On the structure of tree crown on the example of biennial shoot systems of *Ulmus glabra* Huds.

I S Antonova*, M S Televinova¹, M V Kremeneckaia¹, V A Bart²,³

¹Chair of Geobotanics and Plant Ecology, Saint Petersburg State University, 41 Sredniy prospect VO, St. Petersburg 199004, Russian Federation.

²Chair of General Mathematics and Informatics, Saint Petersburg State University, 41 Sredniy prospect VO, St. Petersburg 199004, Russian Federation.

³Research laboratory of biostatistics, Almazov National Medical Research Centre, 2 Akkuratova street, St. Petersburg 197341, Russian Federation.

*Corresponding email: ulmaceae@mail.ru

**Abstract.** Using the example of crowns of *Ulmus glabra* Huds. individuals of the virginal age state, the structure of biennial shoots systems (BSS), the occurrence of different types of them in the crown as a whole and in its different parts are analyzed. Identified features of the structure of the maternal shoot for three functionally different types of BSS: Filling-up, Growth, Basic and Narrow-Outline and Super-growth. Comprehensive analysis of morphology of the maternal axis and lateral shoots revealed the characteristics and enabled us to construct a discriminant function significantly separating the three types of BSS. The predictive accuracy of its classification by sample values is 94 percent. Special zones are identified on the maternal shoots of Growth and Basic BSS, which determine their difference and similarity. The fact that such zonality of the maternal shoot is determined only in the second year of his life corresponds to the idea of BSS as a single module of space-time aggregation in tree crown.

1. **Introduction**

Reconstruction of the spatial structure of the crown of a tree is a problem whose solution is connected with the study of the placement of the photosynthetic surface that provides nourishment of the tree organism. It is known that abiotic components, community and anthropogenic factors affected by the spatial structure of a tree, causing a different density of leaves, and therefore - the power of branching.

It is of great practical interest that spatial structure of the crown of a tree is undoubtedly connected with the number of fruits that a plant can create or that interception of sunlight has a significant impact on all tiers of the plant community located below.

Currently, studies of the spatial structure of crown of tree are carried out on the basis of various methods of mathematical modeling. At the same time, there are few fundamental approaches developed in different schools. Such methods are the L-systems of the Lindenmayer school [1] and Prusinkiewicz school [2], the hidden Markov models [3]. Graph theory was repeatedly used to describe the structure of the crown. The original source of these developments was the work of 1970 Halle and Oldeman [4] on architectural models of tropic woody plants. In Russia, these problems are mainly investigated by experts in the field of the life-form of trees. Much attention here is given to the processes of tree growth [5-8].
The undoubted similarity in the structure of the crown of deciduous woody plants of the middle zone and North-West Russia prompted us to look for shoot system in the crown of the species. Having studied more than 30 species of woody plants in the temperate zone, we managed to distinguish several types of biennial shoot systems (BSS), repeated in crowns of each species [9, 10].

The purpose of this study is to analyze the shoot systems of trees of *U. glabra* in the virginal age stage with the aim of quantitative analysis of some types of BSS and the identification of their features.

2. Materials and methods

*U. glabra* is widespread in the broadleaf forest communities of the European part of Russia. The species has a characteristic branch structure with plagiotropic growth, lateral branching, acrotont shoots and sympodial growth. Growth shoots *U. glabra* described in detail in the works of I A Grudzinskaia [11-13].

The material was collected in the central part of the species distribution *U. glabra*, in the natural habitats of the mountain oak forests of the Belogorye reserve of the Vorskla Forest section. Tree stands here are represented by both natural forest plantations and forest cultures. *Quercus robur* L. has others satellites besides *U. glabra* in this plant communities. *Fraxinus excelsior* L., *Tilia cordata* Mill., *Acer platanoides* L. [14, 15]. In overmature communities, trees of the 1st and 2nd layer fall out. The material was collected in the northern, central, and partly eastern parts of the windows, where optimal conditions are formed for the undergrowth individuals and the virginal age state of *U. glabra* [16]. In the course of the work, biennial shoot systems from 230 individuals aged from 15 to 23 years of the virginal age stage of *U. glabra* were investigated. They were carrying leaf plates and located to the upper part of the crown. The age state was determined according to the classification “Diagnoses and Keys of Age States” [17]. Healthy plants without visible damage was chosen. Ecotopic conditions for all places of material collection can be considered similar in the position in the relief, hydrological and soil conditions. A diagram of the branches was drawn up for each plant with detailed measurements of the lengths of all internodes of the maternal shoots, the time of their formation, the number of leafy organs (bud scale and green leaves). Also were measured branch angles of the lateral shoots, the diameters of the maternal shoots, the total length and number of leaves of the lateral shoots.

In the crown of *U. glabra* the functional types of biennial shoot systems (BSS) are clearly distinguished according to our earlier studies [18]. There are Growth, Basic, Filling up, Narrow-outline and Super-growth. The selection occurs according to the criteria of the function that the system perform in the crown, according to the features of the geometric contour of the system as a whole, which is associated by the metric characteristics of the maternal and lateral shoots, with the duration of the system's existence in the crown and with the location of the maternal shoot of the BSS in the axis of the large branch from the stem.

BSS of Growth type perform the most important function of capturing space for the growth of a tree and the development of its crown. They have a powerful maternal shoot, which is part of the axes of the first or second order of branching. They have a greater (relative to the Basic BSSs) number of lateral shoots, of which the first 3 are most pronounced (counting from the upper end of the axial shoot).

The Basic BSS provide a balance state of the photosynthesizing surface at a time when growth processes in the crown are attenuated and it is more oriented towards generative development. BSS of this type are characterized by a certain number of lateral shoots with gradually increasing sizes to the top of maternal shoot. The difference between the lateral shoots is not as pronounced as in the Growth BSS. The Basic shoot systems are located mainly on the axes of the third and on the aging axes of the second order.

Narrow-outline BSS are formed in virginal age condition. In addition, the presence in the crown of Narrow-outline BSS may indicate a lack of some resources for the life of the tree, for example light. The shoot systems of this type perform the role of axes for the subsequent displacement of small shoot
systems further to crown periphery. The Narrow-outline system is characterized by an elongated maternal axis with short and uniform lateral shoots. A more detailed description of BSS of various types can be found in the article from 2016, which describes the system of hierarchical levels of the crown structure of woody plants of the temperate zone [10].

The Growth systems are located on the axes of the 2nd order, and the Basic ones - on the axes of the 3rd, 2nd and 4th orders. The location of the same axes makes it difficult to determine a system to the specific group. The same can be said about the influence of coenotic and environmental factors. It is the reason of necessity to select the delimiting features.

Based on the data obtained, discriminant analysis was performed in the computer package STATISTICA 10 (StatSoft, Inc.). Mann-Whitney and Kolmogorov-Smirnov non-parametric tests or Student's test (for more subtle comparisons in the case of normal distribution of data) were used for pairwise comparisons of BSS characteristics of different types.

Preliminary studies have shown that the upper part of the crown of a tree is easier to see visually and is the most representative on the composition of the BSS, so it was chosen for analysis.

3. Results and Discussion
Deciduous woody plants of the north-west of Russia differ in the morphological structure of the crown. That is, for example, the crown of a maple differs from an elm or oak crown, but at the same time all plants of the same species have an similar structure of placement of shoot complexes of different scale (from shoots to the most powerful branches). In the course of the work, we studied morphological features and constructed a discriminant rule that separates the type of BSS U. glabra.

Were investigated all foliiferous shoots of 30 the U. glabra trees of virginal age state and with and their maternal axes formed a year earlier. Thus, all bearing leaves biennial shoot systems of crown are considered.

Analyzing the process of growth of the branches, we were convinced that the crown is divided into 3 parts quite successfully: the bottom of crown, where the growth processes have already ended and the process of cleaning the branches is in progress; the middle part of crown, where process of growth and attenuation are in balance but the growth process slightly prevail over the dying off process; and the upper part of crown, where domination of the growth processes is clearly pronounced. The greatest variety of shoot systems is represented in the upper part of the crown (Figure 1). The pie charts in Figure 1 represent the full composition of BSS by types for the most typical tree in the sample. As can be seen in the diagrams (Figure 1), the main variety of BSS appears on the upper part of the tree crown. In the middle part of the crown in addition to Filling-up BSS there is a significant amount of the Basic ones. Filling-up BSS dominates in the bottom part of crown.

The diagram (Figure 2), representing the shares of the main zones of the maternal shoot, distinguished by the contour of the BSS formed on it, is important for characterizing the differences in the types of BSS in the shape of its geometric contour. The Filling-up BSS are excluded from this diagram because of the most of them have degenerated upper and middle zones.
Figure 1. The figure shows the characteristic of the tree according to the composition of the BSS. It is the tree of virginal age state which grew in the northern tip of the window in the ash-oak forest. The total number of shoots on the tree is 971, the number of BSS with lateral shoots of the current year is 247.

The “box-and-whiskers” diagram (Figure 2) shows the ratios of the length of three consecutive zone of internodes on the maternal shoot of BSS to its length: the zone of the three first internodes from the top of the shoot, the zone of remaining internodes with lateral shoots and the zone without lateral shoots. It is clearly seen that in the sequential triad “Basic-Growth-Super growth” the increase of mean length of the shoot is mainly determined by its middle part.

Figure 2. Multiple “box-and-whiskers” diagram of the ratio the lengths of three consecutive zones on the maternal shoot to their length; q1 - the zone of the three first internodes from the top of the maternal shoot, q2 - the zone of the remaining internodes with lateral shoots, q3 - the zone of internodes without lateral shoots.
The diagram in Figure 3 compares the lengths of the lateral shoots of Basic and Growth BSS types. The top down notation of the lateral shoots on the maternal shoot in Roman letters starts with B, since the letter A is left for the axial shoot on the maternal one.

![Diagram showing the comparison of lateral shoot lengths for Basic and Growth BSS types.](image)

**Figure 3.** Decimal logarithm of lengths of lateral shoots of the Basic and Growth shoot systems; B, C, D, E, F, G – the first lateral shoots, sequentially, from the top of maternal shoot.

Dashed lines connect successively the medians of lengths of the 1st, 2nd and 3rd lateral shoots of the Basic BSS and 4th, 5th and 6th – of the Growth ones, numbering from the top. All three lines are almost horizontal. The non-parametric test Mann-Whitney did not find difference in pairwise comparing the distributions of lengths of the lateral shoots connected by these lines \(p(B-E) = 0.35, p(C-F) = 0.36, p(D-H) = 0.95\). We have also checked that the logarithms of the corresponding lateral shoot lengths withstand the Kolmogorov-Smirnov test for normality of distributions, their variances withstand the F-test for pairwise equality of variances, and the means of the logarithms stand t-test for pairwise equality of their maternal shoot. The dotted lines in figure 3 are parallel and close to the medians in both groups of BSS, which indicates a good fit of median regression line by the exponential model in both cases, and with very similar exponential power [19, 20]. In general, all this indicates the correspondence of the lengths of horizontally connected medians of internodes and the presence of a zone in the three upper internodes, specific to Growth BSS and absent from the Basic ones. This zone determines the presence of the most functionally significant lateral shoots on the scale of the tree as a whole, responsible for the capture of space.

In this regard, special attention is paid to the sharp decrease in the range of the values of the longest lateral shoots B in the Growth BSS compared to those located farther from the maternal apex.

Proximity to the exponential model implies the presence of factors of the free growth model, with an increase in both values and their variation. But the longest lateral shoots appear to be controlled by the growth program of the whole tree.

Table 1 shows the descriptive statistics of the main characters studied for 4 types of BSS. Data are presented as Mean ± Std.Dev. or Median [Minimum; Maximum] in case of asymmetrical distribution (Kolmogorov-Smirnov test). For each characteristic in Table 1, the Kruskal-Wallis criterion distinguishes 4 types of BSS at a significance level of \(p <0.0001\).
where, \( L \) – length of maternal shoot; \( Ngr \) – the number of green leaves of maternal shoot; \( N \) – the number of all leaves of maternal shoot; \( a, b, c, d, i \) - length of internodes on maternal shoot from the top; \( Nsh \) – number of lateral shoots; \( NB, NC, ND, NI \) – the number of green leaves of lateral shoots sequentially from the top of the maternal shoot; \( B, C, D, E, F, G \) – lengths of lateral shoots. \( Nal \) – the number of leaves on all lateral shoots.

For the problem of distinguishing BSS types by sampling values, a forward stepwise discriminant analysis was applied. From the totality of 26 variables: the lengths of the first 6 upper internodes of the maternal shoot, its length, the total number of leaves on the maternal shoot, the first four (from the top) and all the lateral shoots together, the lengths of all shoots listed above, and the ratio of the lengths of the first three (from the top) lateral shoots to maternal length (Table 1). Asymmetric variables values were logarithmized. The stepwise procedure left only the following variables in the analysis (Table 2).

| Type of BSS | Super-growth | Narrow-outline | Growth | Basic |
|------------|--------------|----------------|--------|-------|
| \( L \)    | 715 [606; 860] | 447 [279; 710] | 526 [308; 759] | 333 [160; 499] |
| \( Ngr \)  | 15 [12; 16]   | 11.5 [9; 15]   | 12 [9; 15]   | 9 [7; 11] |
| \( N \)    | 23 [20; 24]   | 19.5 [17; 24]  | 20 [17; 23]  | 18 [15; 19] |
| \( a \)    | 36.6 \pm 10.49| 37.8 \pm 8.58  | 43.1 \pm 13.15| 46.2 \pm 13.27|
| \( b \)    | 52.8 \pm 7.93 | 53.4 \pm 11.03 | 59.8 \pm 12.04| 55.9 \pm 11.80|
| \( c \)    | 67.6 \pm 7.65 | 59.0 \pm 8.61  | 67.0 \pm 10.63| 54.5 \pm 10.67|
| \( d \)    | 73.1 \pm 12.21| 62.0 \pm 9.12  | 67.2 \pm 12.36| 51.6 \pm 11.01|
| \( i \)    | 74.9 \pm 8.80 | 58.1 \pm 13.83 | 63.7 \pm 12.61| 44.3 \pm 11.68|
| \( f \)    | 78.9 \pm 6.01 | 53.1 \pm 13.83 | 57.6 \pm 14.10| 34.5 \pm 10.38|
| \( Nsh \)  | 9.6 \pm 1.13  | 6.4 \pm 1.59   | 7.1 \pm 1.19  | 4.4 \pm 0.87 |
| \( NB \)   | 6.9 \pm 1.17  | 5.0 \pm 0.87   | 6.5 \pm 1.16  | 4.8 \pm 0.83 |
| \( NC \)   | 6.6 \pm 1.51  | 4.5 \pm 0.86   | 6.2 \pm 1.28  | 4.2 \pm 0.93 |
| \( ND \)   | 6.7 \pm 1.66  | 4.1 \pm 1.09   | 5.5 \pm 1.22  | 3.4 \pm 0.98 |
| \( NI \)   | 6.1 \pm 1.54  | 3.6 \pm 0.93   | 5.0 \pm 1.16  | 3.0 \pm 0.94 |
| \( B \)    | 142 [91; 361] | 66.5 [38; 138] | 157.5 [89; 328] | 67 [29; 157] |
| \( C \)    | 160 [85; 353] | 54.5 [18; 90]  | 133 [48; 344] | 41 [17; 120] |
| \( D \)    | 152 [67; 391] | 39 [9; 72]     | 87 [19; 226]  | 25.5 [4; 130] |
| \( I \)    | 102 [70; 316] | 35 [11; 60]    | 68.5 [11; 145] | 16 [5; 106] |
| \( B/L \)  | 0.21 [0.13; 0.43] | 0.15 [0.1; 0.2] | 0.29 [0.04; 0.7] | 0.22 [0.1; 0.8] |
| \( C/L \)  | 0.25 [0.11; 0.41] | 0.12 [0.03; 0.2] | 0.25 [0.06; 0.52] | 0.14 [0.05; 0.3] |
| \( D/L \)  | 0.24 [0.08; 0.45] | 0.08 [0.03; 0.15] | 0.18 [0.03; 0.4] | 0.08 [0.03; 0.3] |
| \( Nal \)  | 50.3 \pm 9.34 | 24.1 \pm 7.87  | 40.0 \pm 9.38 | 16.2 \pm 4.42 |
Table 2. The table of factor loadings of discriminant functions.

|              | Root 1 | Root 2 |
|--------------|--------|--------|
| $N_{al}$     | -0.80  | 0.04   |
| $\log B$    | -0.46  | -0.46  |
| $N$          | -0.45  | 0.53   |
| $\log L$    | -0.43  | 0.31   |
| $N_a$        | -0.39  | -0.20  |
| $\log D/L$  | -0.32  | -0.28  |
| $\log C/L$  | -0.32  | -0.42  |
| $\log B/L$  | -0.16  | -0.59  |
| $a$          | 0.06   | -0.25  |

where, $N_{al}$ – the number of leaves on all lateral shoots; $B$ – length of second lateral shoot; $N$ - the all number of leaves of maternal shoot; $L$ – length of maternal shoot; $NB$ – the number of green leaves of first lateral shoot; $B$, $C$, $D$ – lengths of the lateral shoots; $a$ - the first internodes of the maternal shoot from the top; $\log$ – decimal logarithm.

The correlations in shaded cells in Table 2 exceed 0.33 in absolute value.

Root 1 is the discriminator of the Basic and Growth BSS, and Root 2 distinguishes them from Narrow-outline ones (Figure 4).

Figure 4. A joint scatterplot of the two discriminant functions constructed together with 95 percent confidence ellipses for the three studied types of BSS.

4. Conclusion

According to 9 main morphological characteristics: the length of the first upper internode of the maternal shoot, its length; the total number of leaves on the maternal shoot, the number of leaves on the first lateral shoot (from the top), and the number of leaves on all the lateral shoots, the length of the first lateral shoot, and the ratio of the lengths of the first three (from the top) lateral shoots to the length of the maternal shoot, the sample values of the three types of BSS are differed from each other with accuracy of up to 94 percent.
The lateral shoots of the Growth type BSS determine a zone consisting of the three upper internodes of the maternal shoot and this zone is completely absent in the Basic BSS. This zone defines the main difference between the two types of BSS and is the basis for functionally significant lateral shoots responsible for capturing space on the scale of the whole tree.

The fact that zonality of the maternal shoot is determined only in the second year of its life, corresponds to the representation of the biennial shoot system as a single space-time aggregation.

The ratio between of Growth and Basic BSS, which are important in formation and functioning of the crown, allow to specify quantitative estimates of productivity, as well as the production of oxygen, carbon dioxide and organic compound.

References

[1] Lindenmayer A 1968 Mathematical models for cellular interaction in development J. Theoret. Biology 18 280 - 325
[2] Prusinkiewicz P and Lindenmayer A 2012 The Algorithmic Beauty of Plants Springer Science & Business Media 240 p
[3] Durand J-B, Guedon Y, Caraglio Y and Costes E Analysis of the plant architecture via tree-structured statistical models: the hidden Markov tree models New Phytologist 2005 166 (3) 813-25
[4] Halle F, Oldeman R A and Tomlinson P B 1978 Tropical Trees and Forests: An Architectural Analysis (Berlin) 441 p
[5] Gatt suk L E 2008 Modern Approaches to Plant Structure Description [Sovremenny Podkhody k Opisaniiu Struktury Rasteniia - in Russian] 27-47
[6] Gasheva N A 2012 Herald of Ecology, Forestry and Landscape Sci. [Vestnik Ekologii, Lesovedeniia i Landshfovedeniia - in Russian] 12 99-110
[7] Getmanets I A 2008 Herald of TVGU. Series: Biology and Ecology [Vestnik TvGU. Seria: Biologia i ekologija - in Russian] 9 47-50
[8] Mazurenko M T and Khokhriakov A P 1991 Biology Bulletin Reviews [Zhurnal Obsheei Biologii - in Russian] 52 (3) 409-21
[9] Antonova I S and Bart V A 2018 Bulletin of the Botanical Garden of DVO RAN [Bulleten Botanicheskogo Sada DVO RAN - in Russian] 19 23-37
[10] Antonova I S and Fatianova E V 2016 Botanicheskii Zhurnal 101 (6) 628-49
[11] Grudzinskaia I A 1962 Problems of Botany [Problemy Botaniki - in Russian] 6 219–31
[12] Grudzinskaia I A 1968 Proc. All-Union Interuniversity Conf. on Plant Morphology [Vsesoyuznaya mezhvuzovskaia konferentsiia po morfologii rasteniia - in Russian] (Moscow) pp 84-5
[13] Grudzinskaia I A 1974 Botanicheskii Zhurnal 59 (8) 1160–71
[14] Neshtaev Yu N 1986 Proc. Conf. Comprehensive studies of biogeocenoses of forest-steppe oak forests [Kompleksnye issledovaniia biogeotsenosov lesostepnyh dubrav - in Russian] (Leningrad) pp 32–48
[15] Smirnova O M 2017 European Russian Forests ed O M Smirnova, M V Bobrovsky et al (Dordrecht: Springer Science + Business Media B V) 564 pp
[16] Leonova N A 1999 Forestry Sci. [Lesovedenie - in Russian] 6 59–64
[17] Chistyakova A A and Kutina I S 1989 Diagnoses and keys of age conditions of woody plants (Trees and Schrubs vol 1) [Diagnozy i klyuchi vozrastnyh sostoyaniy lesnyh rasteniy (Derevia i Kustarniki tom 1) - in Russian] ed O V Smirnova (Moscow) pp 82–89
[18] Antonova I S and Bart V A 2019 Botanicheskii Zhurnal 104 (2) 71-85
[19] Seber G A F and Lee A J 2003 Linear Regression Analysis (Wiley) 582 p
[20] Koenker R Quantile Regression 2005 (Cambridge University Press) 349 p