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WILLOWS OF THE EUROPEAN PART OF RUSSIA. PART II: LIFE FORMS. POLYVARIABILITY OF DEVELOPMENT

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Abstract. The wide geographical distribution of willows, their rapid growth, and variability of their morphological characteristics ensure their adaptability to various ecological conditions and a significant diversity of willow life forms. The aim of this study is to investigate the polyvariance of the development of boreal willow species in the European part of Russia, which belong to two ecological groups: alluvial and non-alluvial. The research was conducted in the center of the European part of Russia, in its most developed regions: the Moscow, Vladimir, Nizhny Novgorod, and Penza regions. The ontogenetic states of trees and shrubs were determined using conventional methods. The ontogenesis of alluvial species was studied in 2 tree species and 5 shrub species, of non-alluvial species – in 2 tree species and 7 shrub species. Depending on the ecological and coenotic conditions of growth, 11 life forms are formed. The most common life forms are single-stemmed trees, epigeogenic-geoxyl, and hypogeogenic-geoxyl.

Keywords: Salix, European part of Russia, life form, ontogenesis, ontogenesis polyvariance

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ИВЫ ЕВРОПЕЙСКОЙ ЧАСТИ РОССИИ. ЧАСТЬ II: ЖИЗНЕННЫЕ ФОРМЫ. ПОЛИВАРИАНТНОСТЬ РАЗВИТИЯ

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Аннотация. Широкое географическое распространение ив, быстрый рост и изменчивость их морфологических признаков обеспечивают приспособленность к различным экологическим условиям и значительное разнообразие жизненных форм ив. Целью работы является изучение поливариантности развития бореальных видов ив Европейской части России, относящихся к двум экологическим группам – аллювиальным и неаллювиальным. Исследования проводили в центре Европейской территории России в наиболее освоенной ее части – в Московской, Владимирской, Нижегородской и Пензенской областях. Определение онтогенетических состояний деревьев и кустарников проводили общепринятыми методами. Онтогенез особей аллювиальных видов изучен у 2 видов деревьев и 5 видов кустарников, неаллювиальных видов – у 2 видов деревьев и 7 видов кустарников. В зависимости от эколого-ценотических условий произрастания формируется 11 жизненных форм. Наиболее часто образуются жизненные формы одноствольное дерево, эпигеогенно-геоксильный, гипогенно-геоксильный и аэроксильный кустарники.

Ключевые слова: Salix, Европейская часть России, жизненная форма, онтогенез, поливариантность онтогенеза

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Introduction

Willows constitute a fairly large group of plants and are found in Europe, Asia, America and Africa, from the tundra to the tropics [1]. They vary

considerably in their biological properties [20]. The wide geographical distribution of willows, their rapid growth and variability in morphological characteristics ensure their adaptability to various ecological conditions and a significant diversity of life forms.

According to the literature [2, 4–6, 11–13, 22] and previous studies [14–16, 20–21], the genus *Salix* is characterised by a wide range of life forms, including: single-stemmed, few- or multi-stemmed trees of aeroxyl and geoxyl origin, aeroxyl and geoxyl shrubs, dwarf shrubs, elfin, and herbaceous perennials.

In the Arctic and subarctic regions of the North-east, the most common life form among willows is a prostrate shrub with aerial branches and woody epigeal rhizomes (xylorhizomes) [5, 6]; in the Kolyma Highlands, cushion-like life forms predominate among willows of the subgenus *Chamaetia* [10]; among willows of the Southern Urals, the shrub life form is most common [4].

However, there is no complete information on the polyvariance of the development of boreal

willow species in the European part of Russia belonging to two ecological groups – alluvial and non-alluvial.

Materials and methods

Field studies were conducted in the Vladimir, Moscow, Nizhny Novgorod, and Penza regions. Detailed characteristics of the study region and climate are described elsewhere [21].

To identify and characterise the ontogenetic states of willow species, we used Rabotnov's classification [24], supplemented by Uranov [26] and other authors. The ontogenetic states of trees and shrubs were determined using generally accepted methods [3, 7–9, 22, 26–28, etc.] (Table 1).

Table 1

Periodisation of the ontogenesis of trees and shrubs

The ontogenetic period	The ontogenetic stage	Index
1. Latent	(1) Seed	<i>se</i>
2. Pregenerative	(2) Sprout	<i>p</i>
	(3) Juvenile	<i>j</i>
	(4) Immature	<i>im</i>
	(5) Virginile	<i>v</i>
3. Generative	(6) Young	<i>g1</i>
	(7) Middle-aged	<i>g2</i>
	(8) Old	<i>g3</i>
4. Post-generative	(9) Senile	<i>s</i>

Results

The ontogeny of the alluvial group has been studied in seven species, including two tree species (*S. alba* and *S. euxina*) and five shrub species (*S. triandra*, *S. vinogradovii*, *S. acutifolia*, *S. viminalis*, *S. gmelinii*).

The ontogenesis of non-alluvial species has been studied in two tree species (*S. caprea* and *S. pentandra*) and seven shrub species (*S. cinerea*, *S. rosmarinifolia*, *S. aurita*, *S. starkeana*, *S. myrsinifolia*, *S. myrtilloides*, *S. lapponum*).

In adults of alluvial willow species, nine life forms are formed: 1 – single-stemmed tree, 2 – few- and multi-stemmed tree of aeroxyl origin, 3 – few- and multi-stemmed tree of geoxyl origin, 4 – facultative elfin, 5 – epigeogenic-geoxyl shrub, 6 – hypogeogenic-geoxyl shrub, 7 – aeroxyl shrub, 8 – sapling, 9 – facultative elfin.

In non-alluvial species of willow, nine life forms are formed in the adult stage: 1 – single-stemmed tree, 2 – few- and multi-stemmed trees of aeroxyl origin, 3 – few- and multi-stemmed trees of geoxyl origin, 4 – epigeogenic-geoxyl shrub, 5 –

hypogeogenic-geoxyl shrub, 6 – sapling, 7 – aeroxyl shrub, 8 – low long-xylorhizous hypogeogenic-geoxylous shrub, 9 – semi-aquatic long-xylorhizous dwarf shrub. The last two life forms are not found in alluvial willow species. The life forms – aeroxylous tree-shrub and semi-aquatic long-xylorhizous elfin, identified in non-alluvial species, are described for the first time [14, 17–19].

The selected life forms are found in various habitats: river banks and floodplains, the shores of water bodies, the bottoms of wet ravines and ditches, and also far from the riverbed on drier substrates.

A detailed study of the ontogenesis of willow species has revealed that most species exhibit morphological variability in their development, resulting in the formation of two or more (up to four) life forms in adulthood.

In *S. lapponum* and *S. myrtilloides*, this type of polyvariation has not been detected, which is due to the similar growing conditions of these species.

A total of 39 ontogenetic variants have been described, leading to the formation of 11 life forms (Table 2, Fig. 1).

Table 2

Life forms of boreal willow species in the European part of Russia

Types of willows	Life forms										
	1	2	3	4	5	6	7	8	9	10	11
<i>S. alba</i>	+	+	+	+							
<i>S. euxina</i>	+	+	+	+							
<i>S. caprea</i>	+	+	+								
<i>S. pentandra</i>	+	+	+								
<i>S. aurita</i>					+		+	+			
<i>S. starkeana</i>					+		+	+			
<i>S. myrsinifolia</i>					+	+					
<i>S. acutifolia</i>					+	+	+				+
<i>S. triandra</i>						+	+	+			+
<i>S. viminalis</i>						+					+
<i>S. gmelinii</i>	+					+					
<i>S. vinogradovii</i>						+	+				
<i>S. cinerea</i>							+	+		+	
<i>S. rosmarinifolia</i>							+	+			
<i>S. lapponum</i>									+		
<i>S. myrtilloides</i>									+		
<i>n</i>	5	4	4	2	4	6	7	5	2	1	3
<i>%</i>	11,6	9,3	9,3	4,7	9,3	14	16,2	11,6	4,7	2,3	7

Life forms 1– single–stemmed tree, 2 – few- and multi-stemmed aeroxyl tree, 3 – facultative elfin and multi–stemmed geoxyl tree, 4 – facultative elfin, 5 – sapling, 6 – aeroxyl shrub, 7 – epigeogenic-geoxyl shrub, 8 – hypogeogenic-geoxyl shrub, 9 – low long-stem hypogeogenic-geoxyl shrub, 10 – semiaquatic long-xylorizome elfin wood, 11 – elfin

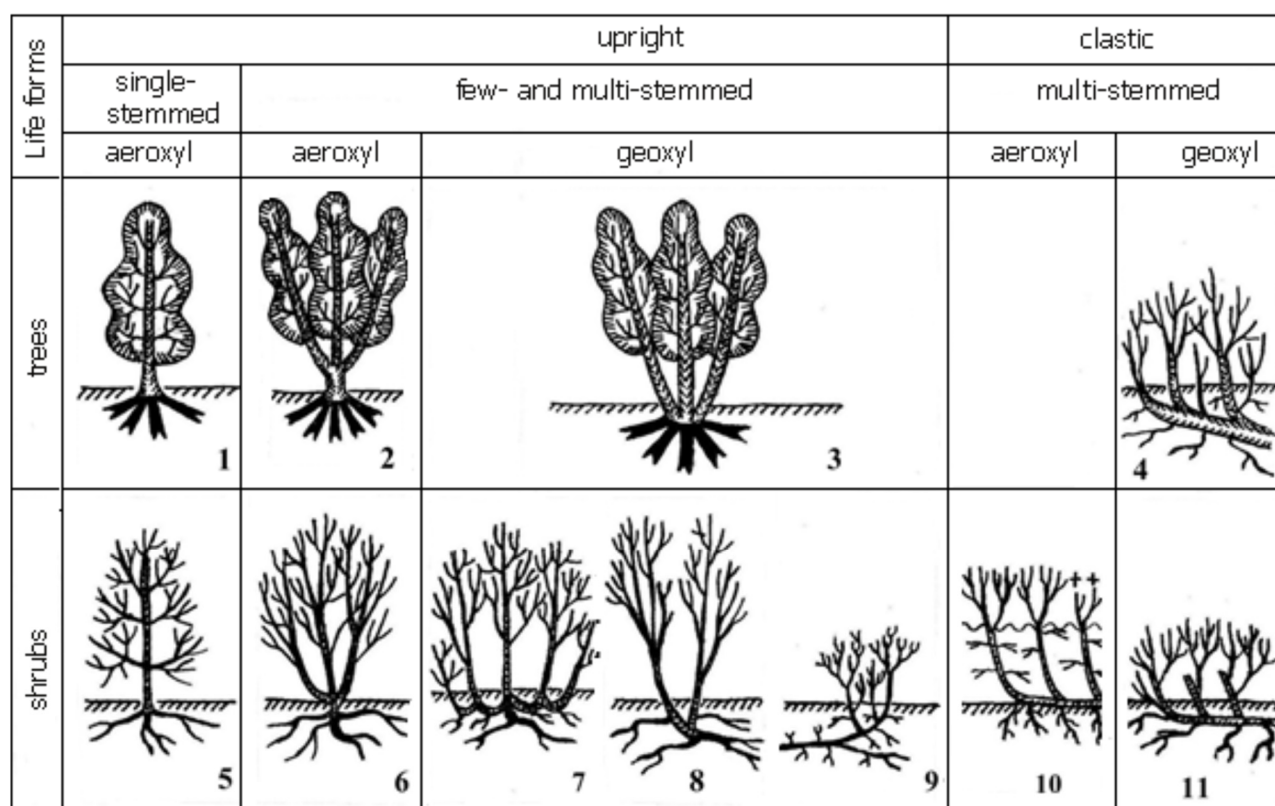


Fig. 1. Life forms of willow trees and shrubs in the European part of Russia. Life forms: 1 – single–stemmed tree; 2 – few- and multi-stemmed tree of aeroxyl origin; 3 – small- and multi-stemmed tree of geoxyl origin; 4 – facultative elfin; 5 – sapling; 6 – aeroxyl shrub; 7 – epigeogenic-geoxyl shrub; 8 – hypogeogenic-geoxyl shrub; 9 – low long-stem hypogeogenic-geoxyl shrub; 10 – semi-aquatic long-xylorizome elfin wood; 11 – elfin

Thus, the selected life forms belong to two major types: trees (*S. alba*, *S. euxina*, *S. caprea*, *S. pentandra*) and shrubs (*S. cinerea*, *S. aurita*, *S. starkeana*, *S. myrsinifolia*, *S. rosmarinifolia*, *S. triandra*, *S. acutifolia*, *S. viminalis*, *S. gmelinii*, *S. vinogradovii*, *S. myrtilloides*, *S. lapponum*). For some species of trees (*S. alba*, *S. euxina*) and shrubs (*S. acutifolia*, *S. triandra*, *S. cinerea*, *S. viminalis*), elfin life forms are also described.

All the studied species exhibit dimensional polyvariance, which is expressed in changes in the size and vital state (normal and reduced vitality) of an individual within the same ontogenetic state. Individuals with normal vitality are characterized by more powerful shoot and root systems; they determine the position of the species in the phytocenosis and ensure the self-maintenance of the population. Individuals with reduced vitality in each ontogenetic state constitute a certain reserve and serve to maintain the territory.

Therefore, the presence of individuals with two levels of vitality (normal and reduced) is an important adaptation mechanism in willow populations. The identified types of polyvariance in development are caused by different phytocenotic conditions for plants of various life forms.

The analysis of the life forms of boreal willow species allows us to identify parallel series of life forms of trees and shrubs in the sense of Serebryakov [25]: they contain single-stemmed forms – few- and multi-stemmed aeroxyl forms – few- and multi-stemmed geoxyl forms – elfin forms of growth (Fig. 1).

The most common life forms are epigeogenic-geoxyl and aeroxyl shrubs (16.2 % and 14 %), hypogeogenic-geoxyl shrubs, and single-stemmed trees (11.6 % each). Less common are the semi-aquatic long-xylorhizome elfin shrub (2.3 %), the facultative elfin and the low long-xylorhizome hypogeogenic-geoxile shrub (4.7 % each). In total, 34 % of the trees have different life forms, while 65.1 % of the shrubs do.

The ontogenesis of individuals of the single-stem tree life form is described in *S. alba*, *S. euxina*, *S. caprea* and *S. pentandra*, which are found away from river floodplains, on drier soils, and in the presence of apical and lateral shading. These conditions are not optimal for willows, so they cannot form more than one skeletal axis due to a lack of light and moisture. The trees grow from 17.5–18 m (*S. caprea*, *S. pentandra*) to 22.5–25.5 m (*S. alba*, *S. euxina*), and have a lifespan of 80 (*S. euxina*) to 100 years (*S. caprea*, *S. pentandra*, *S. alba*).

The ontogenesis of individuals of the life form a few- or multi-stemmed tree of aerobic origin has been studied in *S. alba*, *S. euxina*, *S. caprea* and *S. pentandra*. Individuals of this life form

in *S. caprea* and *S. pentandra* are found in more open areas (edge zones, clearings, and embankments), which are characterized by significantly lower crown density [14–16]. *S. alba* and *S. euxina* are found in open, dry areas of river floodplains and along the banks of water bodies. This life form is formed in the early stages of ontogenesis (im, v) as a result of the formation of new skeletal axes from above-ground dormant buds. Compared to single-stemmed trees, aeroxyl trees have a shorter height and lifespan of the main skeletal axes.

The ontogenesis of individuals of the life form of a few- or multi-stemmed tree of geoxile origin has been studied in *S. alba*, *S. euxina*, *S. caprea* and *S. pentandra*. Individuals of this life form, *S. caprea* and *S. pentandra*, are found within the same plant community as the life forms of aeroxile trees (on forest edges, clearings, and embankments), but they tend to be found in more dense areas of similar coenoses, characterized by significantly higher crown density. Geoxile trees *S. alba*, *S. euxina* are found in the same habitats as aeroxile trees (river floodplains, water bodies), but mainly in more humid areas of similar coenoses. This life form is formed in the early stages of ontogenesis (im, v) as a result of the formation of new skeletal axes from underground dormant buds. Compared to single-stemmed trees, geoxile trees have lower heights and shorter lifespans of their trunks.

The ontogenesis of individuals of the life form of the facultative elfin has been studied in the alluvial species *S. alba*, *S. euxina*, which grow on the banks of large rivers. The individuals experience annual flooding by high water, so all the shoots of the formation (future skeletal axes) lie down in the direction of the water flow, are covered with sand, and take root. During the flood, the skeletal axes are flooded with water up to a depth of 1.5 m, which causes the formation of adventitious roots. These roots, along with the remnants of vegetation carried by the flood, can be observed on the trunks even in the summer. At the point where the lateral branches (skeletal axes) branch off from the trunk buried in the sand, long adventitious roots develop, spreading out in different directions (up to 2.5 m) and anchoring themselves in the mobile substrate. The main skeletal axes have a short lifespan of up to 30 years and reach a trunk diameter of up to 25 cm. When the skeletal axes die, new shoots develop from dormant buds on their basal sections (at the boundary between the soil and the stem).

The ontogenesis of individuals of the sapling life form is described in *S. aurita*, *S. starkeana*, *S. myrsinifolia*, and *S. acutifolia*. Individuals of non-alluvial species (*S. aurita*, *S. starkeana*, *S. myrsinifolia*) are found on dry soils in forests with shading; individuals of the alluvial species *S. acutifolia* are found

on a variety of substrates (clay, gravel), most often within populated areas near houses. The biomorphological life form of the sapling consists of a single main skeletal axis with a lifespan of up to 20 years (*S. aurita*, *S. starkeana*) or 30 years (*S. myrsinifolia*), reaching a height of 1.5 m (*S. aurita*), 2.4 m (*S. starkeana*), or 6.0 m (*S. myrsinifolia*). The lack of light and dryness of the substrate are environmental factors that prevent individuals of this life form from forming more than one stem.

The ontogenesis of individuals of the aeroxy shrub life form has been studied in *S. myrsinifolia*, *S. triandra*, *S. acutifolia*, *S. viminalis*, *S. gmelinii*, and *S. vinogradovii*, which are found in elevated areas of river floodplains and in drier areas with lateral and apical shading. The life form of an aershrib is formed in the early stages of ontogenesis (immaturity, virginal ontogenetic state) as a result of the formation of new stems from above-ground dormant buds. Compared to aero-trees, aero-shrubs have a lower total height and a shorter lifespan of the main skeletal axes. Morphologically, the aeroxyl bush is a system of alternating skeletal axes (up to 80) with a lifespan from 25–27 years (*S. myrsinifolia*, *S. triandra*, *S. vinogradovii*) to 30–33 years (*S. acutifolia*, *S. viminalis*, *S. gmelinii*) years and a height of 5 m (*S. triandra*, *S. myrsinifolia*), 7.0 m (*S. viminalis*, *S. gmelinii*), 8.0 m (*S. vinogradovii*), 10 m (*S. acutifolia*).

The ontogenesis of individuals of the epigeogenic-geoxile shrub life form (Fig. 1) has been studied in *S. cinerea*, *S. rosmarinifolia*, *S. aurita*, *S. acutifolia*, *S. starkeana*, *S. triandra*, and *S. vinogradovii*, which grow in sufficiently moist secondary habitats on a variety of substrates: in open areas of swampy or flooded meadows, and on forest edges in the absence of the upper layer of vegetation. Morphologically, an epigeogenic-geoxile shrub is an above-ground system of main skeletal axes that are subsequently drawn into the soil, forming their own system of accessory stem roots each time. Lifespan up to 20–25 years (*S. aurita*, *S. rosmarinifolia*, *S. starkeana*), 27–30 years (*S. acutifolia*, *S. cinerea*, *S. triandra*, *S. vinogradovii*), height 2.5–3.4 m (*S. aurita*, *S. rosmarinifolia*, *S. starkeana*), 5.0–7.5 m (*S. acutifolia*, *S. cinerea*, *S. triandra*, *S. vinogradovii*).

The ontogenesis of individuals of the hypogeogenic-geoxile shrub life form is described in *S. cinerea*, *S. rosmarinifolia*, *S. aurita*, *S. starkeana*, and *S. triandra*. Individuals of this life form grow along sandy riverbanks on well-aerated substrates (*S. cinerea*, *S. triandra*), and along forest edges with an upper and lateral layer of vegetation (*S. rosmarinifolia*, *S. aurita*, *S. starkeana*). Morphologically, a hypogeogenic-geoxile bush is a small number of underground-forming main skeletal axes of approximately the same age, which do not change their

several orders, which is probably due to a lack of light. Skeletal axes reach a height of 3.2–4.0 m (*S. aurita*, *S. rosmarinifolia*, *S. starkeana*), 5.5 m (*S. cinerea*), and 8.5 m (*S. triandra*), with a lifespan of 25–28 years (*S. aurita*, *S. rosmarinifolia*, *S. starkeana*) or 35 years (*S. cinerea*, *S. triandra*).

The ontogenesis of individuals of the low-length xylorhizome hypogeogenic-geoxile shrub life form is described in *S. lapponum* and *S. myrtilloides*, which grow on the outskirts of sedge and sphagnum bogs with an upper layer of herbaceous and woody vegetation. Morphologically, the low-length xylorhizome hypogeogenic-geoxile shrub is a small number of main skeletal axes of approximately the same age, which are formed on the underground xylorhizome. Skeletal axes reach a height of 1.0–1.7 m, and their lifespan is 13–15 years.

The ontogenesis of individuals of the semi-aquatic long-xylorhizome life form has been studied in the ashen willow, whose basal part constantly grows in water at a depth of up to 1 m, at a short distance from the shore (2–7 m). In plants of this life form, the long xylorhizome is located at the bottom of the water body, and its rooting occurs through adventitious roots that can reach up to 30–45 cm in length. Stolons branch off from the xylorhizome, and their ontogenesis lasts up to 15 years, growing up to 2 m.

The ontogenesis of the elfin species of shrubs *S. acutifolia*, *S. triandra*, and *S. viminalis* has been described. This life form develops under the influence of spring floods in the floodplain banks of large rivers. The main skeletal axis formed at the beginning of ontogenesis lies in the direction of the flow of water, and in subsequent years it becomes buried by alluvial deposits. From this buried part, short-lived skeletal axes of small diameter and height develop. Adjunct bone axes extend from the buried part.

Conclusions

The selected life forms of the boreal willow species are determined by ecological-biological and morphological features: 1) great light-loving, which contributes to the formation of the initial alluvial species near the riverbed; 2) the lying of the trunks under the pressure of flood water, which contributes to the survival of the shoot system; 3) the saber-like bending of the basal parts of the trunks, which contributes to further rooting and spatial fixation of the territory; 4) active adventitious root formation on the lower part of the trunks and xylorhizomes.

An analysis of the ontogenesis of boreal willow species showed that 11 life forms are formed in the studied willow species, depending on the ecological and coenotic conditions of growth. The selected life forms include trees (*S. alba*, *S. euxina*, *S. caprea*,

S. pentandra) and shrubs (*S. cinerea*, *S. aurita*, *S. starkeana*, *S. myrsinifolia*, *S. rosmarinifolia*, *S. triandra*, *S. acutifolia*, *S. gmelinii*, *S. viminalis*, *S. vinogradovii*, *S. lapponum*, *S. myrtilloida*).

For some species of trees (*S. alba*, *S. euxina*) and shrubs (*S. triandra*, *S. acutifolia*, *S. cinerea*, *S. viminalis*), the life forms of elfin are also described.

In boreal willow species, the most common life forms are single-stemmed trees, epigeogenic-geoxyl shrubs, hypogeogenic-geoxyl shrubs, and aeroxyl shrubs.

The populations of all studied willow species are polymorphic in terms of their life forms. Among the studied species, some alluvial species exhibit the greatest variability, while non-alluvial species exhibit the least variability.

The diverse conditions of existence determine the ontogenetic development of trees and shrubs and lead to the formation of various life forms within the same species.

The analysis of literature and own research allowed to allocate parallel series of variability in woody life forms. The studied series of life forms of shrubs and trees contain: single-stemmed forms – few- and multi-stemmed forms of aeroxyl and geoxyl origin – stoloniferous forms of growth. In elfin life forms, the missing link – semi-water long-xylorizomous elfin is described.

This study details the idea of the diversity of life forms of trees and shrubs in general and further smoothes the difference between shrubs and trees in the traditional view. The main differences between trees and shrubs in the studied willow species are: 1) height and 2) age of the skeletal axes of the life forms. At the same time, the change of trunks during ontogenetic development may not always be a distinguishing feature of shrubs, as the life form of the sapling and the hypogeogenic-geoxyl shrub do not experience such a change of trunks during ontogenesis.

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