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Article

On the structure of the crown of a woody plant

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Abstract. The crowns of trees of virginal and generative ontogenetic state of seven species of deciduous plants were studied: *Ulmus glabra*, *Ulmus minor*, *Celtis sinensis*, *Zelkova carpinifolia*, *Aesculus hippocastanum*, *Fraxinus excelsior*, in total more than 500 individuals. A crown of a tree consists of two principal morphofunctional parts: the “skeleton” and the “lace” of the crown. Their functions, appearance, development and time of existence in the crown are related to the geometric space of branches. The presence of these shoot complexes in the crown is based on different spatial and temporal principles. As a result of long-term observations, the types of primary and secondary “lace” of the crown have been identified, including two subgroups of the primary “lace”. The peculiarities of the development of tree branches in ontogenesis have been investigated. At the level of a tree as a whole, it is proposed to consider the entire complex of the crown “lace” as an example of the mathematical model “standing wave” (soliton).

Keywords: shape of a crown, branch from a trunk, biennial shoot system, “skeleton” of a crown, “lace” of a crown, soliton, Kolmogorov-Petrovsky-Piskunov equation

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Научная статья

К вопросу о строении кроны древесного растения

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Аннотация. Исследованы кроны деревьев виргинильного и генеративного онтогенетических состояний семи видов лиственных растений: *Ulmus glabra*, *Ulmus minor*, *Celtis sinensis*, *Zelkova carpinifolia*, *Aesculus hippocastanum*, *Fraxinus excelsior*, всего более 500 особей. Крона дерева состоит из двух принципиальных морфофункциональных частей: «скелета» и «кружева» кроны. Их функции, появление, развитие и время существования в кроне связаны с геометрическим пространством ветвей. Существование этих побеговых комплексов в кроне основано на разных пространственно-временных принципах. В результате многолетних наблюдений выделены типы первичного и вторичного «кружева» кроны, в составе первичного «кружева» выделены две подгруппы. Исследованы особенности развития ветвей деревьев в онтогенезе. На уровне дерева в целом предлагается рассматривать весь комплекс «кружева» кроны, как пример математической модели «стоячая волна» (солитон).

Ключевые слова: форма кроны, ветвь от ствола, двулетняя побеговая система, «скелет» кроны, «кружево» кроны, солитон, уравнение Колмогорова-Петровского-Пискунова

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Introduction

A tree is a structured, multi-level shoot system secured by lignification. The architecture of a crown is determined by the relationship of spatial and temporal factors. The ontogenetic program of a tree organism includes the placement of a photosynthetic surface for several subsequent growing seasons. At the same time, a tree, as an open system, is able to successfully respond to external conditions thus adapting to a specific environmental context. The study of the patterns of the crown complex development in ontogenesis, as well as the possibilities of response of different levels of the crown structure to external conditions, is necessary to understand how the tree crown is structured with its obvious variability. The relationship of the development program of a tree architecture and temporal aspects of its parts realization with spatial capabilities of an organism acquired during the evolutionary process is an urgent task.

The studies of the development of tree crowns and ontogenesis are inextricably related. The crown is formed and transformed throughout the life of a specimen (Morozov, 1930; Serebryakov, 1962). Studies of trees in natural conditions have brought to an understanding of the importance of ontogenesis polyvariance in the formation of its architecture (Notov and Zhukova, 2019; Zhukova and Komarov, 1990). In turn, foreign researchers are developing the concept of the unified tree development program, a plan for its organization (Barthelemy et al., 1991). A tree is studied as an integral modular system, consisting of a set of units and developing along a certain regular path. With technological and computational breakthrough, the models of the crown structure based on various mathematical principles (P.W. Prusinkiewicz et al. (1994) to F. Boudon et al. (2020) and Yang et al. (2021)) began to emerge.

At present, there is no doubt that when studying the crown of a tree as a complex modular hierarchical system, it is essential to identify modular units, the totality of which most fully reflects its structure (Gattsuk, 1994; Getmanets, 2010; Kostina et al., 2018). The elementary modular unit of the woody plant structure is undoubtedly a shoot. At the same time, a collection of shoots is not a tree. The hierarchical system of the crown complex in this case is characterized by the concept of multiscale (emergence), when each subsequent hierarchical level of the crown organization has new properties, not inherent in the elements of the previous level.

When analyzing a tree as a collection of a certain number of repeating elements-modules of different levels of the organization, in order to obtain a complete picture, it is necessary to observe the principle of primacy of qualitative analysis over quantitative (Bart, 2003). In this regard, it is important to take into account the integral structural complexes that naturally stand out in the crown: a trunk of a tree and its branches. The trunk acts as the unifying and coordinating structure inherent in the tree as an integral system (Morozov, 1930; Shitt and Metlitsky, 1940). The presence of a trunk, as a characteristic property of woody plants, makes it possible to distinguish trees into a separate life form (Serebryakov, 1962).

The purpose of this work is to characterize the structure of tree branches in terms of their integrity and integration into the system of the crown complex with the formation of its certain shape. To achieve this goal, the following tasks are set:

1) to identify the levels of structure of a tree branch as a natural integral complex;

2) to investigate the features of the structure and development of branches of virginal individuals of *Ulmus glabra* Huds;

3) to compare the features of the development of shoot complexes of “skeleton” and “lace” at the level of branches of some deciduous woody plants;

4) to characterize the crowns of some woody plants as the systems of branches formed on the trunk at different time of the tree’s development.

Material and methods

The material was collected over a period of more than 20years, from 1999 to 2022. The vitality of trees, crown shapes, heights, places of attachment of lower branches, trunk diameters, characteristics of shoot complexes, biennial shoot systems and branches were studied using the previously approved method (Antonova and Fatyanova, 2016).

In the mountainous forest-steppe oak grove of Belgorod Oblast the crowns of 83 virgin *U. glabra* trees were analyzed. Five model trees were studied separately: the lengths of all shoots were measured and the number of leaves was calculated. In total, 5158 shoots were described in detail. The exact position of each shoot in the tree crown was indicated.

In addition, the crowns of the following trees were examined:

– three generative (g2) *Celtis sinensis* Pers trees (Chinese hackberry) in the Krasnodar Territory;

– virginal and generative (g1, g2) individuals of *Ulmus minor* Mill. (field elm) (50 individuals) in Abkhazia and the Krasnodar Territory;

– virginal and generative (g2) individuals of *Zelkova carpinifolia* (Pall.) K. Koch (Caucasian zelkova) (38 individuals) in Abkhazia;

– virginal, generative (g1, g2, g3) and senile individuals of *Fraxinus excelsior* L. (European ash) in Abkhazia, the Krasnodar Territory, Belgorod and Leningrad Regions. The total number of studied individuals exceeded 240;

– immature, virginal, generative (g1, g2) individuals of *Aesculus hippocastanum* L. (horse chestnut) which grew in the introduction. In total, about 65 individuals were studied in Belgorod Oblast and 68 in St. Petersburg.

Results and discussion

In our previous publications, the hierarchical system of the crown structure levels was formulated and compared with other existing systems of plant organization (Antonova and Azova, 1999; Antonova and Fatyanova, 2016). We propose the following levels of crown organization : 1) metameres; 2) shoot; 3) biennial shoot system; 4) epsion; 5) branch from the trunk; 6) crown; 7) crowns system.

The biennial shoot system (BSS) consists of a mother elementary shoot and lateral shoots developed from its axillary buds, which differ in qualitative and quantitative parameters. BSS has a certain geometry, which is related to its functions in the crown. For woody plants of the temperate zone, a set of morphofunctional types of BSS has been identified, which depends on the development program of the species and is different in different ontogenetic states (Antonova and Fatyanova, 2016).

At the hierarchical level of biennial shoot systems, as a modular unit, BSS has both spatial properties, folding the crown architecture and placing the leaf surface in a certain geometric contour, as well as temporal ones realized over several (usually two) growing seasons. A long-term analysis of biennial shoot systems in the crowns of various species of woody plants of the temperate zone allows us to identify the following morphofunctional types of BSS.

“Growth” BSS are characterized by a continuance mother shoot and one or several upper large lateral shoots. The geometric contour of these BSS has the greatest length and width, as compared to other types. The mother shoots of “growth” BSS are a part of the trunk and axes of low branching orders (second, rarely third), having larger diameters than other shoots.

“Basic” BSS, as was shown earlier, are an undergrown version of “growth” BSS with an underdeveloped upper zone of the largest lateral shoots (Antonova and Bart, 2019). Along with the “growth” they make up axes of the first and second orders, as well as the third and less often the fourth ones.

“Filling” BSS, located throughout the crown, are the most numerous and characterized by the least length and the number of lateral shoots. BSS of this type are formed in the lower zone on the mother shoots of “skeletal” BSS, as well as at the final stages of growth of “skeletal” axes. In crowns, they have the shortest life expectancy relative to other types of BSS.

In addition to these three main types, there are some extra in the crown. These are, for example, “narrow-contour” BSS, which are formed mainly on the peripheral part of the crown, characterized by a long maternal shoot and a large number of small lateral shoots. These BSS are found in crowns occasionally under certain conditions, when the process of branch development requires intensive removal of the photosynthetic surface further to the periphery of the crown. Such systems are formed as a part of axes of the second, third and rarely fourth orders. Also, in the trunk composition at the early stages of tree ontogenesis (mainly in the virgin ontogenetic state) there are large “super-growth” BSS, the maternal shoot of which has several periods of growth.

The properties of BSS in the crown of a tree do not depend on external conditions of its existence and reflect the development program of the crown architecture (Antonova and Bart, 2019). At the same time, in the construction of the crown as an integral hierarchical system, the property of multi-scale is fully manifested (Antonova and Fatyanova, 2013). This work examines the level of a tree branch as an integral, naturally developing natural unit of the crown, which, on the one hand, is a set of BSS and at the same time has its own morphofunctional properties.

A branch from the trunk is the largest single classification unit of the crown in the morphogenetic sense, consisting of a monopodial or sympodial complex of shoots, derived from one axillary meristem of the BSS mother shoot of the trunk (Antonova and Fatyanova, 2016).

The fundamental quality of biennial shoot systems (making up a branch from the trunk) is the difference in lateral shoots BSS formed in different positions on the mother shoot. This is due to zonality of the maternal shoot, which is clearly manifested in the structure of BSS in the second year (Antonova and Bart, 2018; Antonova and Gnilovskaya, 2013). The largest long-lived branches from the trunk develop from the zone of the upper large lateral shoots on BSS (Fig. 1**A**, **B**). Such branches, remaining in the crown for a long time, mark the annual growths of the trunk – biennial shoot systems in its composition (Fig. 1**C**). The morphological property of a greater upper lateral shoots and a longer life span manifested for the first time at the level of a two-year shoot system for branches from the trunk is reflected in crown tiers. It was noted by fruit growers long time ago as an important property of the formation and development of a tree crown (Shitt and Metlitsky, 1940). A branch from the trunk has its own ontogenetic cycle - from bud unfolding on the maternal trunk growth to branch death. The development patterns of branches in the crown are responsible for a consistent change of the tree crown shape in ontogenesis (Fig. 1**C**, **D**).

A new morphological property, which emerges at the level of branches from the trunk, is the presence of two morphofunctional groups of shoots and shoot systems, designated as the “skeleton” and “lace” of the crown. Shitt reported about these two groups, naturally standing out in the composition of tree branches, by the example of fruit tree crowns, calling them “skeletal and fouling” crone parts (Shitt and Metlitsky, 1940).

The geometric formalism leading to the division of crown shoots of *U. glabra* into 3rd and 4th branching orders was previously discussed in detail (Antonova et al., 2021; Bart and Antonova, 2022).

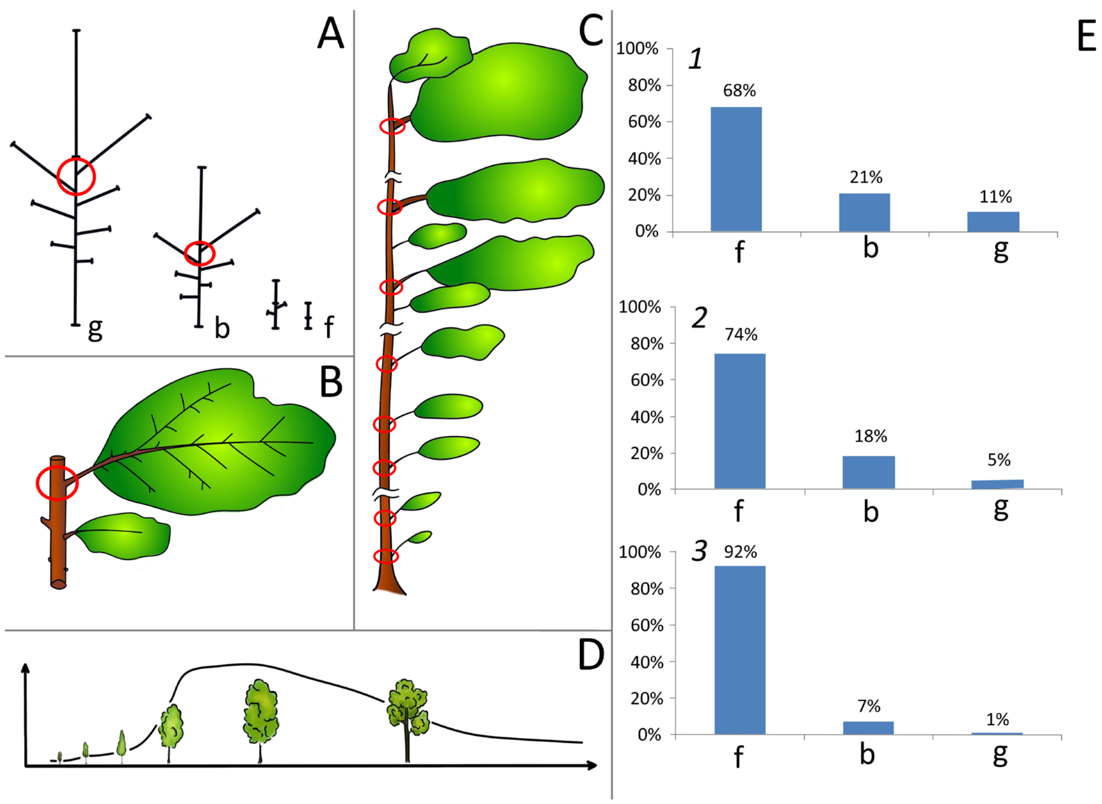

Fig. 1. Branching from a trunk as a hierarchical level of the tree crown structure. **A** – types of biennial shoot systems: g – “Growing”, b – “Basic”, f – “Filling”; **B** – branch from a trunk, the oval marks the zone of formation of large lateral shoots on BSS mother shoot; **C** – branches from the trunk in the tree crown; **D** – development of tree crown biomass in the course of ontogenesis: x axis – ontogenesis time, y axis – biomass; **E** – percentage ratio of “Growing”, “Basic”, “Filling” BSS in the crown of a virginal *U. glabra* for five-, six-, and seven-year branches – 1, 2, and 3, respectively.

This mainly determines the division of shoots into the "lace" of the crown and its "skeletal" part. Indirectly, the separation was confirmed on a large data set. For instance, the spatiotemporal properties of shoots of five *U. glabra* individuals were studied according to a variation series of 5158 shoots. At the end of the virginal stage of ontogenesis, the "skeletal" part made up only about 6% of all shoots of the tree crown (Fig. 2). Meanwhile, just the "skeletal" part determined the architecture of the crown.

The "skeleton" of a tree branch is made up of large mother and lateral shoots of biennial shoot systems. These are "growth", "super-growth", "basic" BSS.

Fig. 1**E** shows percentage change of "growth", "main" and "filling" BSS in the five-, six- and seven-year-old branches of the *U. glabra* virginal tree. The proportion of "growth" and "basic" BSS is noticeably decreasing, but it is the "skeletal" part that sets a visible pattern of the branch, its geometric contour.

Every year a branch grows, the contribution of "filling" BSS to its composition increases (Fig. 1**E**). Already in the 7th year of growth of the branch of the virginal tree of *U. glabra*, the contribution to the total number of "filling" BSS reaches 92% (Fig. 1**D**). As the branch grows, it is intensively filled with small shoot complexes consisting of short shoots. The "filling" BSS branches produce the bulk of leaves during most of their life. Here, the generative organs are formed in the appropriate ontogenetic state (Antonova and Fatyanova, 2016). The combination of "filling" BSS in the branch creates a "lace" of the crown.

During ontogenesis, the "lace" of the crown actively develops as a part of branches, starting from the virginial up to the hydrocyanic ontogenetic state. Fig. 3**A**, **B** shows the development patterns of two branches of the virginal tree *U. glabra* in different parts of the crown. Each branch was formed from a large lateral shoot in the upper position on the mother shoot of "growth" BSS of the trunk.

The seven-year-old branch of the lower part of the crown (Fig. 3**A**) has the "skeletal" axes consisting of maternal shoots, mainly "basic" BSS. Each of the "skeletal" axes in the peripheral part of the branch

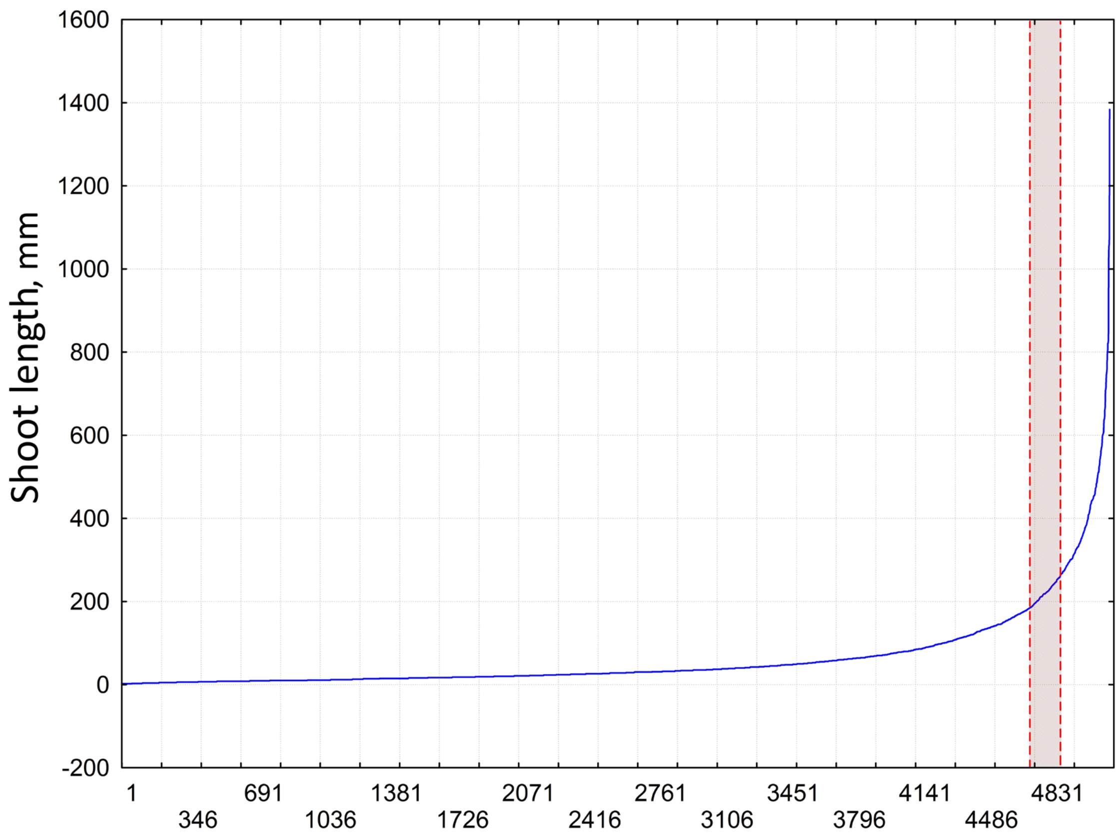

Fig. 2. Distribution of lengths of all shoots of five *U. glabra* forest virginal trees: along the x axis– the number of shoots; along the y axis – the lengths of shoots; dotted lines define a part of the variation series of shorter (transitional between "skeleton" and "lace") shoots; on the left from lines – shoots of the "lace", on the right – shoots of the "skeleton".

began to form the “lace” shoot systems thereby indicating aging and growth of the branch. The “lace” of the crown, consisting of the sequences of “filling” BSS, develops slowly and is up to five years old. The process of the “lace” dying off and exposing the “skeletal” axes, especially at the branch base, is clearly manifested.

The five-year-old branch of the middle part of the crown of the virginial tree of *U. glabra* is characterized by the “skeleton” formation (Fig. 3**B**). The “lace” of the crown is formed on the basis of the lower side shoots of “growth” BSS, and in the started growth process of some “skeletal” axes. The dying off of the “lace” shoot complexes and, accordingly, the thinning of the branches are present, but weakly expressed.

Each branch on the trunk is formed at a certain stage of ontogeny of a woody organism. The ratio of “lace” and “skeleton” in the branch characterizes, on the one hand, the ontogenetic state at the time of branch formation and, on the other – the branch's own development as an integral crown unit.

Using the example of a ten-year-old branch of the middle part of the crown of a generative tree of *C. sinensis*, one can clearly see how the development of “skeletal” axes and the gradual change of shoot “lace” complexes in the branch composition occur (Fig. 3**C**). The “skeletal” part of the branch is built on the basis of the mother and first large lateral shoots of “growth” BSS. The boundary between the “skeleton” and “lace” shoots is more pronounced in this species compared to *U. glabra*. The “skeletal” shoots initially have a greater length and a larger diameter, increasing with age. The “lace” shoot complexes are uniform in structure (Fig. 3**C**), exist within the branch for one to five years, then

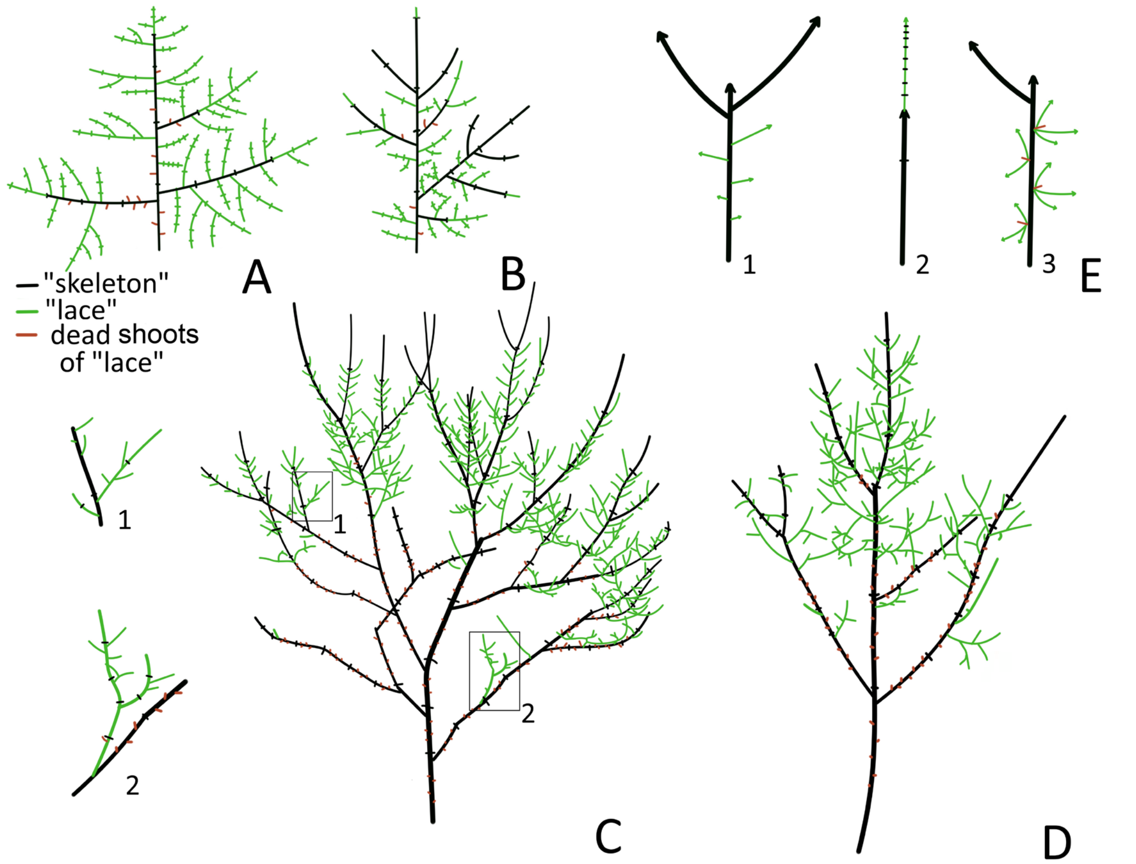

Fig. 3. “Skeleton” and “lace” of the crown. **A** – seven-year-old branch from the trunk of the lower part of the crown of a virgin tree *U. glabra*; **B** – five-year-old branch from the trunk of the middle part of the crown of virginia *U. glabra*; **C** – ten-year branch from the trunk of the middle part of the crown of generative (g2) *C. sinensis*: 1, 2 – detailed image of “lace”; **D** – seven-year branch from the trunk of the upper part of the crown of generative (g2) *C. sinensis*; **E** – scheme of development of crown “lace” axes on “skeleton” axes”: 1 – primary “lace” of the first subtype, 2 – primary “lace” of the second subtype, 3 – secondary “lace”.

die off and the “skeletal” part of the branch becomes bare. The monotony of the structure of the shoot complexes “skeleton” and “lace” is, apparently, associated with ”antiquity” of the species *C. sinensis* (Grudzinskaya, 1980) if it lives in a relatively narrow range of conditions.

The seven-year branch of the upper part of the crown of the generative tree of *C. sinensis* is characterized by a slower rate of development of the “skeleton”, which is expressed in a smaller number of emerging new “skeletal” axes, the general elongated shape of the branch and “lace” dispersion (Fig. 3**D**). The “skeleton” of the branch begins from long growths, which are quickly replaced by shorter ones. Unlike the branches of the middle part of the crown, the “skeleton” contains a single guiding “skeletal” axis.

For different species, at least three different variants of the crown “lace” formation have been identified (Fig. 3**E**). In the first case, the “lace” is formed on the basis of the lower side shoots of the “skeletal” shoot systems and reflects the principle of zoning of BSS mother shoots (Fig. 3**E**, 1). This “lace” is mainly characteristic of the initial stages of branch development and subsequently dies off first. Another version of the “lace” is formed at the final stages of growth of the “skeletal” axes in their peripheral part (Fig. 3**E**, 2). The listed lace types develop directly on the skeletal axes and are designated as the primary “lace”. The secondary “lace” refers to shoot complexes formed from axillary buds of bud scales at the base of dead shoots of the primary “lace” of the first subgroup (Fig. 3**E**, 3). This phenomenon was noted for branches of adult trees of small-leaved fast-growing representatives of the Ulmaceae family and for *Acer negundo* L., also a fast-growing and light-loving species.

Fig. 4 presents the examples of the secondary “lace” for *Z. carpinifolia* and *U. minor*. For *Z. carpinifolia*, the secondary “lace” exists along with the primary one, providing an increase in the photosynthetic surface in the early stages of branch formation (Fig. 4**A**). On the contrary, the formation of the secondary “lace” in *U. minor* occurs when the “skeletal” axis has already been formed (Fig. 4**B**). Here, the secondary “lace” appears due to dying shoot complexes of the primary “lace”. Such a complex of shoots develops over 1–5 years, and then dies off. It is replaced by a new one, arisen at the base of the same shoot of the primary “lace” on the “skeletal” axis. This mechanism allows the leaf surface to preserve the same position within the “skeleton” of the branch for a long time. Meanwhile, growth occurs naturally and a primary “lace” is formed on the periphery of the branch.

The “skeleton” and “lace” properties determine the features of the tree crown in ontogenesis. The ontogeny of *F. excelsior* was studied in detail by L.B. Zaugolnova (1968). In the immature age state of *F. excelsior*, the tree crown consists of a special biennial shoot system, which occurs only once in the ontogeny of the individual (Fig. 5**A**). This BSS is characterized by a large “skeletal” shoot, where a large number of short-lived and uniform lateral shoots develop. They form a leaf mass and quickly die off.

In the virginal ontogenetic state, mainly “growth” and “extension” BSS are formed in the trunk (Fig. 5**B**). This type is functionally close to “narrow” BSS, but differs by the formation of such BSS in the trunk of ash. Unlike “growth” BSS, “extension” BSS do not bear large lateral shoots in the upper part; they allow the “skeletal” axes of the second order and, accordingly, long-lived branches to be spaced on different increments of the trunk.

In the generative ontogenetic state, ash has a formed trunk, which grows monopodially up to a certain point (Fig. 5**C**). As a part of the “skeletal” axes, BSS periodically appear, in which the apical axial bud dies off in the second year, and two large lateral shoots develop forming a “fork”. During the development of the “skeleton” of the crown, this process is repeated, and each time, as the axes grow, the distance between the dead axial buds and, accordingly, the “forks”, becomes less.

In the late generative ontogenetic state (Fig. 5**D**), the axes of the “skeleton” grow (Fig. 5**E**), the long-lived complexes of the primary “lace” are formed on the periphery of the crown (Fig. 5**F**), which are characterized by the smallest shoot lengths and the least number of leaves (up to two on the shoot). Such terminal structures form separate non-branching spherical clusters of leaves, clearly visible in the crown. Thus, a leaf surface is formed in the same crown space for a long time.

“Skeletal” shoot complexes form the trunk and axes of large branches of *F. excelsior* in the virginal age state (Fig. 6**A**). The “growth” BSS in the upper part of the trunk form several large lateral shoots, giving rise to new “skeletal” axes. In the lower part, short-lived shoots of the “lace” of the crown are formed. At the initial development stages of the second-order axes making up the “skeleton” of branches from the trunk, the primary “lace” (of the first subgroup) is practically not formed.

In the generative age state (g2), much smaller BSS are formed in the ash crown as a part of the growing “skeletal” axes forming “lace” side shoots (Fig.6**B**). In the late generative ontogenetic state

Fig. 4. Secondary “lace”: **A** – secondary “lace” on a shoot of the “skeletal” axis of *Z. carpinifolia*; **B** – secondary “lace” on a shoot of the “skeletal” axis of *U. minor*. 1 – place of development of primary “lace” shoot with pool of buds in axils of renal scales, 2 – shoot of primary “lace”, 2* – dead shoot of primary “lace”, 3 – secondary “lace”.

(g3), the “skeletal” axes occasionally branch, and two monopodially growing shoots are formed as a part of BSS with a dead axial apical bud on the mother shoot (Fig. 6**C**). At the last stages of the “lace” development, shoots become small (Fig. 6**D**).

In the crown of *A. hippocastanum,* one can trace several types of branches, regularly changing with development (Fig. 7). In the “skeleton” of branches from the middle part of the virginile tree crown, which, by analogy with types BSS can be called “basic”, a second-order axis demonstrates a prolonged growth (Fig. 7**A**). At a certain stage of branch development, a paired branching is formed on “growth” BSS, and the branch continues to develop, similarly forming new “skeletal” axes. The two upper shoots of “growth” BSS produce a long-lived “lace”, while the lower shoots quickly die off. Depending on the position in the crown and the ontogenetic state, the number of such “skeletal” axes may be different; a branch grows at different rates. The “lace” of this species is represented by shortened shoots, forming on the “skeleton” low-branching long-lived axes.

The “compaction” branch is also formed in the middle part of the crown; it differs from the “basic” branch by the absence or low expression of the zone of increase in the “skeletal” axes number (Fig. 7**B**). Such branches fill the crown space with the “lace” leaf surface without expanding in the distal part. In the upper part of the A. hippocastanum crown, the branches with weakly expressed elongation of the “skeletal” axis are formed; the “lace” axes are represented by numerous short shoots, usually curved upward (Fig. 7**C**).

The regular arrangement of branches with different ratios of “skeleton” and “lace” results in the development of different crown shapes of an adult tree (Fig. 7**D**).

In temperate latitudes, the crown of a tree usually has a cylindrical or rounded shape. Subsequently, in the late generative and senile ontogenetic states, both forms break up into difficult-to-describe complexes of individual branches. It is widely believed that the shape of the crown depends entirely on where the tree grows (in the community or in an open site), in other words, on environmental conditions that directly affect the individual (Bulygin, 1985; Goryshina, 1979; Ipatov, 1970). However, from our point of view, the manifestation of exactly two specific forms cannot be accidental. The idea that a sphere and cylinder have the minimum surface area with a maximum volume is an important geometric consideration, but in arid conditions the umbrella shape and one-sided convex lens (e.g. in acacias, dragon trees, etc) appear.

Thus, the data on the ratio of volume and surface in connection with environmental requirements is clearly insufficient here. At the same time, different crown shapes can be observed in the same species and even in the same genome grown under different conditions (Romanovsky and Shchekalyov, 2014;

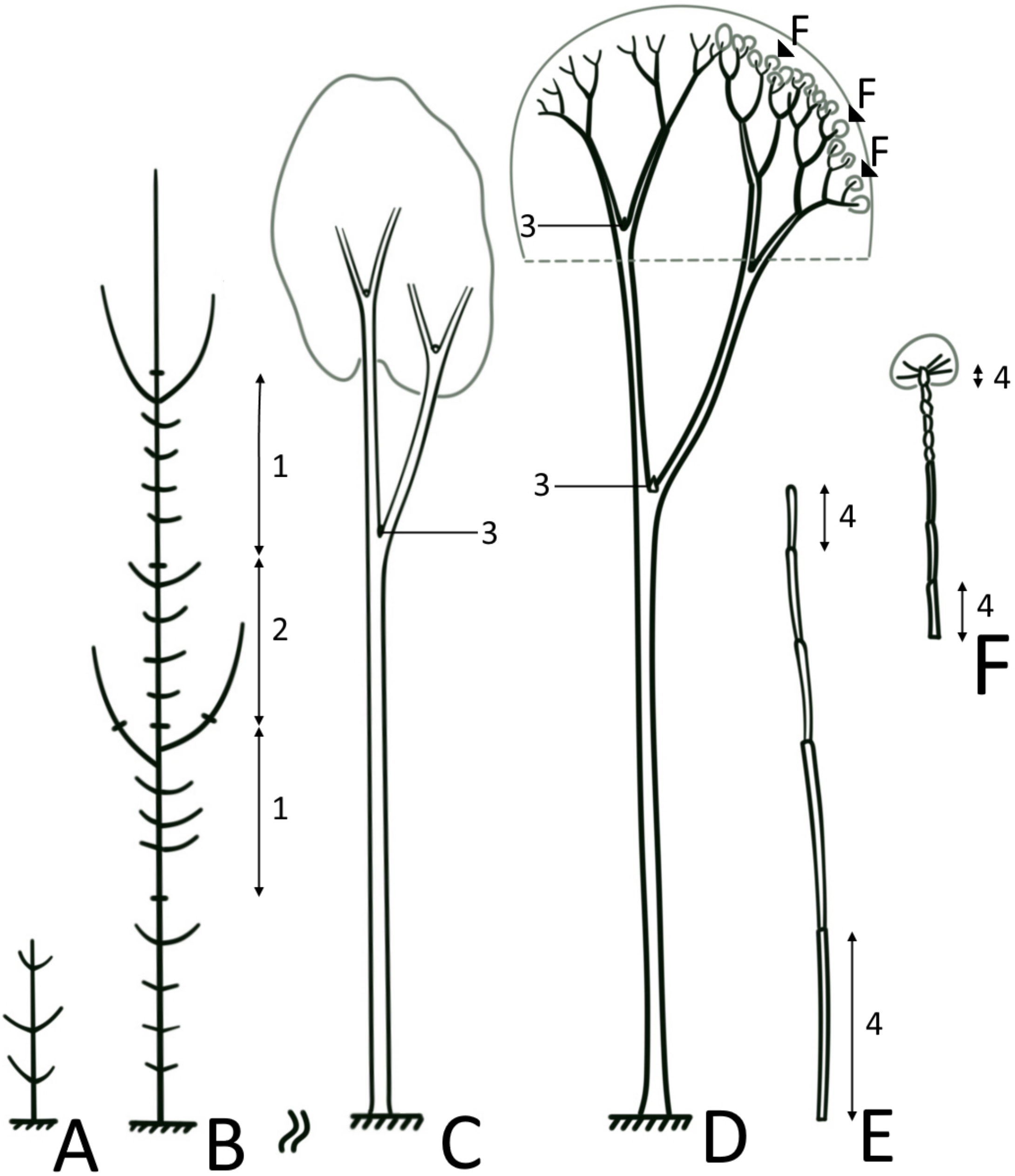

Fig. 5. Development of "skeleton" and "lace" in ontogenesis of *F. excelsior* crown. **A** – immature plant; **B** – virginal plant; **C** – tree in ontogenetic stage of g2; **D** – tree in ontogenetic stage of g3; **E** – growth of "skeleton" axis, **F** – "lace" on crown periphery. 1 – "growth" BSS, 2 – "spreading" BSS, 3 – place of axial bud death, 4 – annual shoot.

Zhuk, 2010). Light-loving pines, birches, and aspens growing in the community have a highly raised rounded crown and a long branchless trunk. The same species growing in an open place, first acquire a broadly cylindrical, then an oval-rounded crown shape, where most of their ontogenesis occurs – from the end of g1 to the g2 stages. These two variants of a tree crown shape are distinguished by an elongated trunk in the community and a short dense trunk in the open site. The transition to the formation of a rounded crown completion in the open-standing trees begins early, and the leading axis is lost among the large branches. This complex of large branches, expressed much weaker, is also present in forest plants, but only in the uppermost part of the crown.

When discussing the shape of the crown of isolated trees, we can probably talk about the loss of the developmental stage of long annual growths of the trunk. They form a long trunk and allow the branches of the crown to be spread relative to each other that is observed in forest plants. In

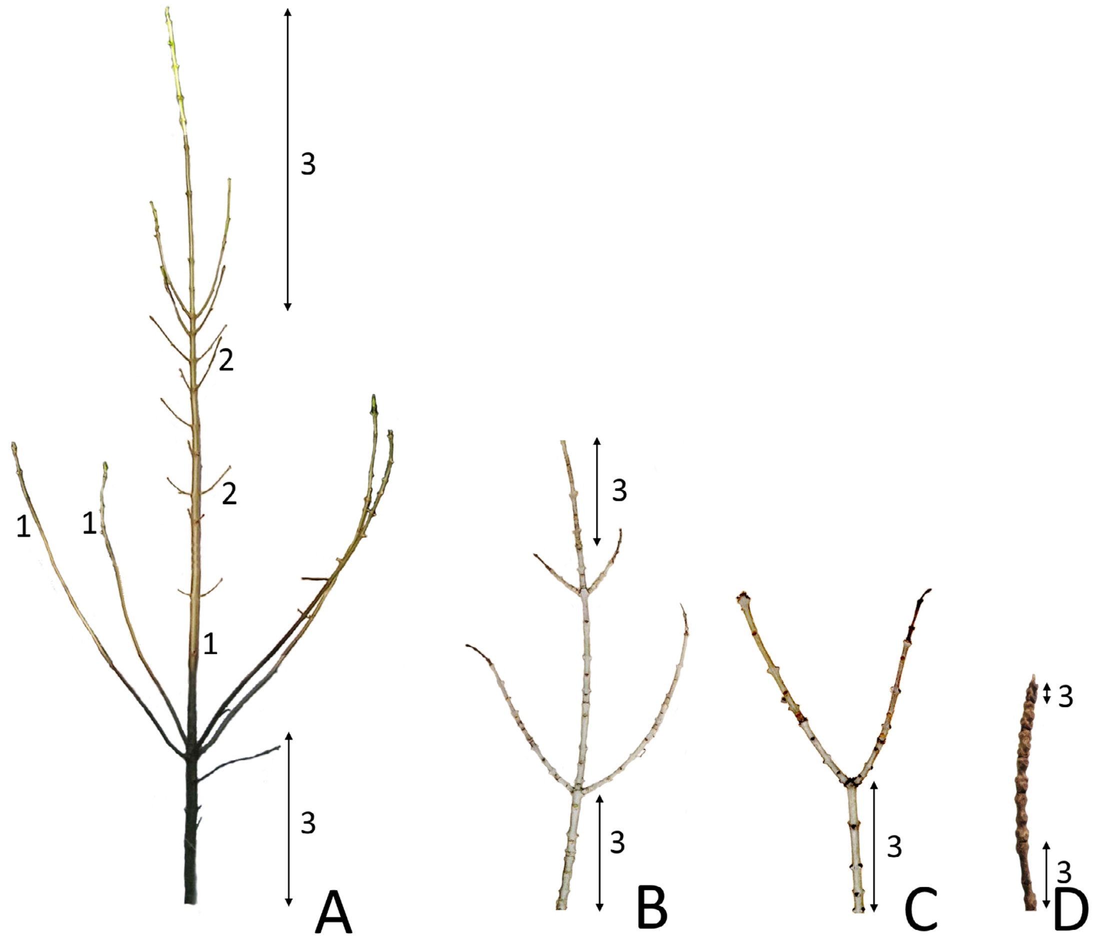

Fig. 6. Shoots of "skeleton" and "lace" complexes in the crown of *F. excelsior* in different ontogenetic states. **A** – crown apex in virginal ontogenetic state; **B** – three-year lateral "skeletal" axis in generative ontogenetic state (g2); **C** – three-year lateral "skeletal" axis in late generative ontogenetic state (g3); **D** – perennial "lace" axis of crown periphery in late generative ontogenetic state (g3). 1 – "skeletal" axes, 2 – "lace" axes, 3 – annual shoot.

other words, the ontogenetic formation of the g1 stage and partially the g2 one changes, and the polyvariance of ontogenesis manifests itself. Evolutionary theory suggests the selection of appropriate types of ontogenesis on the Earth thereby providing better adaptation to conditions. At the same time, the existence of geometrically defined crown shapes fluctuating around the shapes of a cylinder and a ball indicates, first of all, the existence of a general program for the development of the crown shape, the parts of which are realized in different conditions in temperate zone species.

Branches from the trunk are formed and function at different stages of ontogenesis, while the crown does not cease to be an integral structure (Antonova and Bart, 2018). Fig. 8 presents the diagrams of the structure of tree crowns under different growing conditions. Based on the structure of the branches from the trunk in both cases, one can distinguish similar zones of their location on the trunk. Thus, in the second zone of the trunk, feeding of the leading vertical axis of the trunk may serve as the main functional feature of branches. In the third zone of the trunk, the branches occupy a position more "equal" and even "competing" with the top of the trunk and with each other. Earlier, we showed the zonality of the maternal shoot of the two-year-old shoot system for the species *A. negundo* and *U. glabra*. It was revealed that the formation of the "main" BSS occured by eliminating the zone of the upper internodes of the BSS maternal shoot and, accordingly, the upper lateral shoots (Antonova and Bart, 2020; Antonova et al., 2019).

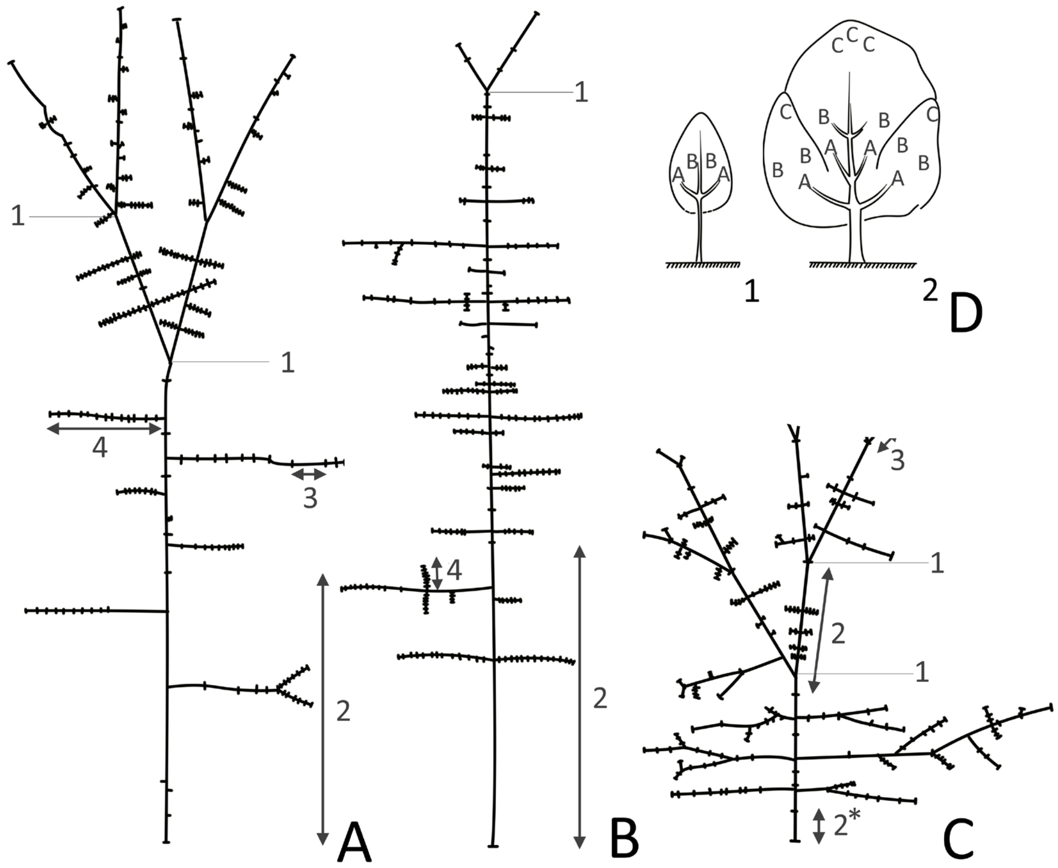

Fig. 7. Branch types in crown ontogeny of *A. hippocastanum*. **A** – branch of the middle part of the crown "main"; **B** – branch of the middle part of the crown "compaction"; **C** – branch in the upper part of the crown: 1 – places of branching of "skeletal" axes; 2 – increase in "skeletal" axis of branch; 3 – increase in branch "lace"; 4 – axis of branch"lace"; **D** – diagram of branch arrangement in the crown of a virginal tree (1) and generative tree g2 (2); the diagram demonstrates location types of branches in the crown given in Fig. 7**A**, **B**, **C** with corresponding symbols.

This is confirmed by the presence of a special segment of "skeletal" axes at the end of each branch of the third zone of the trunk consisting of almost identical sequences of many shoots representing the mother for several shoot systems and giving equal axes. Moreover, one branch can have several such end axes forming an end zone already on the branch itself. On branches from the second zone of the trunk, such a zone of terminal axes is usually absent, being, apparently, a program effect.

Both, the development of the tree trunk itself and each branch from the trunk is a combination of the processes of aging and rejuvenation according to N.P. Krenke (1940). Cyclicity of these processes is noted with a movement up the trunk or along each of the branches. Aging can be considered as the construction of large axial shoots, that is, the process of building a "skeleton", and rejuvenation is the accumulation of small shoots, i.e. the "lace" development. At the same time, the construction of terminal "skeletal" axes of the same structure clearly confirms this thesis since it is directly involved in both processes.

From an observer point of view, two processes are engaged in the development of a tree crown. One, the most noticeable (external), is responsible for the development (and growth) of the "skeletal" part of the crown. In Fig. 9, it corresponds to successive images of tree crowns over the course of ontogenesis. The second process is the dynamics of the crown "lace", no less intense than the first, but hardly noticeable and taking place at significantly higher frequencies (indicated by rounded arrows). Both processes go on continuously during the tree crown's life, but the first prevails at the first stages of ontogenesis, whereas the second in the last ones. The latter are characterized by a higher rate of changes in the composition of the crown "lace" at a low speed of movement of the entire crown as a whole, that is, the development of the "skeletal" part.

The wave propagation model – the propagation of a gene in a population – was described by the Kolmogorov-Petrovsky-Piskunov differential equation (KPP) (Shiryaev and Khimchenko, 2003) in 1937. Since then, many authors (not only geneticists) have applied this equation to describe other biological processes (Kalinin, 1972; Müller and Köhlmann, 2009; Vlasov and Logunov, 1986). The theory of solitons ("lonely", "standing" waves) deals with studying the "nonlinear Schrödinger equation" (NS), which coincides with the KPP equation of cubic nonlinearity (given in abbreviated form) (Takhtadzhyan and Faddeev, 1987):

$$\psi_t = D\psi_{xx} \pm \kappa\psi(\psi^2 - 1),$$

where ψ is a function of spatial and temporal coordinates, D – a linear operator, κ – a positive coupling coefficient.

Note that when choosing the minus sign in the right side of NS, the equation takes the form of the well-known FitzHugh–Nagumo equation (the Hodgkin–Huxley modified model) for distribution of the electrical potential of a nerve impulse along the axon of a neuron (see, for example, Riznichenko, 2010, etc.).

The first term on the right side of the NS equation is responsible for the speed of movement of the wave itself, while the second - for its shape. Here, just the cubic function of ψ is important. Any form is a manifestation of a latent process, invisible to the observer. The function ψ, which describes the motion of a soliton, has two important properties: it retains its shape and energy, and also has non-reflectivity, that is, the ability to avoid any obstacles. Mathematically, these properties were discussed by L.A. Takhtadzhyan and L.D. Faddeev (1987) for the case of solving the NS equation in explicit form and under sufficiently simple initial conditions.

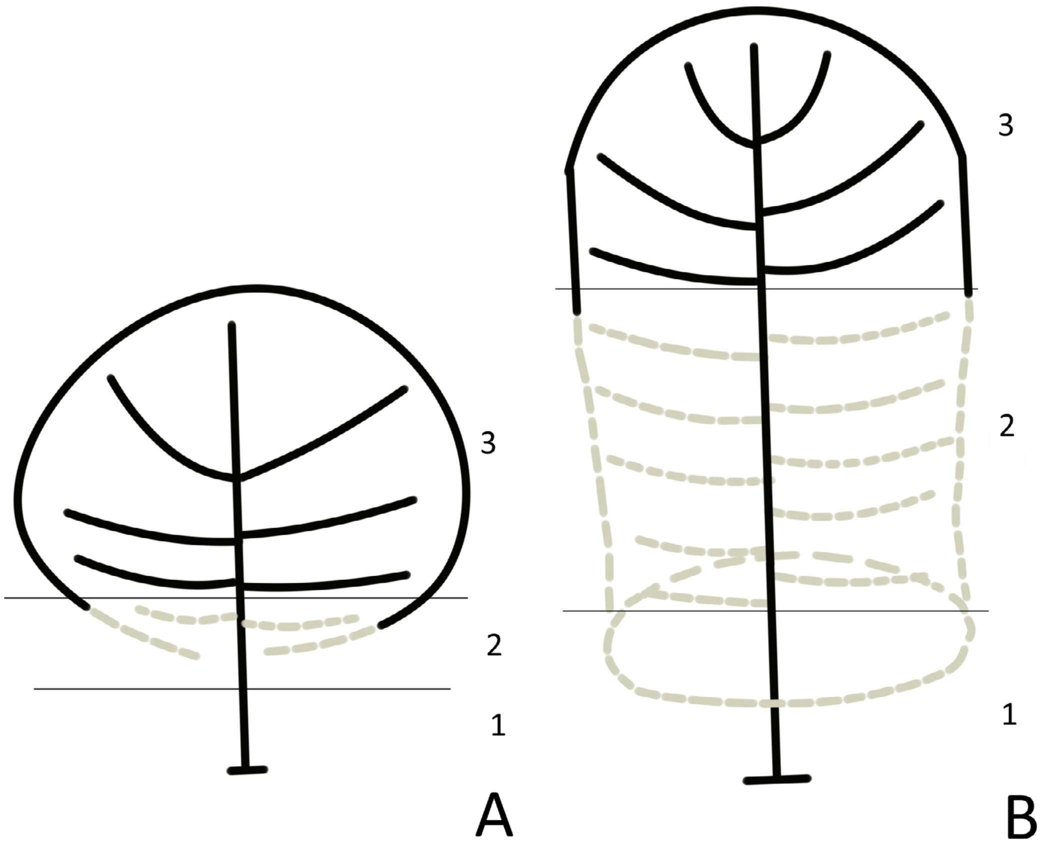

Fig. 8. Scheme of the crown development of a solitary tree and that growing in the community: **A** –crown of a solitary tree; **B** – crown of a tree in the community. 1 – trunk zone without branches, 2 – trunk elongation zone, 3 – zone of branches of the upper crown part.

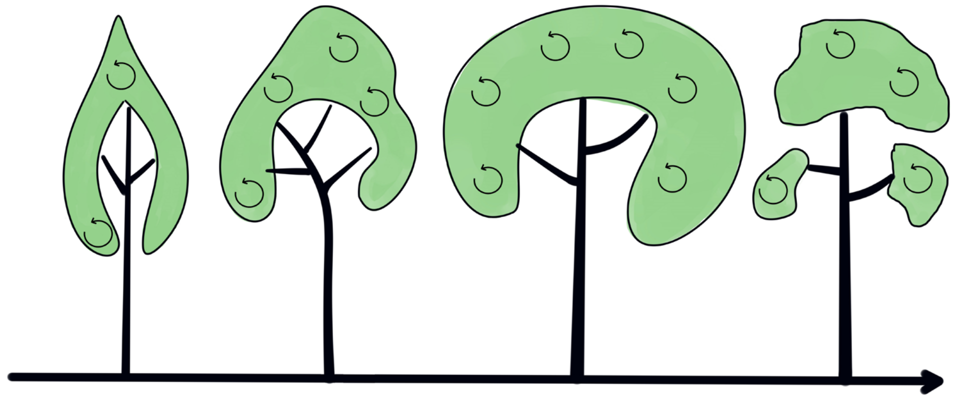

Fig. 9. Dynamics of the crown as a whole in ontogenesis in terms of modeling: from left to right – a diagram of sequential changes in the shape of the tree crown, rounded arrows – development of the crown “lace”.

We also find out that “a soliton is an essentially nonlinear phenomenon” since the existence of such a solution “is possible only due to the nonlinear term in the NS equation” (Takhtadzhyan and Faddeev, 1987). This means that there is a hidden “oscillation process” that determines the shape of the soliton as it moves (sometimes this process spills out in the form of “flaps” on the wave). If we consider the function ψ to be complex-valued (Takhtadzhyan and Faddeev, 1987), then the real part will describe the wave itself, and the imaginary part – the process of oscillation in the internal “latent” time.

These are precisely two processes: external (the construction of the “skeleton”) and internal (the development of the "lace"), which manifest themselves in the crown development. In Fig. 9, the first two states correspond to the “assembly” of the soliton, and the fourth – to its gradual destruction, breaking into parts associated with loss of energy.

Conclusions

1) A tree branch, as a complex of shoots and shoot systems, consists of two large morphofunctional spatiotemporal parts: the “skeleton” and the “lace”. These structures are inherent in the branch as an integral formation, and appear for the first time at this hierarchical level of the crown structure.

2) The primary and secondary “lace”, including two subgroups within the primary “lace’, have been identified in the branch in accordance with its position on the “skeleton” and the time of occurrence,

3) The crown of a tree is a spatiotemporal complex, which naturally develops in ontogenesis. Program-induced growth of the crown begins at the end of the virginal stage of tree ontogenesis. The “skeletal” part of the tree represents many “skeletal” axes both on top of the trunk and at the ends of branches from the trunk. These axes become the basis for the main part of the crown “lace” of each branch and a tree as a whole.

4) The development of the “skeletal” part and the “lace” of the crown are the external and internal (latent) processes of the crown development. At the tree level, the entire complex of the crown “lace” can be considered as an example of the “standing wave” (soliton) mathematical model.

5) The crown shape of an individual tree or that in the community is determined by its development program. In particular, the formation of round and cylindrical shapes of the crown depends on time of development and trunk zoning. The phenomenon of multiple trunks in a single tree is associated with a reduction in the time period of zone 2 (trunk elongation zone) of the tree crown.

6) The development of both the branch from the trunk and the trunk itself is consistent with the Krenke theory of cyclicity.

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