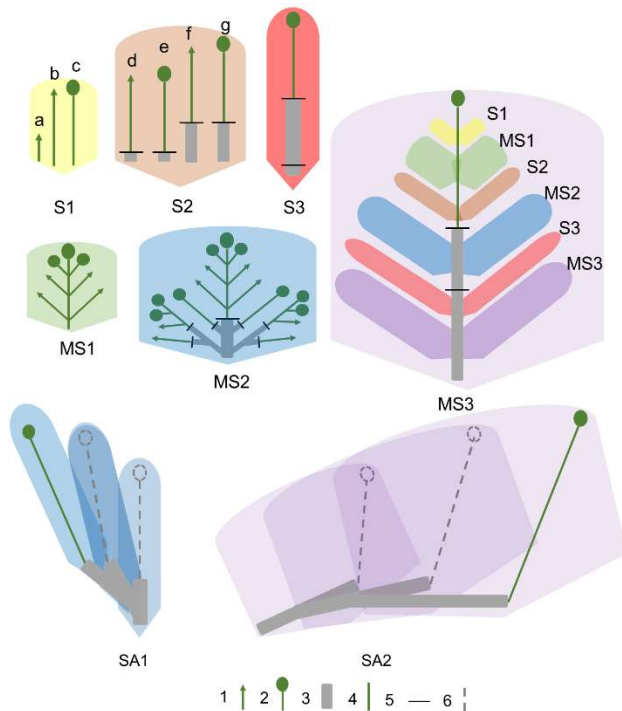
Fig. 2. Variations of the axes. **S1**, monocyclic shoots: a-short shoot, b-long shoot, c-reproductive shoot; **S2**, bicyclic shoots: d, e-first growth unit is short, second-long, vegetative or reproductive; **S3**, polycyclic shoot-first growth unit is short, second-long, and third-long, reproductive. **MS1**, 1-year monopodial system of shoot; **MS2**, 2-year monopodial system of shoot; **MS3**, 3-year monopodial system of shoot. **SA1**, orthotropic sympodial axis; **SA2**, plagiothropic sympodial axis. 1-vegetative shoot, 2-reproductive shoot, 3-lignified part, 4-herbaceous part, 5-border between growth units, 6-dead part.

and remained in winter. The second growth unit was herbaceous, vegetative (Figure 2 d, f) or reproductive (Figure 2 e, g). These shoots proleptically developed in the middle part of the main stem.

S3. Polycyclic reproductive shoots grew for three years and consisted of three growth units: the first was short and completely lignified, the second was long and completely lignified, and the third was herbaceous and reproductive. Polycyclic reproductive shoots proleptically formed in the proximal or middle parts of the main stem and had a plagiotropic growth direction. Often, polycyclic reproductive shoots had an anisotropic growth direction. When the first and second growth units were plagiotropic, the third was orthotropic.

Variations monopodial system of shoots

Monopodial systems of shoots differed depending on the growth cycle of the main stem (Figure 2).

MS1: 1-year monopodial system of shoots. Branches are monocyclic vegetative or reproductive shoots (S1). In winter, they completely die off. In some habitats (CP 1 and 3), the proximal part of the main stem becomes woody and persists in winter.

MS2: 2-year monopodial system of shoots. Branches are monocyclic (S1) or bicyclic (S2) vegetative or reproductive shoots. Branches S1 and the 1-year MS1 of the n + 2 order developed sylleptically (acrotonic branching of the main stem). Branches S2 and 2-year MS2 of the n + 2 order developed proleptically (mesotonic and basitonic branching of the main stem). In winter, S1 and 1-year MS1 of the n + 2 order die off completely, and the herbaceous annual shoots of S2 and 2-year MS2 of the n + 2 order also die. The lignified parts of main stem and lateral axes are preserved and become perennial.

MS3: 3-year monopodial system of shoots. Branches are monocyclic (S1), bicyclic (S2) or polycyclic (S3) vegetative or reproductive shoots. S1 and 1-year MS1 of the n + 2 order developed sylleptically; S2 and 2-year MS2 of the n + 2 order developed mesotonically, and S3 and 3-year MS3 of the n + 2 order developed basitonically. In winter, the lignified part of the main stem was preserved, as well as lignified parts S2, S3, 2-year MS2 of the n + 2, and 3-year MS3 of the n + 2 order.

Variations of sympodial axes

There were two types of sympodial axes in the architecture of *T. marschallianus*: orthotropic SA1 and plagiotropic SA2 (Figure 2). Orthotropic SA1 developed in the time period from 2 to 5 years and contributed to the compaction of the bush, plagiotropic SA2 developed from 3 to 8 years, its provided seizure of new areas of the territory. Plagiotropic SA2 formed partial bushes. Sympodial axes die off gradually, beginning in the distal part. As a general rule, orthotropic SA1 die off completely, and in plagiotropic SA2, the proximal parts with dormant buds are preserved, subsequently unfolding in an old form.

Architectural modifications of *Thymus marschallianus* in different environmental conditions

The high diversity of axes contributes to the diversity of the architecture of *T. marschallianus* on the whole. We identified three architectural modifications (Table 3; Figure S1). *T. marschallianus* with the same architecture was found in the same conditions. Using cluster analysis, we distinguished the habitats of populations depending on the type of steppe, herbaceous cover, dead grass and stones, topography (Figure 3). The first cluster united populations 7–9. Their habitats were confined to petrophytic steppes located on a slope, a flat mountain top and an intermountain plain. The common factor among these habitats was the high cover of stones (40–45%). Under these conditions, the architecture of *T. marschallianus* corresponded to modification III.

The habitats of populations 1–6 and 10 united in the second cluster, in which two subclusters were distinguished. The first subcluster united populations 1 and 3. Their merging in the dendrogram occurred earlier

Table 3. Modifications of the *Thymus marschallianus* architecture.

Modification	Shoot			Monopodial system of shoots			Sympodial axis	
	S1	S2	S3	MS1	MS2	MS3	SA1	SA2
I	+	+	+	+	+	+	+	+
II	+	–	–	+	–	–	+	+*
III	+	+	–	+	+	–	+	–

Note. Shoots: S1 – monocyclic shoot; S2 – bicyclic shoot; S3 – polycyclic shoot. Monopodial system of shoots**:** MS1 – 1-year monopodial system of shoots; MS2 – 2-year monopodial system of shoots; MS3 – 3-year monopodial system of shoots. Sympodial axis: SA1 – orthotropic sympodial axis; SA2 – plagiotropic sympodial axis. I, II, III, modifications of architecture; «–», absence; «+» presence; «+*» axis is rare.
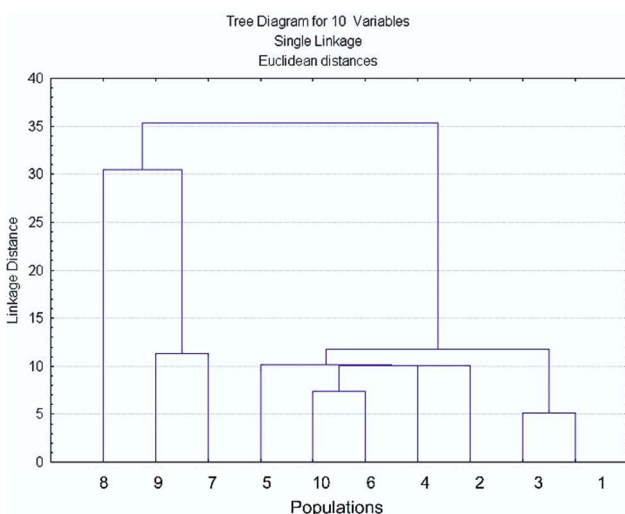

Fig. 3. Dendrogram of the similarity of habitats of *Thymus marschallianus* populations. Depending on the type of steppe, the cover of herbaceous, dead grass and stones, topography, three clusters of habitats united. The first cluster unites populations 7–9. The second cluster unites populations 1–6 and 10, in which two subclusters are distinguished: the subcluster with populations 2–6 and 10; and the subcluster with populations 1 and 3.

than the others, indicating a greater similarity with each other. The habitats of these populations were steppe with a high cover of herbaceous plants (95–100%) and of dead grass (25–58%). Under these conditions, the architecture of *T. marschallianus* corresponded to modification II.

Populations 2, 4–6 and 10, whose ranges were mainly confined to steppes with up to 50–80% herbaceous coverage, were located in the second subcluster. The similarity of these conditions is demonstrated in parameters such as the cover of herbaceous plants (up to 70%) and stones (up to 5%). Under these conditions, the architecture of *T. marschallianus* corresponded to modification I.

Correlation between *Thymus marschallianus* sympodial axes quantitative characteristics and environmental conditions

We investigated whether environmental factors influence the variability of signs of the plagiotropic

Table 4. Characteristics of plagiotropic symodial axes of the n+1 order.

№	Modification	Length (cm)	SA n + 2 order (it.)	AR (it.)	Age (year)
1	II	29.9 ± 0.4	1.2 ± 0.3	11.1 ± 0.2	3.3 ± 0.3
		24–42	1–2	9–13	3–4
2	I	25.6 ± 0.7	2.0 ± 0.1	3.8 ± 0.6	4.5 ± 0.6
		15–40	1–6	2–8	3–6
3	II	36.8 ± 0.9	1.1 ± 0.2	15.5 ± 1.6	5.1 ± 0.6
		26–42	1–2	3–19	4–6
4	I	17.3 ± 0.8	5.1 ± 1.4	10.1 ± 2.9	6.5 ± 0.8
		11–25	2–10	3–20	4–8
5	I	17.0 ± 0.9	2.1 ± 0.4	9.0 ± 0.9	4.4 ± 0.3
		13–21	1–3	4–18	4–5
6	I	22.0 ± 0.3	2.4 ± 0.7	7.6 ± 0.7	3.2 ± 0.2
		14–36	1–9	2–22	3–4
10	I	12.9 ± 0.8	3.1 ± 0.7	1.7 ± 0.7	4.1 ± 0.8
		6–20	1–10	1–3	3–6

Note. № - number of populations. Modification **-** modification of architecture. Length of the plagiotropic SA (cm). SA n + 2 order **-** number of symodial axes of the n + 2 order (it.). AR **-** number of adventitious roots (it.). Age **-** age of symodial axis (year). Data are presented in the numerator as mean ± standard deviations and in the denominator as minimum–maximum values.

symodial axes. The analysis revealed the influence of environmental factors such as topography ($F = 11.57$; $p = 0.002$), cover of stones ($F = 16.97$; $p = 0.01$) and cover herbaceous ($F = 43.12$; $p = 0.03$) on the length of plagiotropic symodial axes only, other environmental factors (slope steepness, cover of dead grass, cover of stones and bare soil, height above sea level) were not significant for other characteristics of the plagiotropic symodial axes.

Variation quantitative characteristics *Thymus marschallianus* symodial axes in different environmental conditions

The testing characteristics of plagiotropic SA n + 1 order (length and age, number of SA n + 2 orders and adventitious roots) in *T. marschallianus* with modifications I and II of architecture showed their differences (Table 4).

In *T. marschallianus* with modification I of architecture (population 2, 4–6, 10), the length of plagiotropic SA on average reached 25.6 cm. Differences in habitat preferences for *T. marschallianus* with modification I of architecture were evident from correlations between length of plagiotropic SA with environmental factors of topography, cover of stones and cover of herbaceous plants. The average values of the length of plagiotropic SA increased on the plains (including the intermountain plain) with a low value cover of stone and cover of herbaceous plants. The intense branching of plagiotropic SA was determined: the number of SAs n + 2 order showed the largest of magnitude; it reached 5.1 on average. Along the entire length of the lignified part, SA was rooted by adventitious roots. Their number on the axis reached an average of 10.1. Symodial axes were characterized by continuous growth in all populations. On average, the age of axis

ranged from 3.2 to 6.5 years.

T. marschallianus with modification II of architecture (population 1, 3), the length of plagiotropic SAs was the greatest importance due to the long last orthotropic annual Unlike plants with modification I of architecture, plants with modification II, SAs were characterized by the lowest values of the number of plagiotropic SA of the n + 2 order. The accumulation of dead grass (cover 25–58%) and herbaceous cover hindered the development of plagiotropic ASs; their number did not exceed 1.2 on average. On the contrary, plagiotropic SA had the highest number of adventitious roots: up to 15.5 on average. Adventitious roots were usually thin and developed in the proximal part of the sympodial axis.

DISCUSSION

T. marschallianus in Central and North Asia is characterized by a high diversity of architecture. The variety of shoots is related to the number and structure of growth units, growth direction, and flowering characteristics. Their main role in plant life is assimilation and seed propagation (for reproductive shoots). The lignified parts of polycyclic shoots remain after fruiting and become perennial. In this case, it takes part in the construction of the long-term basis of *T. marschallianus*. The monopodial system of shoots corresponds to the module previously characterized when we studied species of *Thymus*, a common species distributed in the Tien Shan mountains (Central Asia) (Talovskaya and Cheryomushkina, 2022). The repetition of this structure in other species of *Thymus* in different habitats indicates its universality and great importance to plant life. The lignified part of the monopodial system of shoots is the basis for the further construction of the sympodial axis. A similar structure was characterized by Millan *et al.* (2019) for *T. vulgaris* L. and called the "branched complex", which is composed of a dichasial succession of modules. They proposed the use of the type branching of branched complexes (basitonic, mesotonic and acrotonic) to describe the «shrub-like» and «bush-like» growth forms of chamaephytes or woody plants with a dwarf body. Our study shows that *T. marschallianus* is characterized by basitonic branching and it determines not the growth form, but the life form of the dwarf subshrub (Warming, 1909; Serebryakov, 1962). We previously described this fact in other Asian species of *Thymus*, such as *T. brevipetiolatus* Cáp, *T. diminutus* Klokov, *T. dmitrievae* Gamajun, *T. extremus* Klokov, *T. indigirkensis* Karav., *T. jenisseensis* Iljin, *T. karatavicus* Dmitrieva, *T. pavlovii* Serg., and *T. seravschanicus* Klokov (Talovskaya *et al.*, 2019; 2020; Talovskaya and Cheryomushkina, 2022). The growth form of *T. marschallianus* is determined by the growth direction of the sympodial axes. Modifications I and II of architecture with orthotropic and plagiotropic sympodial axes constitute a prostatic growth form, or "trellis" plant

(Serebryakov, 1962; Vareschi, 1970). Modification III of the architecture, which only has orthotropic sympodial axes, is an erect or shrub-like growth form.

Earlier, Gogina (1990) and Cibanova (1977) described the structure of *T. marschallianus*, which is widespread in the lowland communities of the European part of Russia. They described the plant as a compact clone consisting of primary bush and closely spaced partial bushes. The biomorph type is monocentric. We compared our data and determined that Asian *T. marschallianus* individuals form longer plagiotropic sympodial axes reaching 40 cm. In the rooting parts of the axis, partial bushes develop, which are located much further from the primary bush, and a loose clone is formed. Thus, unlike the data of Gogina (1990) and Cibanova (1977), the spatial structure of *T. marschallianus* is not monocentric, but implicitly polycentric. This modification of the architecture allows *T. marschallianus* to spread on plains, in steppes with a covering of herbaceous up to 50-80%, a slight covering of stones (up to 5%) and the absence of dead grass. Statistical analysis revealed a positive relationship between the characteristics of the plagiotropic sympodial axis (length and age, number of SA n + 2 orders) and environmental conditions. Modifications II and III of architecture are given by us for the first time and are formed in the species of *Thymus* only in the Asian part of the range. Plants with the II modification of architecture have mastered the growing conditions, which are characterized by a high coverage of herbaceous plants (up to 90%) and withered grass. In *T. marschallianus* individuals, long orthotropic herbaceous shoots are formed, the intensity of branching and the duration of growth of the sympodial axes are decreased. *T. marschallianus* plants with modification III grow in petrophytic steppes located on a slope, a flat mountain peak and an intermountain plain. The absence of a free substrate, a large number of stones (40–45%) prevent the overgrowth of *T. marschallianus*. There are no plagiotropic sympodial axes in the structure of individuals, the primary bush persists throughout its life. *T. marschallianus* with modifications II and III of its architecture is a monocentric biomorph type.

Comparing the modifications of *T. marschallianus* architecture, we come to the conclusion that modification I manifests itself much more often than the others. On the one hand, this is due to the phytocenotic preferences of the species, namely flat steppes with a grassy surface of up to 50-80% are most typical for the species in the Asian part of its range. On the other hand, modification I is the most advantageous, since an implicitly polycentric biomorph is formed. The individual forms several growth centers that allow it to occupy new territories and receive more resources from the environment.

In demonstrating the diversity architecture of *T. marschallianus*, it is clear that none of the models described by Hallé *et al.* (1978) are suitable for describing

the dwarf subshrub *T. marschallianus*, combining the sympodial development of the main and lateral axes, basitonic branching, plagiotropic and orthotropic growth direction of the axis, and terminal position of inflorescences. To some extent, the sympodial version of the Scaronne model, also proposed for the *T. hyemalis* Lange shrub (Navarro *et al.*, 2009), corresponds to modification III of architecture *T. marschallianus* but does not reflect basitonic branching. Often, in cases where architectural features of a particular type do not fit into one of the architectural models, its variants are described or a new model is highlighted (Hallé, 2004; Bartha, 2011). This trend is increasingly observed in the study of dwarf shrubs and dwarf subshrubs (Gambino *et al.*, 2016). Thus, the architectural model of *T. marschallianus* is a model of a perennial dwarf subshrub with a sympodial development of the main and lateral axes, basitonic branching and terminal position of inflorescences. We propose distinguishing, depending on the direction of growth of the sympodial axes, submodel **A** with an orthotropic growth direction (modification III of the architecture) and submodel **B** with an orthotropic and plagiotropic growth direction (modifications I and II of architecture).

Currently, the question of the evolution of morphological features of *Thymus* is becoming more and more relevant (Gogina, 1990; Millan *et al.*, 2019). In this regard, it is necessary to understand what permanent and fundamentally important signs for the genus appear in species in different habitat conditions. Using the architectural analysis of *T. marschallianus* we have identified a variety of architecture, growth forms and differences in the quantitative characteristics of the sympodial axes, which should be considered as features of its evolutionary transformations, which allowed the species to spread widely not only on the plains, but also in the mountain communities of Central and Northern Asia. At the same time, the ability to modify architecture increases the likelihood of *T. marschallianus* surviving in changing environmental conditions.

AUTHOR CONTRIBUTIONS

Conceptualization, E.T. and V.C.; methodology, E.T. and V.C.; software, E.T.; validation, E.T., V.C. and A.A.; formal analysis, E.T.; investigation, E.T.; resources, E.T., V.C. and A.A.; data curation, E.T.; writing - original draft preparation, E.T.; writing - review and editing, E.T., V.C. and A.A.; visualization, E.T.; supervision, A.A.; project administration, E.T.; funding acquisition, V.C. All authors have read and agreed to the published version of the manuscript.

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LITERATURE CITED

Abdusalam, A., Li, O. 2018 Morphological plasticity and adaptation level of distylous *Primula nivalis* in a heterogeneous alpine environment. Plant Divers. **40(6)**: 284–291.

Astashenkov, A. Yu., Godin, V. N., Cheryomushkina, V. A., Talovskaya, E. B. 2022 Analisis of functional traits and the structure of their relationships in the coenopopulations of *Panzerina lanata* (Lamiaceae). Botanicheskii Zhurnal. **107(6)**: 544–560.

Bartha, D. 2011 Architectural models and types of the woody plants in the Pannonian Basin. Acta Bot. Hungarica. **53(3-4)**: 215–224.

Barthélémy, D. 2003 Botanical background for plant architecture analysis and modeling. In: Hu, B.-G., Jaeger, M. (eds.), Plant Growth Modeling and Applications. The First International symposium on plant growth modeling, simulation, visualization and their applications. Tsinghua University Press, Beijing China, pp.1–20.

Barthélémy, D., Caraglio, Y. 2007 Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Ann. Bot. **99(3)**: 375–407.

Burns, K.C. 2019 Evolution in Isolation: the search for an island syndrome in plants. Cambridge University Press, Cambridge. 226pp. doi:10.1017/9781108379953

Caraglio, Y., Pimont, F., Rigolot, E. 2007 *Pinus halepensis* Mill. architectural analysis for fuel modelling. In: Leone, V. Lovreglio, R. (eds.) Proceedings of the international workshop MEDPINE 3: conservation, regeneration and restoration of Mediterranean pines and their ecosystems, ser. A., vol. 75. Ciheam, Bari, Italy, pp.43–59. http://om.ciheam.org/om/pdf/a75/00800314.pdf

Charles-Dominique, T., Edelin, C., Bouchard, A. 2010 Architectural strategies of *Cornus sericea*, a native but invasive shrub of Southern Quebec, Canada, under an open or a closed canopy. Ann. Bot. **105(2)**: 205–220.

Charles-Dominique, T., Edelin, C., Brisson, J., Bouchard, A. 2012. Architectural strategies of *Rhamnus cathartica* (Rhamnaceae) in relation to canopy openness. Botany **90(10)**: 976–989.

Cibanova, N.A. 1977 Life cycle and age structure of the coenopopulations of *Thymus marschallianus* Willd. (Lamiaceae) in the Northern steppe (Kursk region). Botanicheskii Zhurnal **6(1)**: 101–105.

Das, D.S., Rawat, D.S., Maity, D., Dash, S.S., Sinha, B.K. 2020 Species richness patterns of different life-forms along altitudinal gradients in the Great Himalayan National Park, Western Himalaya, India. Taiwania **65(2)**: 154–162.

Esau, K. 1977 Anatomy of Seed Plants, 2nd ed. Wiley, New York, USA. 550pp.

Frolov, P.V., Zubkova, E.V., Shanin, V.N., Bykhovets, S.S., Mäkipää, R., and Salemaa, M. 2020 CAMPUS-S – The model of ground layer vegetation populations in forest ecosystems and their contribution to the dynamics of carbon and nitrogen. II. Parameterization, validation and simulation experiments. Ecol. Model. **431**: 109183.

Gambino, S., F. Ratto, F., and Bartoli, A. 2016 Architecture of the genus *Gutierrezia* (Asteraceae: Astereae, Solidagininae). Bol. Soc. Argent. Bot. **51(4)**: 657–663.

Glantz, S.A. 1998 Primer of Biostatistics (translated from English into Russian), 4th ed. Praktika Press, Moscow, Russia.

Grabherr, G. 2003 Alpine vegetation dynamics and climate change – a synthesis of long-term studies and observations. In: Grabherr, G. *et al*. (eds.), Alpine Biodiversity in Europe Vol. 167. Springer, Berlin, Heidelberg Germany, pp.399–409.

Grime, J.P. 2006 Plant Strategies, Vegetation processes, and Ecosystem properties. John Wiley & Sons, UK.

Gogina, E.E. 1990 Variability and morphogenesis in the genus *Thymus* L. Nauka, Moscow, Russia. 208pp.

Guo, Y., Fourcaud, T., Jaeger, M., Zhang, X., Li, B. 2011 Plant growth and architectural modelling and its applications. Ann. Bot. **107(5)**: 723–727.

Hallé, F. 2004. Architectures de Plantes. Francis. Publisher, Montpellier, France. 180pp.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B. 1978 Tropical trees and forests. An architectural analysis. Springer-Verlag Berlin, Heidelberg New York. 444pp.

IPCC. 2014 Climate Change 2014: Synthesis report: Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva, Switzerland. Available from https://www.ipcc.ch/report/ ar5/

Irl, S.D.H., Obermeier, A., Beierkuhnlein, C., Steinbauer, M.J. 2020 Climate controls plant life-form patterns on a highelevation oceanic island. J. Biogeogr. **47(10)**: 2261–2273.

Jalas, J. 1972 *Thymus* L. In: Tutin, T.G. *et al*. (eds.) Flora Europaea: Diapensiaceae to Myoporaceae. Vol. 3. Cambridge University Press, Cambridge, UK, pp.172–182.

Klimešová, J., Martínková J., Herbenb T. 2018 Horizontal growth: An overlooked dimension in plant trait space. Perspectives in Plant Ecology, Evolution and Systematics. **32**: 18–21.

Klimešová, J., Martínkováa J., Pausasc J.G., Moraesd M.G., Herbenb T., Yuf F.-H., Puntierih J., Veskj P.A., Belloa F., Janečeka Š., Altmana J., Appezzato-da-Glóriam B., Bartuškováa A., Crivellaron A., Doležala J., Ottp J. P., Paulaq S., Schnablováe R., Schweingrubers F.H., Ottaviania G. 2019 Handbook of standardized protocols for collecting plant modularity traits. Perspectives in Plant Ecology, Evolution and Systematics. **40**: 125485.

Klokov, M.V. 1954 Genus 1299. Thyme – *Thymus* L. In: Schischkin, B.K. (ed.) Flora of the USSR. Vol. 21. Publishers of the Academy of Sciences of the USSR, Moscow & Leningrad, St. Petersburg, pp. 470–591.

Kolegova, E.B., Cheryomushkina, V.A., Makunina, N.I., Bystrushkin, A.G. 2013 Ontogenetic structure and status assessment of *Thymus marschallianus* (Lamiaceae) coenopopulations in South Ural and Altai. Rastitelnye Resursy **49(3)**: 341–352.

Körner, C. 1992 Response of alpine vegetation to global climate change. Catena. Supp (Giessen) **22**: 85–96.

Laliberté, E. 2017 Below-ground frontiers in trait-based plant ecology. New Phytol. **213(4)**: 1597–1603.

Lavorel, S., Garnier, E. 2002 Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct. Ecol. **16(5)**: 545–556.

Millan, M., Rowe, N.P., Edelin, C. 2019 Deciphering the growth form variation of the Mediterranean chamaephyte *Thymus vulgaris* L. using architectural traits and their relations with different habitats. Flora **251**: 1–10.

Nagy, L., Grabherr, G. 2009. The Biology of Alpine Habitats. Oxford University Press, Oxford. 336pp.

Navarro, T., Pascual, V., Cabezudo, B., Alados, C. 2009 Architecture and functional traits of semi-arid shrub species in Cabo de Gata Natural Park, SE Spain. Candollea **64**: 69–84.

Orlovsky, N.S., Zonn, I.S., Kostianoy, A.G., Zhiltsov, S.S. 2019 Climate change and water resources in Central Asia. The Herald of the Diplomatic Academy of the MFA of Russia. Russia & World **1**: 57–75.

Rabotnov, T.A. 1950 Life cycle of perennial grasses in meadow coenosises. In: Proceedings BIN AN SSSR., pp. 179–196.

Raunkiaer, C.C. 1934 The life-forms of plants and statistical plant geography: Being the collected papers of C. Raunkiaer. Clarendon Press, Oxford, U.K.

Serebryakov, I.G. 1959 Types of development of shoots in herbal perennial plants and their formation factors. Uchenye Zapiski Moskovskogo Gosudarstvennogo Pedagogicheskogo Instituta. Voprosy biologii rastenii **100(5)**: 3–38.

Serebryakov, I.G. 1962 Ecological Morphology of Plant. Vyshaya Shk., Moscow, Russia. 378pp.

Serebryakov, I.G. 1964 Comparative analyses of some rhythm peculiarities of the seasonal development of plants in different botanic and geographic zones of the USSR. Bull. Mosc. Soc. Natur. Biol. Ser. **69(5)**: 62–75.

Smirnova, O.V., Palenova, M.M., Komarov, A.S. 2002 Ontogeny of different life forms of plants and specific features of age and spatial structure of their populations. Russ J. Dev. Biol. **33(1)**: 1–10.

Subedi, S.C., Ross, M.S., Sah, J.P., Redwine, J., Baraloto, C. 2019 Trait-based community assembly pattern along a forest succession gradient in a seasonally dry tropical forest. Ecosphere **10(4)**: e02719.

Talovskaya, E., Cheryomushkina, V. 2022 Morphological variations of *Thymus* L. in the vegetation belts of the Tien Shan mountains (Central Asia). Botany **100(6)**: 499–508.

Talovskaya, E.B., Cheryomushkina, V. A., Barsukova, I.N. 2020 Architecture of the dwarf shrub *Thymus petraeus* (Lamiaceae) in the conditions of Southern Siberia. Contemp. Probl. Ecol. **13(1)**: 85–94.

Uranov, A.A. 1975 The age spectrum of coenopopulations as a function of time and energy wave processes. Biol. Sci. **2**: 7–34.

Vareschi, V. 1970 Flora de los Páramos de Venezuela. Universidad de Los Andes, Mérida, Venezuela. 429pp.

Warming, E. 1909 Oecology of Plants. Clarendon Press, Oxford. 422pp.

Wilson, R.J., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R., Monserrat, V.J. 2005 Changes to the elevational limits and extent of species ranges associated with climate change. Ecol. Lett. **8(11)**: 1138–1146.

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