bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Fractal model of emergence of a proto-plant

V.V. Galitskii

Institute of Physical-Chemical and Biological Problems of Soil Science RAS
Pushchino, Moscow region, Russia

ABSTRACT Sectional model of the tree's system branches, which was published earlier, was extended in the range (0,1) for model's allometric parameter μ, binding magnitude of the green biomass of a tree and its size (for spruce μ ≈ 1.83). The model has shown presence of a biomass of branches in this range that indicates, according to fractal geometry, on the placement of a green biomass in the form of set of "points". In turn according to contemporary notions about endosymbiotic character of appearance of organelles in eukaryotic cell this was interpreted as begin of endosymbiosis of cyanobacteria and a host (protist) and has been modeled by the groups placement of growing number of points on an interval under initial limitation the number of points per group. The limitation is connected to the initial absence in protist an infrastructure which is need for the growing number of cyanobacteria. It has been demonstrated that initially in course of increasing total number of points the parameter μ decreases from 1.0 to 0.25 under the fixed number of points per group and then increases to 1.0 under the fixed number of groups. This gives an initial deceleration of growth of proto-plant's size (a characteristic geometrical size of the point set) and then the exponential growth after deliverance from limitation of point number per group in course of host evolution. Similar initial deceleration of growth can be seen now also in higher plants. Morphological analogy of situations of beginning the plant embryogenesis and of seed germination with the situation described by the model of proto-plant appearance is discussed.

Keywords: *sectional model of a tree, fractal parameter, set of photosynthetic points, group placement, endosymbiosis, trajectory of evolution, proto-plant, initial deceleration of growth.*

INTRODUCTION

In [1] has been allocated the sectional tree structure with periodic growth, which can be described by a simple model of the dynamics biomass of section using the notion of co-axial adjacent virtual trees, nested each to other and periodically appearing on the top of the tree. Biomass of each next virtual tree is part of previous one and accordingly, the biomass of each section consisting of biomasses of its branches, may be calculated as the difference between biomasses the two adjacent virtual trees. Considering the dynamics of real tree biomass known and taking it for the virtual tree as

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

an initial approximation, we can thus obtain the dynamics of biomass distribution along sections (and height) of the real tree [1]. When using assumption about the monotony and limited dynamics of the green biomass of a tree this model has demonstrated some of the properties of a tree existing in reality. The model showed also the possibility by varying the three parameters to obtain the biomass distributions in height (sections) of the tree that may be associated with a rather distant from each other tree species [2]. This model has been used as a basis for analyzing the dynamics of distribution and distant transport of assimilates along the freely growing tree using "diffusion" formulation of transport mechanism of mass-flow. The model of distant transport has shown the possibility of the so-called "a respiratory barrier" associated with the power-law dependence of costs on the breath on the magnitude of biomass, as well as the effect of the stratification of the tree by interleaving groups of the donor and acceptor sections [3]. Combination of sectional model and the two-dimensional model of biomass dynamics of a tree growing not freely [4] has demonstrated that the lower sections of a tree growing in a limited area (polygon) in the community are in oppression and die (more rapidly in comparison with the freely growing tree). As a result, at the top of the tree new sections appear and they are growing freely, and the bottom sections die, i.e. occurs wave of biomass that moves up along the tree stem [5].

In [6] the sectional tree model was extended to the branches system that carry green biomass of respective sections of tree. Parametrizing model of branches system using nature data [7] about lifespan $t_{D,j}$ of spruce branches of four orders (j = 1, ..., 4) showed that in this case model of system of regular branches must also take into consideration two known features of spruce – initial growth deceleration [8] and existence and role of inter-verticil branches [9, 10]. The combined model is in good agreement with natural data and with other publications. Model only regular branches showed only the branches of the 1st order, and when it is complemented by sub-model of the initial deceleration of growth it shows the branches of all 4 orders [6, fig. 2b, d]. This article discusses some of the consequences of interpretation of the allometric parameter μ linking green biomass B and geometric size H of a tree

$$B \sim H^{\mu} \tag{1}$$

as a fractal parameter, and dissemination of model to the range μ (0, 1). For spruce the value of parameter was obtained μ ≈ 1.83 [6]. It lies in the range [1, 2) corresponding to a set of linear elements (conifer needles) [11].

Figure 1 shows dependence $t_{D,j}(\mu)$ of lifespan for system of the j-orders branches. It shows features of the model system of regular branches, which was augmented by the sub-model of initial growth deceleration for the range of fractal parameter μ (0, 1) with the set of other parameters of spruce from [7, 12]. This range according to the ideas of fractal geometry [11] corresponds to the set of points. In

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

this range of μ there are the branches of first 3 orders, i.e. biomass is placed along height of "tree" in the form of green "dots" what is not observed visually in the higher plants. The article [12] demonstrated that the appearance of branches of orders j = 1, 2 and 3 in this range of μ is a consequence of accounting initial deceleration in growth model.

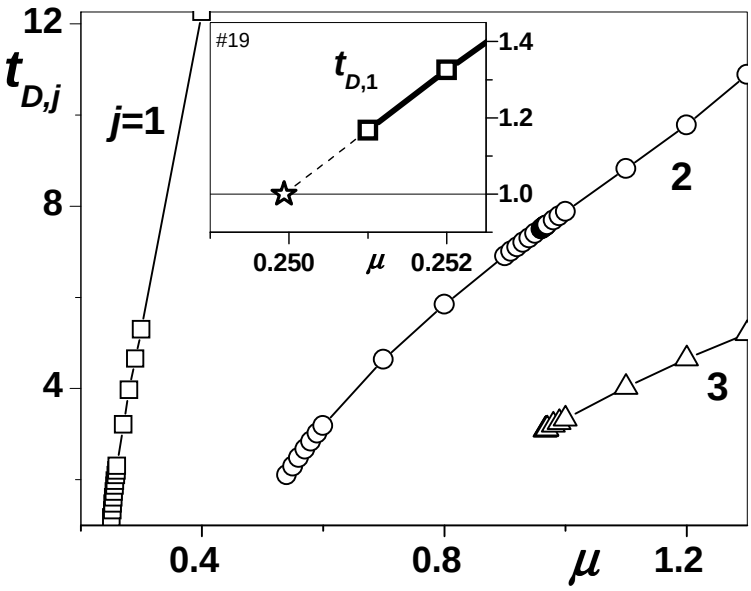

Fig. 1. The dependence of the lifetime of the j-branches $t_{D,j}$ of regular branches' model with adding of the sub-model of initial growth deceleration [6]; other parameters are as for spruce [6, 7]. Inset for the 1-branch in a larger scale, an asterisk □ the appearance of the 1-branch for parameter set μ#19 [6].

ON THE FRACTAL PROPERTIES OF SETS OF POINTS ON THE INTERVAL

The mechanisms of photosynthesis of higher plants and cyanobacteria are practically identical. This is due to the history of the appearance of plants in symbiosis and / or endosymbiosis of cyanobacteria and protists. According to [13-15], chloroplasts of modern plants are the descendants of the cyanobacteria which undergone transformation in the course of evolution after the organization of endosymbiosis with protists. Thus, photosynthesis in plants and is now being performed by "point" elements (chloroplasts), placed in the cells of green biomass of plants [15, 16]. Features of placing a set of points in space affect the value of a fractal parameter and thus the efficiency of using of sunlight in the plant growth. It should be noted that a tree and set of points are natural objects of the fractal geometry, which allows using its methods directly [11].

Assuming that the initial invasions of cyanobacteria into the cell of endosymbiosis' host were sporadic and have not lead directly to a compact placement and considering that protists are by several orders bigger than cyanobacteria, we can estimate the parameter μ for the set of N_p points in an interval using the usual algorithm of box counting [11]. Placing points of a set not in the groups of points on an

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

interval but with uniform random placement or with placement with fixed step leads to $\mu \approx 1.0$. Placement in groups of points on the interval gives $\mu < 1$. It can be noticed that Cantor point sets, which often considered as a simple example [11], are actually group placements with $\mu < 1$.

For group placements of points on the interval [12]: 1) the value μ is practically independent of A – relative value of on-off space ratio for stepper placement of groups; 2) μ depends on type of the placement of points in the groups; 3) for stepper placement of groups the value μ quite resistant to accidental and rather large deviations of groups' location.

FRACTAL TRAJECTORIES OF PROTO-PLANT EVOLUTION

Endosymbiosis is cohabitation of protist and cyanobacteria within it, as a natural development of their symbiosis during the trophic relations between "heterotrophic protists" and "photosynthetic prokaryotes" [13: 25]. Thus cyanobacteria, being in the capsule, the inner wall of which has the same properties as the outer wall of the host, appeared in natural conditions close to them in symbiosis and in result continued normal existence in endosymbiosis [17]. Endosymbiosis begins with a minimal number of cyanobacteria inside the host – $N_p = N_g * n_g$ and in groups – n_g (N_g is the number of groups). This is determined by the initial lack in host of a necessary system for supplying cyanobacteria and distribution of their products (i.e. an infrastructure). The number of groups N_g, seems less critical, since supplying them in this case is local and may be carried out at symbiotic level. During evolution of endosymbiosis, the number of groups N_g containing 1 and / or 2 dots at first should increase and then upon reaching a certain level of supplying (appearing infrastructure) quantity n_g of cyanobacteria per group may start to increase. Fig. 2 shows the dependence of $\mu(N_g)$ (empty symbols) for some fixed values of n_g. The parameter μ decreases from 1 to ≈ 0.25 with the growing number (from 1) of groups N_g and a minimum fixed number ($n_g = 2$) of points per group. The same figure shows the dependence of $\mu(n_g)$ with increasing n_g for several fixed values N_g (black symbols). The parameter μ increases weakly with the number of points in the group n_g at a small fixed number of groups N_g (≥ 2). When N_g value is large then the parameter μ increases at first rapidly with n_g and then slowly, remaining slightly less than 1. The abscissa in Fig. 2 shows the evolutionary "time" T_2 as the total number of doublings corresponding active (not fixed) variable – N_g or n_g (chloroplasts reproduce by dividing in half).

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

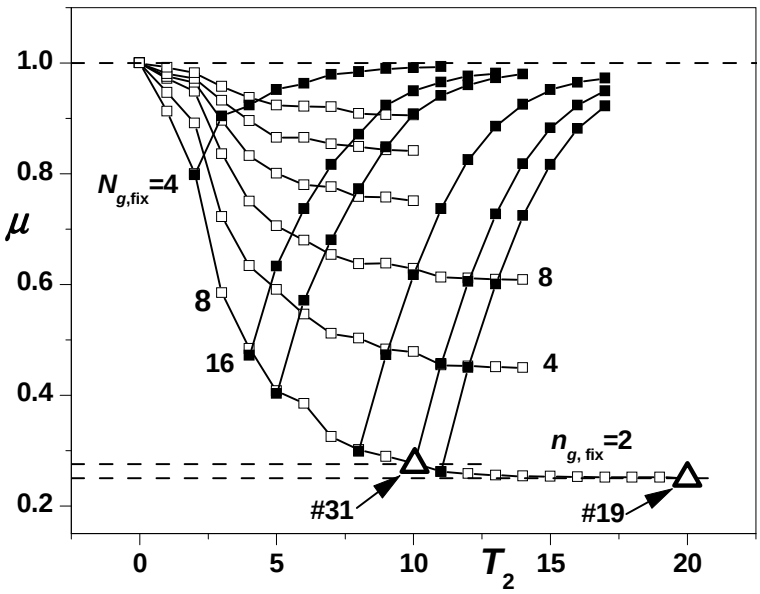

Fig. 2. Two-dimensional images of three-dimensional trajectories of dependencies $\mu(N_g,n_g)$. Examples of combined trajectories: part $n_{g,\mathrm{fix}}$ at a fixed value n_g (empty squares) and part $N_{g,\mathrm{fix}}$ at a fixed N_g (filled squares), A = 0.005. Empty triangles - $\mu_{\#19}$ and $\mu_{\#31}$ correspond to nature data [7] and their model interpretations [6] (see inset in Figure 1, #19).

Consider the possible trajectories of the endosymbiotic proto-plants in space (μ,N_g,n_g). It is evident that the proto-plant begins as a series of infestations by solitary cyanobacterium into the host's body in random places of an interval. Since the reproduction of it is not possible, then $\mu = 1$ regardless of the number of points. When cyanobacterium gain an opportunity of dividing with the restriction $n_g \leq 2$, and is removed the restriction (if it was) on the number of groups N_g, evolution begins on a trajectory $n_{g,\mathrm{fix}} = 2$ (Fig. 2) going with decreasing to $\mu \approx 0.25$. When at some moment T_2 immediately or gradually in the course of evolution is removed the restriction of division cyanobacteria in groups, the evolution of proto-plant goes over to the appropriate trajectory $N_{g,\mathrm{fix}}$ (Fig. 2), which leads to an increase in magnitude of μ to the value of 1. When fractal parameter μ reaches 1 the situation is already corresponds to the sets of linear elements, i.e., the piecewise linear or continuous filling of interval (considering the real size of the green "point"). This assembly procedure is shown in Fig. 2 for multiple combinations of fixed values $n_{g,\mathrm{fix}}$ and $N_{g,\mathrm{fix}}$. Thus, during the evolution of proto-plant the dependence $\mu(T_2)$ of the fractal parameter must go out from the 1, to pass through a minimum and then again tends to the value 1. In this picture, obviously, profound detalization is possible, depending on symbiotic "experience" of protist and cyanobacteria – for example, trajectory could start with $n_{g,\mathrm{fix}} = 4$, as shown in Fig. 2, or depending on value N_g of host, at which the trajectory type is changed, but it does not change the nature of the trajectory of the proto-plant. It may be noted that it follows from this the countability of set of variants of this evolution, which led every the proto-plant into state of a plant

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

with μ = 1 in different evolutionary times T_2 and, consequently, could give different previous and / or subsequent histories of plant evolution. In Fig. 2 positions at the trajectory $n_{g,\mathrm{fix}} = 2$, corresponding to the values μ (#19 and #31) received for the two sets of natural values of $t_{D,j}$ for spruce [7], are marked by asterisks. It is evident that a proto-spruce (# 19) spent on the evolution approximately twice as much "time" than of the proto-spruce (# 31), and this was reflected in their "descendants" [6, fig. 5].

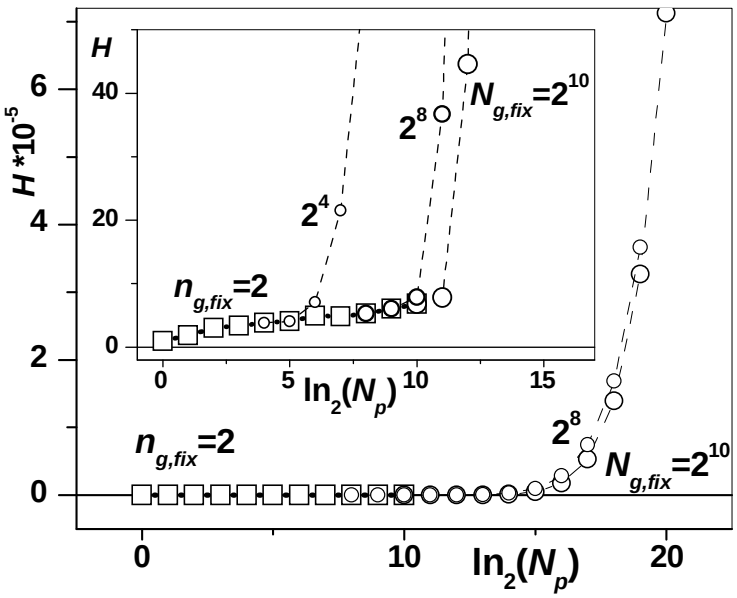

Fig. 3. The initial deceleration of the proto-plant growth during endosymbiosis. The dynamics of the size $H \sim B^{1/\mu}$ of system of green "points" corresponds to an increase in their biomass (population, unit of biomass – a mass of cyanobacterium). Inset: movement along trajectories $\mu(n_{g,\mathrm{fix}}, N_{g,\mathrm{fix}})$ with an increase in the number of groups of N_g in the first portion, where the number of $n_{g,\mathrm{fix}}$ points in the group (the squares) is fixed, and in the second portion $N_{g,\mathrm{fix}}$ (circles, dashed) – increasing total $N_p = N_g * n_g$ by way doubling the number of "points" n_g in groups with using the combined dynamics of the fractal parameter $\mu(T_2)$ (see Figure 2.)

INITIAL GROWTH DECELERATION OF PROTO-PLANT

As seen from the foregoing, green biomass (i.e., the number of cyanobacteria involved in endosymbiosis) is the leading variable in the evolution of proto-plant. Therefore, "turning over" the ratio (1) and using the obtained dependence $\mu(T_2)$, we can calculate dynamics of the characteristic size H of the system of points – $H(T_2) \sim (N_g(T_2) * n_g(T_2))^{1/\mu(T2)}$. Fig. 3 shows examples of the dynamics of $H(T_2)$ demonstrating a very weak growth at the stage $n_{g,\mathrm{fix}}$, which is replaced by an exponential rise on stage $N_{g,\mathrm{fix}}$.

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

DISCUSSION

According to modern evolutionary theory (biogenetic law) "in embryonic development have sometimes can be reproduced stages of evolutionary history" [14], i.e., may be the so-called recapitulation, as which is usually understood a visually discernible similarity some stages of a modern organism in embryogenesis and ontogenesis of its evolutionary ancestors. In this sense apparently, the "punctiform recapitulations", which repeat visually sufficiently "strictly" the situation of occurrence of proto-plant (at the beginning of the range μ <1.0 in Fig. 1), can be detected generally speaking in higher plants twice.

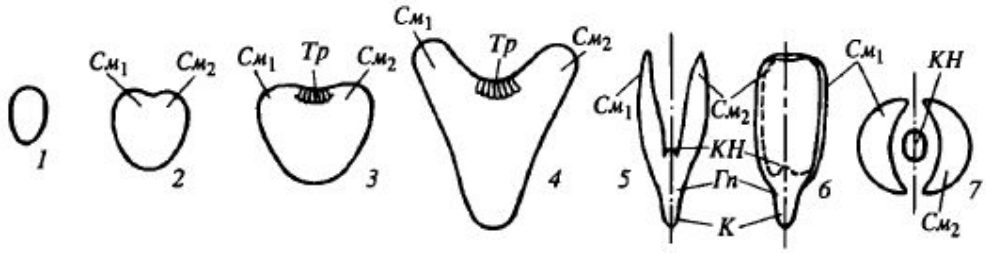

Fig. 4. The scheme of development of dicotyledons embryos. 1-4 - the early development of the embryo; 5, 6 - fully formed embryo; view of two mutually perpendicular planes; 7 - a cross-section in the plumule embryos; CM1 and CM2 - cotyledons, TP - growth point (before forming cone of growth CN); Hp - hypocotyl; R - root. Dashed line shows the plane of symmetry (after [19: 144, Figure 70]).

The first time – in dicotyledons during embryogenesis when the seed embryo begins to turn green due to the transformation of the existing leucoplasts into the chloroplasts [18] in course of the transition from globular to heart phase of embryogenesis (Figure 4). [19]. The form (two cotyledons) of the embryo in a heart phase and placement of chlorophyll [20] may be associated with the appearance of "branches" of the first order in of proto-spruce (Fig. 1) with μ ≈ 0.25. Obviously, there is no complete coincidence and can not be. The matter is that the proto-plant appeared at initial absence of appropriate infrastructure and elements of the genome in the host, whereas a seed of higher plant in early embryogenesis it all in some form already has. According to the model, we can assume that the embryogenesis moves along a composit trajectory (of course, far more rapidly than a proto-plant has appeared), which is similar essentially to that shown in Fig. 3, taking into account the differences of their starting positions and structures. A distinctive feature of recapitulation, apparently, can be considered a group character of plastids placement with fixed number of $n_{g,\mathrm{fix}}$ in the group (Fig. 2, open squares) during the growth of the total number thereof on the globular phase of embryogenesis (Fig. 4 (1)) before and after the transition to the heart-shaped phase. The result of the plant embryogenesis is the appearance of typically yellow, mature dry seeds, which have no active

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

chlorophyll (chloroplasts when ripe are converted to colorless plastids – leucoplasts [18, 21]), and are able in this way to wait the appropriate conditions for germination.

The second time recapitulation can assume occurring during germination of mature dry, initially yellow seed of a plant when embryo with the formed cotyledons begins to turn green as a result of the transformation of existing colorless leucoplasts back in the green chloroplasts. Typically, this is a natural process of increasing the number of active chloroplasts which is expressed in normal ontogeny a plant. However for some economically important crops is observed, and it remains unclear [22] why the seeds, sometimes remaining green when ripe, i.e., during germination having an additional ("extra") chlorophyll, show poor germination, give low yields, and the poor quality of the product for oilseeds. If we assume that the situation at the beginning of seed germination and activation of "systemic" chlorophyll is reflected by the proto-plant model, then the role of "non-systemic" or excess chlorophyll become clear. It is obvious that the activation of chloroplast in the embryo, having the appropriate infrastructure is controlled by the genome. "Non-systemic" chloroplasts are not consistent with infrastructure of embryo, are located quite randomly and are generating extra, "non-systemic" oxygen that can damage cell structures [20, 23], i.e. adversely affect the process of germination and further ontogeny. In addition, not only the quantity but also the spatial distribution of the additional chloroplasts may be important as unacceptable for the existing infrastructure.

Thus formally in the ontogeny of the seed plants, there are two situations of recreating the photosynthetic system, which are similar at least morphologically at a model situation of emergence of proto-plant. In both uses the same elements that are in one of two states – leucoplasts and chloroplasts, and presumably similar technologies switching them from one state to another. Evolution following the principle of «Occam's Razor» not produces superfluous entities.

Apparently, in connection with the presented model it would be advisable conducting experimental studies and model analysis of placement and transformation leucoplasts and chloroplasts in embryos and plantlets of wild and related mutants of Arabidopsis in the early embryogenesis and germination using fluorescence confocal microscopy [20].

REFERENCES

1. Galitskii V.V. Dynamics of the Distribution of Free-Growing Tree Biomass with Respect to Height: Model Analysis. *Doklady Biological Sciences.* 2006. V. 407. # 4. P. 166-168. doi: 10.1134/S0012496606020153).

2. Galitskii V.V. The sectional structure of a tree. Model analysis of the vertical biomass distribution. *J. General Biology*. (Zhurnal Obshchei Biologii). 2010. **71**(1): 19-29. (Russian).

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

3. Galitskii V.V. Models of tree and trees' community dynamics: evolution from 2D to 3D models. *Math. Biol. and Bioinform.* 2012. **7**(1): 54-80. (Rusian). http://www.matbio.org/2012/Galitskii2012(7_54).pdf

4. Galitskii V.V. Sectional model of non-free tree growth. *Comp. Res. and Modelling*. 2016. **8**(2): 307-322. (Russian). http://crm.ics.org.ru/uploads/crmissues/crm_2016_2/16.08.09.pdf

5. Galitskii V.V. Biomass Dynamics of Higher-Order Tree Branches: An Analysis of the Model. *Biol. Bull. Rev.* 2013. **3**(5): 412-421. doi: 10.1134/S2079086413050034

6. Tsel'niker Ju.L. The structure of spruce crown. *Russian forest science*. 1994. (4): 35-44. (Russian).

7. Kazimirov N.I. *Spruce forests of Karelia*. Leningrad: NAUKA Publ. 1971. 139 p. (Russian)

8. Kramer P.J., Kozlowski T.T. *Physiology of trees*. NY: Academic Press. 1979.

9. Treskin P.P. Regularities of morphogenesis of the crown's skeletal part of mature tree. In: *Structure and productivity of spruce forests of south taiga*. Leningrad: NAUKA Publ. 1973. 222-240. (Russian).

10. Feder J. *Fractals*. NY: PLENUM PRESS. 1988.

11. Galitskii V.V. Evolutionary trajectories in the parameter space of the sectional model of green spruce crown biomass. The emergence of a "proto-plant". *J. General Biology*. (Zhurnal Obshchei Biologii). 2016. 77(6): 409-422. (Russian).

12. Margulis L. *Symbiosis in Cell Evolution.* W.H. Freeman and Company. 1981.

13. Borisov N.M., Vorob'ev F.Ju., Gilarov A.M., Es'kov K.Ju., Zhuravlev A.Ju., Markov A.V., Oskol'sky A.A., Petrov P.N., Shipunov A.B. *Evidencies of evolution*. Ed.: A.V. Markov. 2010. (Russian). http://evolbiol.ru/evidence.htm

14. Gamalei Ju.V. The nature of the trophic tract in vascular plants. *TSITOLOGIYA.* 2009. **51**(5): 375-387. (Russian)

15. Hanson M.R., Kohler R.H. A Novel View of Chloroplast Structure. *Plant physiology online.* 2006. http://6e.plantphys.net/essay07.01.html

16. Malachov V.V, Great symbiosis: origin of eukaryotic cell. *V mire nauki*. 2004. (2): 70-79. (Russian).

17. Zhukova G.Ja. *Embryo plastids of flowering plants*. Doct. thesis, Botanical Inst. RAS, SPb. 1992. (Russian).

bioRxiv preprint doi: https://doi.org/10.1101/083543; this version posted November 2, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

18. Serebrjakova T.I., Voronin N.S., Elenevski A.G., Batygina T.B., Shorina R.I., Savinych N.P. *Botany with fundamentals phytocenology: Anatomy and morphology of plants.* 2006. 543 p. (Russian).

19. Tejos R.I., Mercado A.V., Meisel L.A. Analysis of chlorophyll fluorescence reveals stage specific patterns of chloroplast-containing cells during Arabidopsis embryogenesis. *Biol. Res.* 2010. **43**: 99-111. doi: 10.4067/S0716-97602010000100012.

20. Allorent G., Courtois F., Chevalier F., Lerbs-Mache S. Plastid gene expression during chloroplast differentiation and dedifferentiation into non-photosynthetic plastids during seed formation. *Plant Mol Biol.* 2013. **82**: 59-70. doi: 10.1007/s11103-013-0037-0.

21. Nakajima S., Ito H., Tanaka R., Tanaka A. Chlorophyll b Reductase Plays an Essential Role in Maturation and Storability of Arabidopsis Seeds. *Plant Physiology.* 2012. **160**: 261-273. doi: 10.1104/pp.112.196881.

22. Smolikova G.N., Medvedev S.S. Photosynthesis in the seeds of chloroembryophytes. Russian Plant Physiology. 2016. **63**(1): 1-12. doi: 10.1134/S1021443715060163)