The branching orders of the crown of virginal tree of *Ulmus glabra* Huds

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**Abstract.** Tree crown formation in ontogenesis is a realization of spatial and temporal development program. Based on the study of young individuals of *U. glabra* growing in a natural oak forest, the presence of two groups of axes was shown. One group creates the axes of crown base - "skeleton". The other one appears at a certain age and creates the so-called "crown lace" - a short-lived and replaceable base for photosynthesis. The transition from the formation of the skeletal part of the crown to the next stage, which occurs in the 4th branching order, the shoots of which are significantly shorter, and their number is greater, is quantitatively shown. It is shown that the lengths and number of leaves on shoots in the axes of the first three orders of branching vary within a large range. The maximum variability is reached on the third order of branching, after which it decreases. When crown development reaches the 4th order, spatial growth limitations, which are determined by angles of shoot branching, leaf size, lifetime of axes and shoots, begin to play their roles. Here, more structured crown space is required to optimize the photosynthetic surface.

1. **Introduction**

Unfolding of spatial and temporal structure is essentially the realization of ontogenesis of a tree organism [1]. The process of structure unfolding is realized through annual formation and growth of new shoots as more or less autonomous units [2, 3]. This principle clearly dominates in studies of ontogenesis [4-6]. Formation of tree crown in this case occurs on the basis of formation of branches of different structure. Just a branch from a trunk is a natural form of shoots arrangement in space and time. It is present in any branching tree.

What is the difference between a shoot and a branch in space? A shoot is a linear form of mastering space, a branch consisting of certain correlated shoots represents the volume and area mastered by a plant [7, 8]. It is known that branches significantly change their structure both in the course of ontogenesis and depending on environmental conditions, which significantly complicates their study. In plagiotropically developing plants, a branch realizes the development of space in two dimensions. It should be noted that even in tree species with "three-dimensional" distribution of lateral shoots on maternal one we can show that this distribution is controlled by only two parameters [9]. The tree solves the geometrical problem of arrangement of shoots - segments on the plane - so that they get an...
opportunity to photosynthesize in optimal conditions without shading each other. Identification of features of plagiotropic branch structure is an important problem in the study of tree ontogenesis.

The aim of this work is to determine the role of axes of different branching orders in the branch architecture of the virginal pregenerative stage of _U. glabra_. We are also interested in constant features peculiar to different parts of the crown branch plane. Such areas are organized by the axes of different orders, i.e., by shoot systems, the minimum of which is the biennial shoot system [10].

2. Methods and Materials
The material for the work was 87 plants from the gaps of a decaying oak forest located on the right high bank of the Vorskla River in the Belgorod region. All investigated individuals belonged to the virginile pregenerative age group, formed from seeds and outgrown stage of umbrella-like undergrowth [9-11]. Multiyear features of development of vegetation cover of forest-steppe oak woodland are described in detail in the works of Y N Neshataev [12]. The oak forest is located on the territory of the reserve "Belogorye". Having studied on a large material the characteristics of branches and trees of _U. glabra_, 5 trees were selected for which detailed schemes of all 5158 shoots were made in the laboratory conditions, 23 characteristics of shoots, axes and branches were studied (the order of branching of each shoot was determined). All data were entered into the computer, and an individual code was made for each shoot, allowing to get any shoot from the table. The research was based on biological features of the species, the listing of which can be reduced to the following. _U. glabra_ is a sympodial growing plant with plagiotropic branch growth [13]. Each axial shoot in the process of branching is characterized by pronounced acrotony, in which the first and second lateral shoots from the apex considerably prevail in length and biomass over the remaining lateral shoots. Leaf arrangement of the species is alternate spiral [14, 15]. The sequence of axial shoots composing the tree trunk is characterized by a three-dimensional arrangement of lateral shoots. Axes of the second order start from developed lateral buds of trunk shoots and form plagiotropically growing shoot complexes. Accordingly, their lateral buds give rise to third-order axes, etc. The biennial shoot system (BSS) is a shoot of any order and year with the next-order shoots developed on it in next year. Due to acrotonic development, each BSS has maximum development in length and phytomass on the first two upper lateral shoots. The remaining lateral shoots have significantly smaller sizes. BSS, development of which is suppressed for one reason or another, may have only one strongly developed upper lateral shoot. Besides, there are BSS in the crown on which only the apex shoot develops, continuing the axis, and the lateral shoots are not developed.

The Kolmogorov-Smirnov criterion was used to estimate the type of distribution of quantitative characteristics of shoots and axes. The main conclusions were made on the basis of descriptive statistics and correlation analysis. In comparisons of the lengths and numbers of shoots we used the Mann-Whitney and Clopper-Pearson tests. Statistical processing was performed using STATISTICA 10 package (StatSoft, Inc.).

3. Results and Discussion
Table 1 shows the number, medians and ranges of length distributions of all axes of different branching orders for the trees studied (except for the trunk). Any axis begins with a lateral shoot, and the most axes in the crown has no other shoots. The greatest number of axes (with a relatively small length) has the fourth order.

To study the branch ontogenetic properties, all 5158 shoots of the studied trees were combined together. In figure 1, they are divided into axial and lateral ones and are arranged according to all branching orders encountered. On the first three orders, a zone of intensive (one can say "free") growth of shoots number with increasing order number is distinguished. This is followed by a short plateau in transition from the 3rd to the 4th order and further – by the same sharp decrease in the number of all shoots. Up to the 3rd order, the numbers of axial and lateral shoots grow almost indistinguishable from each other. Then, in the 4th order, their clear division occurs(chi-square test, p<0.0001) and remains until the end of all branching.
Table 1. Descriptive statistics for the investigated axis of trees (Med [Min; Max]).

| Order of axis | N of axis | Length     |
|--------------|-----------|------------|
| 6            | 52        | 13 [2; 95] |
| 5            | 455       | 18 [1; 259]|
| 4            | 1225      | 30 [1; 812]|
| 3            | 920       | 70 [3; 1405]|
| 2            | 186       | 228 [3; 2553]|

| N of shoots in axis | N of axis | Length     |
|---------------------|-----------|------------|
| 1                   | 1591      | 19 [1; 639]|
| 2                   | 693       | 69 [4; 1143]|
| 3                   | 282       | 94.5 [7; 1696]|
| 4                   | 162       | 126.5 [19; 2553]|
| 5                   | 60        | 174.5 [34; 1636]|
| 6                   | 35        | 294 [75; 1519]|
| 7                   | 11        | 608 [163; 4262]|
| 8                   | 4         | 557.5 [208; 1176]|

Figure 1. Total number of axial (color 1), lateral (color 2) and all (color 3) 5158 shoots distributed by branching order. Abscissa axis – branching order, ordinate axis – number of shoots.

In order to understand in more detail the role of different branching orders in the branch architecture of *U. glabra*, a group of shoots (group A) was formed, in which only those shoots were selected which were descendants of the BSS trunk at levels 1 and 2 on top of the lateral shoots, 4,261 shoots in total.

Since the shoot lengths had a pronounced lognormal distribution on each branching order (Kolmogorov-Smirnov test), they were presented in logarithmic scale. Figure 2 shows the curves of dependences of shoots number and sums of logarithms of shoot lengths from branching order. Increase
of total number with simultaneous decrease of shoot length of the fourth order together with the data of table 1 and figure 2 indicates a fundamental change in the structure of this order axes in comparison with the axes of previous orders (Mann-Whitney and Clopper-Pearson tests for the 3rd and 4th orders, both give p<0.00001).

**Figure 2.** Sums of logarithms of lengths and number of shoots from all 4261 shoots of *U.glabra* on different branching orders. Abscissa axis–branching orders of shoots (2, 3, ..., 6); Ordinates axis – axis of trait values; color 1 – number of shoots; color 2 – sum of logarithms of shoot lengths.

Figure 3 shows the change in average size and variability of shoots of group A. The maximum variability is reached in the third order, after which it falls.

When modular organism of a tree is mastering space, its most important task is to arrange the shoots at a convenient distance from each other for photosynthesis. One strategy is to move as far away as possible from the photosynthetic planes of past years to avoid overlap in the internal architecture of the crown. It is best to release new axes in planes orthogonal to those ones. An axis directed so will not overlap them regardless of its length or time of growth. This justifies naming such a strategy as a free growth strategy.

At the initial stage of development of the first three orders of branching of a young tree, this strategy gives good results. "Skeleton" composed of such shoots and BSS remains for many years, sometimes – for the rest of the tree’s life (figure 5) [16, 17]. In figure 4, such axes are represented by solid arrows.

But in our space, it is possible to build no more than three planes perpendicular to each other. The axis of the fourth order (dotted line in figure 5), orthogonal to its parent alone under unrestricted development, would necessarily cross some old photosynthetic surface, which would result in partial shading. It happening, because lateral shoots located lower than the first and second above lateral shoots on the same annual growth will form a plane by short linear axes of shoots, whose leaves are located in the same old photosynthetic surface.
Figure 3. Distribution of mean and standard deviations of logarithms of lengths of 4261 shoots of *U. glabra* by branching orders. Abscissa axis—branching orders of shoots (2, 3, ..., 6); Ordinates axis—axis of the statistics values; color 1—mean values of shoot length logarithms; color 2—their standard deviations.

Figure 4. Scheme of mutual arrangement of first-order axes in free-growth strategy. α, β, γ—photosynthetic planes; v1, v2, v3, v4—vectors corresponding to their mutually perpendicular directions.

Figure 5. The upper part of the crown of *U. glabra*. The ellipses mark the preserved "skeleton" of the axes of the first orders of branching.

All this means that for the axes of the fourth and larger orders of it, the strategy must be changed. At least now it must also take into account the sizes of shoots and axes. The branching angles, leaf size, lifetime of the axis and shoot, and these of their neighbors begin to play a role.

The systems of shoots from the fourth order and higher become smaller and more structured. The latter can be seen from figure 3 where shoots of each next order, starting from the 4th one, have lower variability, and the number of shoots (axes) of the 4th order significantly exceeds all the others (see also table 1). Such properties of the axes having the order greater than the third one lead to formation of a special system of shoots on the tree, which is called "crown lace". The combination and
arrangement of the crown "skeleton" and its "lace" is unique for the species and makes it recognizable in the leafless state. Such structuredness is associated with a decrease in the number of high order axes, and in the end, explains the limited number of total branching orders in the tree. This has significance including tree pruning [18].

In this age stage, the fourth order is of such importance as the real crown of a mature specimen is formed here. A strongly shaded young plant may have more orders. But these orders are very short-lived and in most cases are flat and easily lost, leaving no geometrical trace in the structure of the plant crown.

Relative branching of a shoot for each order is defined as a ratio of the number of lateral shoots of the next order to the number of all shoots of this order. Figure 6 shows a graph of branching distribution for different orders of shoots of the trees under study.

![Graph showing branching distribution](image)

**Figure 6.** Relative branching of all possible orders for all 5158 examined shoots. Abscissa axis – branching orders of shoots (1, 2, 3, ..., 6); Ordinates axis – values of relative branching.

Elm is characterized by a short petiole, with a leaf size of 6-7 cm in length. Figure 3 makes it possible to calculate an approximate geometrical average of shoot lengths of different orders: for the 4th order it is 25 mm, for the 5th order - 14 mm, and for the 6th order - 10 mm. The commensurability of ashoot length with a leaf length makes branching of the first one practically impossible. It is calculated that average number of leaves on a shoot of 4th order is 3.3, of 5th order - 2.7, of 6th order - 2.5 leaves.

The fact that average branching ability of 3rd order shoots is less than unit indicates that the increase in number of 4th order shoots is connected, first of all, with the change of shoot formation strategy of such axes.

4. Conclusion

Axes of the fourth order of branching play a special role at virginial stage and in development of a tree as a whole. It is from this order that construction of tree "skeleton" ends and formation of "crown lace" begins. This can be clearly seen in graphs of distribution of length and number of shoots and crown axes of virginial stage by all possible branching orders. Axes of "skeleton" are characterized by intensive branching. Branching of the 4th and subsequent orders is significantly lower, which limits the total number of branching orders on the tree. Size characteristics of a leaf, especially with a small petiole, do not allow unlimited reduction of shoot length in the "crown lace". Further survival of a tree is connected with stiffer stacking of shoots in flat shoot systems while creating photosynthetic surface.
Acknowledgments
We express our gratitude to A S Shapovalov, director of the Belogorye Nature Reserve, and the staff of the reserve for the opportunity to work fruitfully in the reserve.

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