



Dynamics of competition in uniform communities of trees

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Abstract: Earlier, as a result of processing maps of trees and crown projections of 90-year-old spruce stands in the Moscow suburbs, nonuniform trends of correlation coefficients between areas of tree crown projections and areas of Voronoi polygons was detected in a series of sites ranked by increasing coefficient of variation of stem diameter. The observed behavior was analyzed using an original two-dimensional model of the dynamics of a plant community. Theoretical measures of competition in a community, which base on the definition of competition show that the process of competition in relatively uniform communities is not uniform. The coefficients of correlation mentioned above can be considered as measures of competition and such competition is not regular or uniform especially in uniform communities. The latter circumstance gives possibility to estimate the duration of biomass growth of *freely growing* spruce in the Moscow suburbs for ≈ 1000 years. Because of limitation of a two-dimensional resource model some characteristics of communities, such as coefficients of variation and correlation features of neighborhoods, differ from experimental values rather significantly.

Introduction

Competition among plants – their indirect interaction in the course of partition and repartition of resources insufficient for all of the plants in the community (Clements et al. 1929) – is the leading process in the development of any plant community. Thinning – the decrease of community density by many times in the process of growth of community members – is the most demonstrative manifestation of this process.

It should be noted that phytocenologists (for example, Rabotnov 1978), in the analysis of natural data prefer to speak about competition for a specific resource (light, water, elements of mineral nutrition). However, with the assumption (natural, on initial consideration) that the territory of a community is homogeneous, the area occupied by the community may be taken as a united resource. Resource is an additive quantity, and upon partitioning of the territory, the material resources are shared proportionally.

Competition in a community of plants is manifested locally by interactions of neighboring plants resulting in changes in individual parameters such as mass and shape. It is also manifested at the community level by changes of

community characteristics such as average values and features of distributions of plant parameters, coefficients of variation, density of the community and intensity of thinning, and correlation relationships that vary as a result of localized interactions.

Investigations of problems connected with competition in plant communities and, in particular, of measures of the “force” of local interaction of plants in a community have been carried out for at least a century (for example, Clements and Weaver 1929, Sukachev 1973, 1975, Pielou 1960, Mack and Harper 1977, Weiner 1984, Duncan 1995). Competition on a local level is not discussed here, rather the behavior of competition measures in a plant community is considered.

The investigation was because of a strange behavior of coefficients of correlation between areas of tree crown projections and the appropriate Voronoi polygons which was noted during an analysis of maps of trees and their crowns for a series of experimental sites that were ranked according to increasing coefficients of variation of crown areas. The sites were from planted tree stands (cultures) of identical age (90 years) and differed practically only in initial density of planting (Abaturov and Galitskii 1995).

Table 1. Several site characteristics ([S]pruce, [P]ine, [B]irch,[A]spen,[O]ak).

Sites	H56	D22	AL5	R22	AL7
age, (year)	S-90	S-90	S-90	S-100	S-70
	P-90				P-70
density, (stems/ha)	S-264	S-612	S-528	S-504	S-716
	P-139	P-51		A-46	P-80
	O-15	B-126		P-27	
yeld, (m ³ /ha)	S-309	S-352	S-330	S-340	S-355
	P-219	P-63		P-45	P-65
	O-5	B-27		A-21	
				B-6	
closeness (for curtains)	0.7(0.9)	0.8	0.5 (0.8)	0.7 (0.9)	0.8

The mentioned correlation coefficients became very small in the middle of the series of sites, which was in order of increasing coefficient of variation of stem diameter.

A hypothesis based on a model of plant communities about an opportunity of nonuniform growth of biomass of a homogeneous community was suggested earlier (Galitskii 1979). It was assumed that in a series of sites there is some analogue of an age (time) series and that the behavior of correlation coefficients along a series is a manifestation of an overall behavior of growth and competition in a uniform community.

For the analysis of this experimental effect, a two-dimensional model of dynamics of community of plants developed earlier (Galitskii 2000, 2003) was used. Brief descriptions and definitions of terms of the models of individual plant and community of plants are given in the Appendix. We use two-dimensional models of a plant and a plant community based on Voronoi polygons as territories occupied by a plant in a community. In these models, heuristic algorithms for the partition and re-partition of contested resources between the neighboring plants were not applied. Such algorithms, generally speaking, are a replacement of the third dimension absent in two-dimensional models. We believe that similar approximations are useful based on a comparative analysis of behavior of two- and three-dimensional models, consequently a similar analysis may be made with a using of quasi-three-dimensional models of a tree and a plant community (Galitskii, 2005).

Results from field surveys

More than 30 sites (from 0.25 ha to 2.25 ha with a total of more than 10 000 trees), which included all main tree

species of the region, were chosen in mature, closed tree stands of the Moscow forest belt. The majority of the sites were characterized by a prevalence of spruce. For this research, five even-aged tree stands (old cultures without human interference) were taken (Table 1). All sites had initial densities of more than 5000 trees per ha except for site H56, where the estimate was about 1250 trees per ha.

For each site, trees having a stem diameter at breast height $D_{1.3} > 6$ cm were enumerated; location maps of trees, stumps, juveniles, and contours of crown projections of individual trees were made; and stem diameters $D_{1.3}$ were measured. Model trees were measured in more detail. The following features were calculated: (1) geometrical parameters of crown projections (area S_{cr} , perimeter, and index of the form), (2) average crown projections, (3) usual statistics, (4) type of placement of trees on a site (the method of Greig-Smith, Zahl 1977), (5) the Voronoi mosaics for the point set (Voronoi 1908) and the polygon areas S_{pb} , (6) correlations between parameters of trees and some regressions, and (7) correlations of parameters of neighboring trees (Tables 2-4).

Ranking of the sites was based on the following notions: (1) the coefficients of variation for individual characteristics increase during competition and (2) the initial distributions of $D_{1.3}$ and S_{cr} up to closing of crowns and beginning of thinning are normal. Ranking was performed by comparing (1) parameters of distribution functions (normality and asymmetry) of stem diameters $D_{1.3}$ and areas of crown projections S_{cr} and (2) coefficients of variation for $D_{1.3}$ and S_{cr} (Table 2). Rankings of the coefficients of variation for $D_{1.3}$ and S_{cr} in ascending order are rather close.

The start of the competition processes is characterized by meaningful normality of distributions (Table 2)

Table 2. Statistical parameters for 90-year old spruce stands. $D_{1.3}$ - stem diameter, S_{cr} - area of crown projection, N - size of sample, -/+ : rejecting or accepting normality hypothesis for the distribution, $P < 0.05$.

Sites	H56		D22		AL5		R22		AL7	
N	240		267		163		468		204	
Parameters	$D_{1.3}$	S_{cr}	$D_{1.3}$	S_{cr}	$D_{1.3}$	S_{cr}	$D_{1.3}$	S_{cr}	$D_{1.3}$	S_{cr}
average, $\bar{X}$	32.8	19.9	23.2	14.2	25.0	9.4	26.4	16.4	21.2	9.3
dispersion, S^2	38.4	60.0	42.7	42.7	58.7	26.1	74.9	74.9	73.4	51.0
asymmetry	0.28	1.0	0.18	0.88	0.14	0.98	0.79	1.5	1.1	2.9
normality	+	+	-	-	-	-	-	-	-	-
variation coeff.	0.19	0.39	0.28	0.46	0.31	0.54	0.33	0.52	0.40	0.77

Table 3. Coefficients of correlation between characteristics of individual trees in a 90 year old spruce stand. The primed values are for mosaics built for alive trees only, otherwise for all fixed trees; underlining indicates that the linearity hypothesis is rejected, $P < 0.05$; * difference from zero is significant, $P < 0.05$.

correlation coeff.	H56	D22	AL5	R22	AL7
$(D_{1.3} - S_{cr})$	<u>0.72*</u>	<u>0.66*</u>	<u>0.82*</u>	<u>0.76*</u>	<u>0.78*</u>
$(S_{cr} - S_{pl})$	<u>0.34*</u>	-0.061	-0.009	0.008	<u>0.59*</u>
$(S_{cr} - S'_{pl})$	0.14	0.12	0.024	0.007	0.014
$(D_{1.3} - S_{pl})$	<u>0.19*</u>	0.037	<u>0.35*</u>	<u>0.38*</u>	<u>0.40*</u>
$(D_{1.3} - S'_{pl})$	0.12	0.079	0.017	0.003	0.014

Table 4. Correlation coefficients of tree diameters and the areas of the crowns' projections for a focal tree and its neighbors in a mosaic. N - size of sample, r_D - correlation coefficient ($D_{1.3} - D_{1.3,n}$), r'_D - correlation coefficient ($D_{1.3} - D'_{1.3,n}$), r_{cr} - correlation coefficient ($S_{cr} - S_{cr,n}$) for focal tree and its neighbors on a mosaic; the primed - neighbors are taken on the mosaic built for alive only, otherwise for all fixed trees; difference from zero significantly: * - $P < 0.02$, ** - $P < 0.01$.

all of pairs					average neighbor			
Sites	N	r_D	r'_D	r_{cr}	N	r_D	r'_D	r_{cr}
H56	924	-0.098**	-0.088**	0.080*	314	-0.282**	-0.252**	-0.252**
D22	832	0.009	0.068*	0.042	282	0.027	0.142**	0.118
AL5	369	0.146*	0.026	0.016	121	0.298**	0.124	-0.005
R22	1419	0.090**	0.080**	0.086*	481	0.184**	0.162**	0.181**
AL7	572	0.089**	0.077	0.147**	190	0.226**	0.202**	0.307**

and negative correlations of stem diameters of neighboring trees (Table 4). Normality then disappears (more quickly for crown projections), as does negativity of the correlation coefficient r_D for stem diameters $D_{1.3}$ of neighboring trees. The reason for the latter effect is that, after thinning, the surviving trees become neighbors. Table 2 shows a rather small positive asymmetry of the dis-

tribution of $D_{1.3}$. The analogous characteristic for the areas of crown projections is 1.5-5 times greater. This may mean that the distribution of S_{cr} is a more sensitive indicator of competition.

Table 3 presents estimations of correlation relationships between individual characteristics of trees for each of the sites. There is an essential distinction between the

correlation dependences ($S_{cr} - S_{pl}$) and ($D_{1.3} - S_{pl}$) on the one hand and ($S_{cr} - S'_{pl}$) and ($D_{1.3} - S'_{pl}$) on the other hand. For the first group, the Voronoi mosaics were constructed and the polygon areas S_{pl} were calculated taking into account all available trees – live, dry, and stumps, while, for the second group – S'_{pl} – only live trees were taken into account. In the second group, the significance of values of coefficients is lower and analogues of significant values of the first group are much less.

In Table 4, coefficients of correlation between diameters r_D (all trees) and r_D' (live trees only) and between the crown areas r_{cr} of neighboring trees are shown. The neighborhood was determined by using the Voronoi mosaics. As neighbors, either all pairs of neighbors on the appropriate mosaic or the average neighbor was taken. In the case of correlation with the average neighbor, absolute values of coefficients increased 2-3 times.

Thinning as a result of competition destroys the relationships between tree parameters and the geometrical structure of the community: (1) correlation coefficients ($S_{cr} - S_{pl}$) do not differ significantly from zero for sites D22, AL5, and R22, nor does the correlation coefficient ($D_{1.3} - S_{pl}$) for site D22 (Table 3); (2) coefficients r_D for D22 and r_{cr} for D22 and AL5 also do not differ significantly from zero. By the end of the series (site AL7), the relationship is to a considerable degree restored, and for ($D_{1.3} - S_{pl}$) and ($S_{cr} - S_{pl}$) the correlation coefficients are approximately twice those for site H56.

The correlation coefficient r_{cr} for neighboring trees is positive, small, and significant at the beginning and the end of the site series. The coefficient of correlation between crown projection area and the corresponding Voronoi polygon area ($S_{cr} - S_{pl}$) differs significantly from zero at the ends of the series. Together with the mentioned dynamics of the distribution characteristics, it also allows one to assume that the tree stand at the beginning of the series (H56) is on the first wave of aggravation of competition and the tree stand at the end of the series (AL7) enters into a new wave which can occur with sufficient uniformity of a tree stand and energy of tree growth.

Competition in dynamics

Although Clements et al. (1929) pointed out that competition is a “dynamic process,” this aspect of competition has still not been adequately considered because of a lack of methods that define the resource requirements of an individual plant and the total needs of plants during the development of a community, as well as the difficulty (or impossibility) of observing a community over sufficient intervals of time. Moreover, study of natural tree stands

usually begins at that tree stand age when the process monotonously decreases (Khilmi 1957), and it usually comes for cultures to an end when the process has just begun to develop. A theoretical analysis of this problem, most significant for rather spatially uniform communities, requires the use of spatial dynamic models and certain computer possibilities. For example, in the well-known JABOWA model of a forest ecosystem (Botkin et al. 1972) the total death rate of trees is set to obtain the given density of a population at a given age. Earlier, with a 2D model of a plant community for a spatially relatively uniform community, the possibility of nonuniform dynamics of production characteristics related to self-thinning, which accompanies competition in such a model community, was demonstrated (Galitskii 1979).

Computer processing of maps of sites in even-aged spruce stands located in the Moscow suburbs was interpreted as a manifestation of a nonuniform competition process in initially uniform tree stands (Abaturov and Galitskii 1995, Galitskii and Abaturov 1996). This phenomenon was analyzed with a 2D model of plant community from a class of spatial tessellation models (Kenkel 1990). Short formulations and symbol definitions of these models of a plant and plant community are presented in the Appendix.

On selecting the integral measure

The integral measure used here is as a method of estimation of the value of or intensity of competition in a community of plants. It is obvious that several measures that give values for a fixed range, for example $[0, 1]$, should be considered. Two groups of methods are discussed below.

The first group consists of theoretical measures based on the definition of competition. According to the definition, measures should be constructed from values describing the resource requirements of an individual plant of a community and measures of the available resources for each plant. Assume the territory occupied by the community to be homogeneous and, as a measure of the resources accessible to an i -th plant the area of the appropriate Voronoi polygon (Voronoi 1908) $S_{pl,i}$ is used and as is the area of free growth $A_{F,i}(T)$ as a measure of the growth area necessary for a tree at age T .

According to Clements et al. (1929, p. 317), an integral measure of competition in a community, C_{cb} , should take the ratio of the total deficiency of a resource over the community to the total requirement of members of the community for this resource:

$$C_{C1} = \sum_{A_{F,i} > S_{pl,i}} (A_{F,i} - S_{pl,i}) / \sum_{i=1}^N A_{F,i} \quad (1)$$

where the first summation is made for all plants of the community experiencing competition and N is the total number of trees. It should be noted that this formulation ‘divides’ individual shortages of resources into the entire community.

Using the same model concepts, it is possible to propose another formulation of an integral measure of the competition experienced by individual plants of a community on the part of their neighbors, namely, the average (over the community) ratio of individual shortages of a resource to individual requirements for it:

$$C_{av} = 1/N \sum_{A_{F,i} > S_{pl,i}} (A_{F,i} - S_{pl,i}) / A_{F,i} \quad (2)$$

Both expressions are normalized to the interval $[0,1]$: if each plant has $S_{pl,i} \ll A_{F,i}(T)$, then both values are close to 1, and if for all plants $S_{pl,i} > A_{F,i}(T)$, both values are equal to 0.

Since $A_{F,i}$, $S_{pl,i}$ and N vary in time, C_{C1} and C_{av} , generally speaking, depend on T also. It can be noted that, according to these expressions, the integral measure of competition is defined by the geometrical design of the community and a characteristic of a freely growing plant that is dependent on the plant species and ecological conditions in the community.

The expressions (1) and (2) coincide with each other in case of a single-species even-aged community, and for a multi-species and/or uneven-age community when plants differ in sizes $A_{F,i}$, the values satisfy to inequality $C_{av} > C_{C1}$. The inequality follows from structure and ‘philosophies’ of these expressions – ‘socialist’ measure C_{C1} takes into account resources of the individual plants having different requirements, and ‘capitalist’ C_{av} takes into account real oppression of individual plants. Only one-species even-age communities are considered hereinafter.

The other group comprises practical measures to estimate the competition force, in which data obtained from natural environments are used. These competition measures are constructed with the use of values showing the state of plants in the community such as phytomass, biomass, height, stem diameter (Galitskii 2003) and values representing resource allocation in the community. The parameters showing the state of plants can, in turn, be divided into two groups.

The first group has parameters that are of a cumulative character, i.e., those whose current values are defined by the entire previous history (of competition) of the plant

and uniform increases with age. In the first groups are phytomass, height, and stem diameter. The model of a plant’s phytomass dynamics is the time integrated value named the biomass and does not include directly the parameters related to the resources that the plant has.

The second group includes parameters that directly depend on the resource provision of the plant including plant biomass, which is understood as the physiologically active part of the whole plant. According to the model used here (Galitskii 2003), the rate of biomass change is directly connected with the resources accessible to a plant, and would be appropriate as a measure of competition intensity. However, experimental data are lacking for such measure, therefore we shall limit ourselves to the biomass proper. From among the integral characteristics of a community, the correlation relationship between biomass and area of territory occupied by plants is preferred because the measure should be dimensionless and normalized.

Model analysis of the competition dynamics in the plant community

In a previous study (Abaturov and Galitskii 1995), maps of placement for tree stands of one age were fixed only for one moment of time and the function $A_F(T)$, generally speaking, was unknown. Consequently, the direct and dynamic estimation of C_{av} with the available natural data of mapping and, hence, validation of nonmonotonicity was impossible. Processing of results of modeling similar to that used for natural data was, therefore, one of the primary goals of the analysis of uniform community dynamics with 2D models of the plant and the community (Galitskii 2000, 2003, Appendix).

Dynamics for communities in which trees are initially placed near to nodes of a rectangular grid in a uniform placement, and also for communities with random (Poisson) initial placement at identical values of other parameters were carried out with a 2D model of a plant community. Uniform placement was realized on a site of a 1×1 square grid, with one tree randomly placed in one of 100 locations of each of the square 100×100 grids. The initial number was taken to be 10,000 trees. The initial density varied with change in the size of a square site. Hereafter, the following designations (in parentheses is the relative density of placement of trees) of model sites are used: uniform $g89$ (0.83), $g93$ (0.94), $g90$ (1.00), $g94$ (1.06), and $g95$ (1.66) and Poisson $p90$ (1.00). In calculations, the following values of biological, growth, and physiological parameters of the plant model (Galitskii 2003) were used: $A_0 = 0.004$, $A_1 = 100$, $\mu = 2.5$, $\alpha = 10.0$, B type of growth,

$k = 0.8$, $\varepsilon_M = 0.2$, $\tau_M = 0.1$ and $c_G = 0.1$; the shape of the polygon was not taken into account.

Here it is important to note that this plant model gives values of biomass and phytomass, and it is not related directly with any dimensions of a plant. The data of natural observations available to us, on the contrary, were results of linear measurements, from which values of the areas of crown projections were obtained. To interpret the results of the model notions about allometric relationships between characteristics of a tree were used. The value $s_{cr} = B^{2/\mu}$ (μ is an allometric parameter; its isometric value in the case of the B type of growth is $\mu = 2.0$ (Galitskii 2003)) was taken as the area of a crown projection of a tree with biomass B . Analogously, the value $d_{1.3} = P^{1/(1+\mu)}$, where P is the physiologically passive part of the tree

mass, or the phytomass, was taken as the “stem diameter”.

Measures of competition

In Fig. 1a, the model dependences $C_{av}(T)$ for several uniform communities of various initial density and for one Poisson community are exhibited. A uniform community, unlike the Poisson community, really demonstrates irregular dynamics of the integral measure of competition C_{av} . After the first largest peak corresponding to initial competition of the community's members, peaks of decreasing amplitudes occur with some periodicity, and with time the curve of the uniform community approaches the corresponding dependence of the Poisson community. With a decrease in planting density, curves C_{av} are shifted on the axis T , but essentially are not changed.

Dynamics of C_{av} are shown in Fig. 1b for comparison with the time dependence of the number of oppressed members of community $N_{opr}(T)$. The behavior of the dependencies on the appropriate scale is rather close.

Statistics

The dynamics of the coefficient of variation and normality of “stem diameter” $d_{1.3}$ and “crown projection area” s_{cr} distributions were examined. Regularities similar to natural ones occur in some model communities. The normality of distribution for s_{cr} disappears earlier than that for $d_{1.3}$. In Fig. 2a, the dynamics of some characteristics for uniform $g90$ and Poisson $p90$ communities are shown, in particular, coefficients of variation for $d_{1.3} - CV_P$, and for $s_{cr} - CV_B$. In general, the behavior of these model coefficients does not contradict natural observations (Table 2): with the emergence of competition in the community, they increase, though in the course of model competition their dynamics is more complicated (especially for s_{cr}). The difference in behavior of these (random and uniform) communities is most clearly expressed in the behavior of the coefficient of variation for s_{cr} . In time, the characteristics of both communities approach each other.

In Fig. 2b, the dynamics of the coefficients of variation for $d_{1.3}$ for the gXX communities are shown (in the inset, the part of interest to us is shown on an enlarged scale). In time, the differences between communities practically disappear. Obviously, the coefficient of variation cannot be used as a competition measure but rather as a directional indicator of the course of competition.

Correlation of the individual characteristics

In Figs. 3a–3c are shown model dynamics of correlation coefficients $(s_{cr} - S_{pl})$ and $(d_{1.3} - S_{pl})$ for the areas of

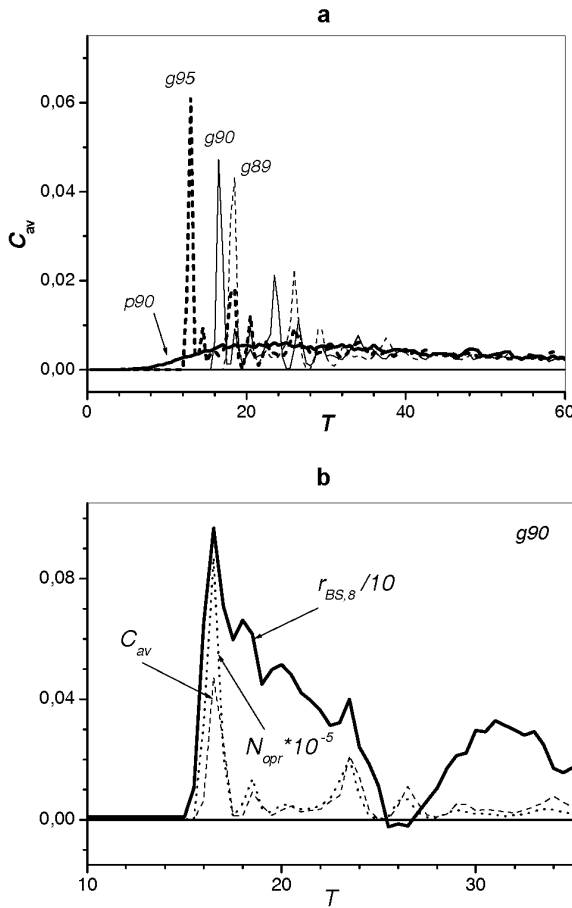


Figure 1.a. Dynamics of measure of the competition intensity – average oppression because of limitation of area for growth – C_{av} (2) for uniform communities gXX of various density and poisson $p90$ (see section 5), **b.** comparison C_{av} , amounts of plants N_{opr} oppressed by competition and model coefficient of correlation $(S_{cr} - S_{pl}) - r_{BS}$ at $lag=8$ for community $g90$; for explanation of a designation lag see text.

the polygons calculated for the given moment of time T ($lag=0$) and the previous moment $T - lag$ ($lag=8$). In the latter case, the situation was imitated in which, in processing of data of natural observations (construction of a Voronoi mosaic), positions and diameters of tree stems dead at the given moment were also taken into account. It can be seen that the dependencies of the coefficients with change in the initial density qualitatively do not vary strongly and with reduction of the density are shifted toward greater T . This, together with the substantial non-monotonicity of the dependencies, makes possible sharp distinctions between values of coefficients of correlation in a ranked series of sites (Table 3).

In the figures, the moment of time, section A-A, is when model correlation coefficients are rather close to the natural ones presented above (Table 3). Model and natural coefficients of correlation are shown in the inset in Fig. 3a. The graphs in Fig. 3a show that, in section A-A, variant

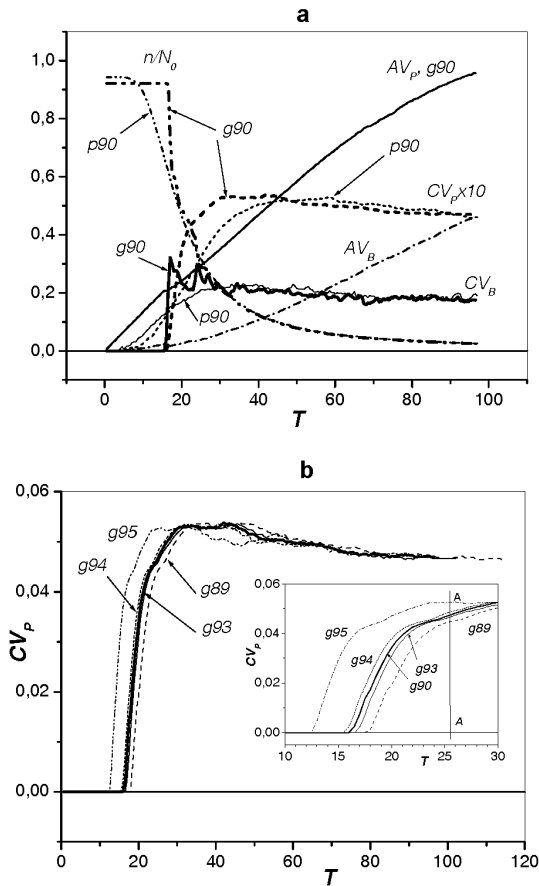


Figure 2.a. Model dynamics of number of alive plants n/N_0 , average phytomass AV_p and biomass AV_B , coefficients of variation of phytomass CV_p and biomass CV_B for communities g_{90} and p_{90} ; **b.** dynamics of coefficients of variation of phytomass for communities g_{XX} of various density (inset) on the increased scale near section A-A.

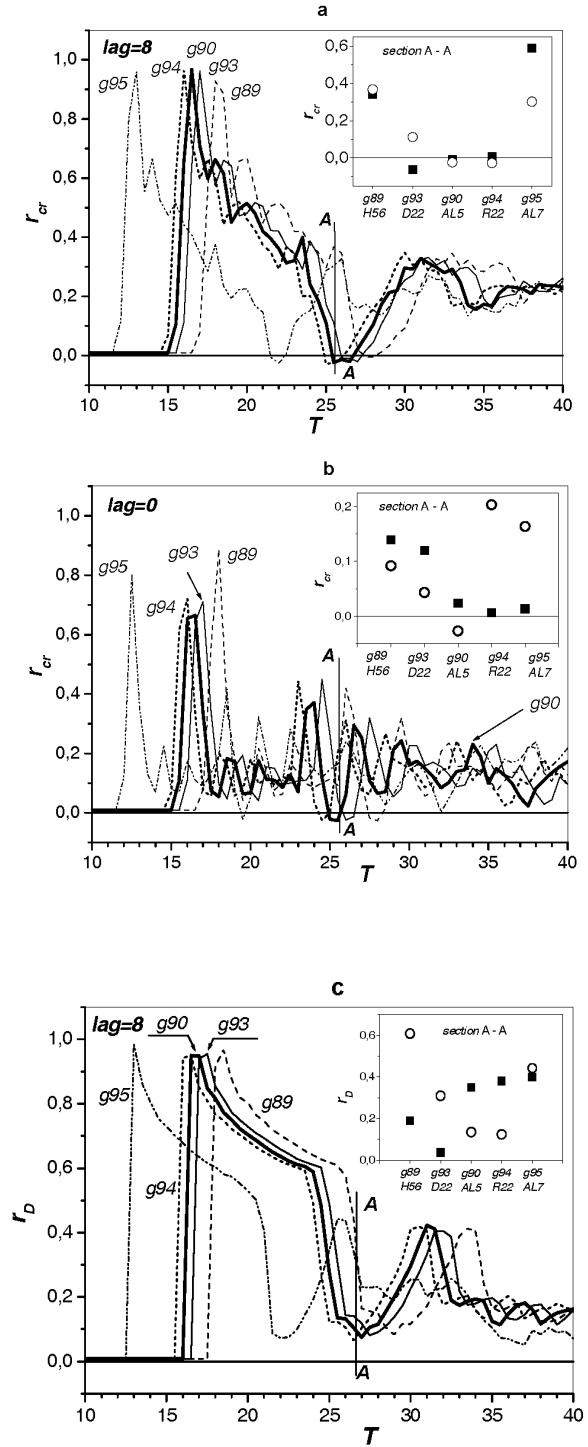


Figure 3.a and b. Model dynamics of the correlation coefficients $(s_{cr} - s_{pl}) - r_{cr}$ for communities g_{XX} at $lag=8$ and $lag=0$ accordingly; **c.** model dynamics of correlation coefficients $(d_{1.3} - s_{pl}) - r_D$ for communities g_{XX} at $lag=8$. On insertions comparison of values of corresponding correlation coefficients for the model communities in section A-A (circles) and coefficients of correlation for sites in spruce cultures (black squares) in order of increasing of densities.

Table 5. Correlation coefficients between characteristics of trees in the model uniform communities. $d_{1.3}$ - “diameter of a stem”, s_{cr} - “the area of a crowns projection” for moment of section $A-A$ (see Fig. 3a and compare with Tab. 3); for explanation of a designation lag, see text.

correlation coeff	$g89$	$g93$	$g90$	$g94$	$g95$
$(s_{cr} - d_{1.3}), lag=0$	0.730	0.605	0.716	0.714	0.698
$(s_{cr} - S_{pl}), lag=8$	0.368	0.113	-0.024	-0.027	0.303
$(s_{cr} - S_{pl}), lag=0$	0.093	0.044	-0.026	0.202	0.164
$(d_{1.3} - S_{pl}), lag=8$	0.608	0.309	0.135	0.123	0.441
$(d_{1.3} - S_{pl}), lag=0$	0.004	-0.037	-0.034	-0.028	0.031

Table 6. Variation coefficients for trees’ characteristics in the model uniform communities. $d_{1.3}$ - “diameter of a stem”, s_{cr} - “the area of a crowns projection” for moment of section $A-A$ (see Fig. 3a).

variation coeff.	$g89$	$g93$	$g90$	$g94$	$g95$
$d_{1.3}$	0.045	0.047	0.047	0.049	0.053
s_{cr}	0.210	0.27	0.24	0.25	0.21

Table 7. Correlation coefficients of parameters of focal tree for uniform (gXX) of various density and poisson ($p90$) model communities. $d_{1.3}$ - “the diameter of a stem” and s_{cr} - “the area of a crowns projection” at the moment of section $A-A$ (see Fig. 3a); over lined - average values for neighbors on a mosaic; for explanation of a designation lag, see text.

correlation coeff.	$g89$	$g93$	$g90$	$g94$	$g95$	$p90$
$(d_{1.3} - \overline{d}_{1.3,n}), lag=0$	0.049	-0.0079	-0.015	-0.0084	-0.031	0.041
$(s_{cr} - \overline{s}_{cr,n}), lag=0$	-0.0048	0.042	0.046	0.050	0.046	0.067
$(s_{cr} - \overline{s}_{pl,n}), lag=0$	-0.098	-0.036	-0.024	0.075	0.0063	0.102
$(s_{cr} - \overline{s}_{pl,n}), lag=8$	0.016	0.015	0.015	0.0013	-0.028	0.021
$(d_{1.3} - \overline{s}_{pl,n}), lag=0$	-0.056	0.0069	-0.0022	0.0035	-0.044	0.038
$(d_{1.3} - \overline{s}_{pl,n}), lag=8$	0.016	0.044	0.027	0.029	0.045	-0.0071

$g89$ (the analogue of site H56) is on the first wave of aggravation of competition, and variant $g95$ (the analogue of site AL7) is on the second wave.

In Table 5, other coefficients of the pairwise correlation of model communities for the moment of section $A-A$ are shown. The correspondence is quite satisfactory not only for the row of coefficient $(s_{cr} - S_{pl}), lag=8$, whose values were the basic ones in choice of the location of section $A-A$, but also for the majority of other rows. The location of the section is chosen with accuracy not worse than step of the integration equal 0.1. The theoretical minima of the dependences $(s_{cr} - S_{pl})$ with time, appropriate for comparison with the natural data, are rather sharp, and the differences in correlation coefficients $(S_{cr} - S_{pl})$ for sites D22, R22, and AL5 (Table 3) are very small. There-

fore, these sites are accepted as being rather similar, including initial density of plant communities.

A change in the parameters of the model of a plant (Galitskii 2003) – the value α by an order of magnitude, or the parameter ϵ_M by twofold, results in a change in the position of section $A-A$ (Fig. 3) by approximately 1. This allows us to conclude that in the functions of free growth $A_F(T)$ and $B_F(T)$ used in the model (Galitskii 2003), it is possible to estimate the parameter of the time scale A_1 as the value $A_1 \approx 360$ years and the age of the practical end of growth of the biomass of a freely growing spruce tree as ≈ 1000 years.

It can also be noted that the positions of the extreme of the time dependences of $(s_{cr} - S_{pl})$ and the measure of competition C_{av} described above are rather close (Fig. 1b)

which serves as one more argument in favor of this measure of competition.

For the obtained moment of section *A-A*, it is possible to compare the values of the coefficients of variation for $d_{1.3}$ and s_{cr} of variants *gXX* (Table 6) with the corresponding coefficients of variation of the stem diameter and the area of a tree crown projection (Table 2) that were used for ranking of sites in a natural study. The model values are much less than the natural ones – for diameters by 4–6 times and for crowns by 1.5–2 times.

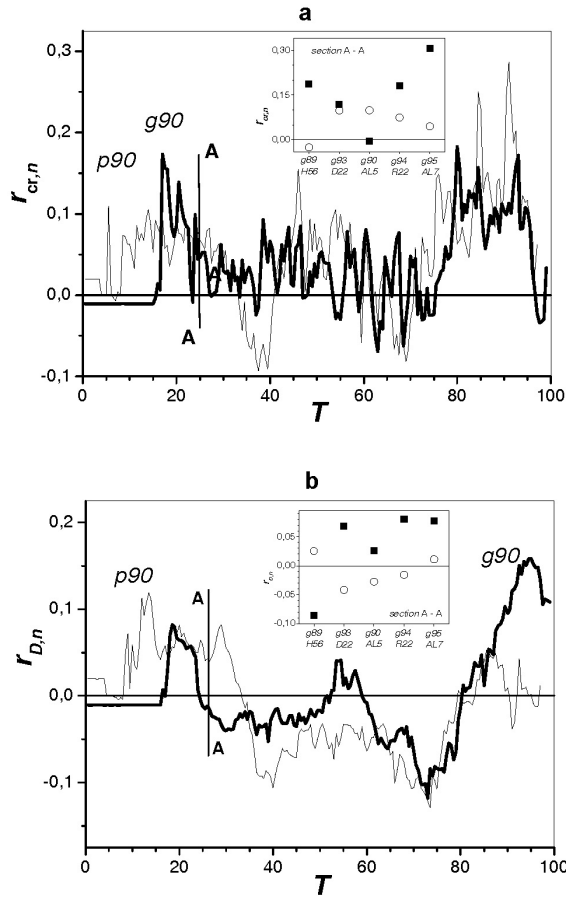


Figure 4. Model dynamics of correlation coefficients of characteristics of a focal tree and its “average neighbour”. **a.** “the area of a crown projection” ($s_{cr} - s_{cr,n}$) – $r_{cr,n}$ and **b.** “the diameter of a stem” ($d_{1.3} - d_{1.3,n}$) – $r_{D,n}$ for uniform *g90* and poisson *p90* communities. Insets contain comparison of values of corresponding correlation coefficients for the model communities *gXX* in section *A-A* (circles) and correlation coefficients for sites in spruce cultures (black squares) in order of increasing of densities.

Correlation with neighbors

In Table 7, values of correlation coefficients between some characteristics of a focal tree and characteristics of its neighbors for the moment of section *A-A* (see Fig. 3) are shown. The average values of characteristics of the neighbors of the focal tree at a given moment, and in some cases with some lag as well, were obtained.

Comparison of the first two rows of the table with the corresponding values of Table 4 shows that distinctions are rather significant, first of all, in values of coefficients: model values are much smaller. The last four rows of Table 7 contain correlation coefficients between characteristics of focal plants and average values of resources of neighbors. These coefficients are also rather small. The dynamics of model coefficients of correlation with neighbors look rather casual, especially for biomass. For example, in Figs. 4a and 4b model dependences of ($s_{cr} - \bar{s}_{cr,n}$) and ($d_{1.3} - \bar{d}_{1.3,n}$) with time for the homogeneous *g90* and Poisson *p90* placements of trees are shown ($lag=0$). Model dynamics of correlation coefficient between diameters of focal and ‘average’ neighboring trees, shown in Fig. 4b correspond quite well to results of Reed and Burkhart (1985) who concluded that correlation is positive at low and rather high levels of plant competition and negative at intermediate levels. In the beginning the neighboring trees not exposed to competition have an identical history and correlation is positive. This is followed by a stage of strong competition and the correlation is negative. After strong thinning due to competition, the surviving trees become the neighbors and correlation is again positive. Consideration of the dynamics indicates that a third stage (one of positive correlation) corresponds to weakening of plant competition following thinning.

Discussion

The results of the 2D model analysis indicate that the effect of nonuniform changes in the correlation coefficients of areas of crown projections of trees in a ranked series of sites of 90 year old spruce stands in the Moscow suburbs with resources available to each tree is similar to that found in natural studies and is not an artifact. It is considered to be a consequence of the pattern of competition in uniform plant communities.

The effects revealed by this model over a range of parameters are considered adequate to estimate the temporal scale of the model $A_1 \approx 360$ years and, accordingly, the time of growth of the biomass of freely growing spruce trees in the Moscow suburbs as ≈ 1000 years. We believe this manner of estimating a temporal parameter could also be applied to stands of other species.

Integral measures of competition

Two measures of competition in a plant community are derived directly from a definition of competition and for a single species, equal aged community are considered, however, they are mainly theoretical values. Their divergence for multispecific and/or uneven-age communities may indicate their areas of application, namely (1) an estimation of sufficiency of resources for community, or (2) an estimation of oppression of plants in community because of lack of resources. Our indices of plant competition are similar to a family of indices of relative competition intensity RCI (Weigelt and Jolliffe 2003, Table 1, 2b), which are usually used to estimate the intensity of competition of individual plants.

A third measure of competition considered here – the correlation coefficient between the area of crown projection of real tree S_{cr} (in nature), or a derivative modeled quantity based on biomass of a tree $s_{cr}=B^{2/\mu}$, and the area of an appropriate Voronoi polygon fit into a family of indices expressing outcome of competition (Weigelt and Jolliffe 2003, Table 3). These dynamics are rather close to dynamics of theoretical measures C_{av} and number of oppressed plants in a plant community N_{opr} . The dynamics of biomass (physiologically active part of tree mass) and dynamics of phytomass (a passive part) are rather variable reflecting their different biological functions which usually are not taken into account in the analysis and modeling of competition in plant communities. Similar correlation coefficients for tree stem diameter $D_{1.3}$ (in a nature) or for the appropriate quantity $d_{1.3}=P^{1/(1+\mu)}$ (in model) cannot be effectively used to estimate the intensity of competition because the process relates to much shorter times. According to our model (Galitskii 2003), biomass of a tree is described by a differential equation of the first order, and only the rate of change of biomass is directly expressed by a resource area for growth. The results indicate the necessity of introducing of some time lag between values of tree biomass and the appropriate environment of a tree (the neighbors determining its current Voronoi polygon) when calculating correlation coefficients.

Insufficiency of two-dimensional models

Although coefficients of variation of “diameters of tree stems” and “areas of crown projections” in our 2D model as well as in their natural analogues, increase with increasing competition in a plant community, their dynamics are more complex than was possible to assume. First of all, the model values are much less.

At the beginning of competition, normality of distributions of biomass and phytomass disappear in the same order as in the natural study. However, this occurs very quickly, even at the first steps of the model. The correlation coefficients of characteristics of plants with characteristics of their neighbors, in particular, of ‘average’ neighbors, are smaller than those for their natural analogues.

The discrepancy of natural and model correlations with neighbors mentioned above is a consequence of the simplicity of the models. In the model of a plant community used, plants only interact at the time when a polygon is repartitioned because their neighbors die off. In between such times, each plant grows and dies off independently on its Voronoi polygon. Correlation relationships between neighboring plants are not very strong as each focal plant interacts with an average of six neighbors. Discrete interactions between neighbors in the models are also weaker because many plants which did not interact before become neighbors as the result of death of intermediate neighbors.

The two-dimensional form of the models used with their excessive ‘rigidity’ can be considered also as a reason for these discrepancies. For example, the model plant that has fallen into an oppressed state and has no time to receive an increase in the area of growth from its dying neighbors, dies off rather quickly. In nature, a plant experiencing lack of resources has an opportunity to try to solve this problem within the third dimension, i.e., growth in height. Stoll et al. (2002) named this situation “shade avoidance”. It extends the time interval of dying off and increases the coefficients of variation. Cutoff of the left tail of distributions as in our 2D model does not occur, and the affinity of distributions to the normal type is retained longer. Conclusions about insufficiency of two-dimensional models in the description of a competition of plants within some model parameter domains corresponding to asymmetry of competition were made also for the -3/2 rule (Galitskii 1998) and under analysis of competition experiments (Purves and Law 2002).

On three-dimensional modeling

Thus, it is possible to conclude that a more satisfactory way of modeling plant community dynamics within model parameter domains corresponding to asymmetry of competition, is three-dimensional modeling of three-dimensional objects. Development of a three-dimensional model of a plant and then of a community is a significantly more complicated problem for which various approaches are possible.

Among these is an approach of joint modeling of the material processes connected with functioning of a tree and algorithmic modeling of the dynamics of the form of a tree based on so-called growth grammars describing the spatial and functional structures of a tree. Such an approach is being intensively developed in a number of European centers (Kurth 1994, De Reffye et al. 1995, Perttunen et al. 1996). Such an approach, rather simply realized in three dimensions, allows one to pictorially formulate, realize, and interpret models of both an individual plant and small communities. It is thought that this promising approach can be an effective, perhaps the main, source of parameters and characteristics for models of a freely growing plant and algorithms of interactions of plants used in models of large communities.

Models of large communities of plants consisting of tens of thousands of elements and more, necessitate studying the behavior of communities in connection with the properties of the plants included, with structure of the community and with properties of the environment. Such models require the development of submodels of an individual plant adequately describing the interaction of a plant with its neighbors in the community yet being simple in internal construction. The simplicity should allow one to determine correctly the destiny of an individual plant in conditions of the community. Work with models of plants and plant communities as demonstrated allow us to presume that they can be a base for development of quasi-three-dimensional models (Galitskii 2005). In these models the biomass sections of a plant will be “visible” ones, and the movement of assimilates in a plant in the third dimension will be described but should not include ‘surplus’ information on smaller details of the construction.

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Appendix

Models of a plant and a community of plants are described in (Galitskii 2003).

The plant is characterized by biomass B – physiologically active part and phytomass P – passive part of total mass accordingly. In the model the dynamics of a plant in community are considered relative to a free-growing plant, which does not experience competition for resources on the part of its neighbors. A free-growing plant is a plant growing in ideal conditions of a community, but without the spatial (resource) restrictions caused by near neighbors. Dynamics of free-growing plant are given by two functions of age T – the area necessary for free growth

$$A_F(T) = A_0 \operatorname{th}^2(T/A_1) \quad (\text{A1})$$

and biomass of free-growing plant

$$B_F(T) = B_0 \operatorname{th}^\mu(T/A_1), \quad (\text{A2})$$

where A_0, A_1, B_0 – parameters, μ – allometric parameter (at isometry it equals 2), function $\operatorname{th}(x)$ is used in (A1 and A2) according to a Poletaev (1966) model of limitation of growth of tree height.

The resources, possessed by plant, are measured by size of area $A(T)$ accessible to a plant, and dynamics of biomass B of a plant are described by differential equations:

$$dB/dT = \kappa(T)(B/\tau(B,T) + f_1(B/B_F) dB_F/dT) - B/\tau(B,T) \quad (\text{A3})$$

where

$$\kappa(T) = \min(1, A(T)/A_F(T)), \quad (\text{A4})$$

$$\tau^{-1}(B,T) = (\alpha B^{k-1} + 1/\tau_M) / (1 + c_G(1 - \kappa(T))) \quad (\text{A5})$$

$$f_1(B/B_F) = (B/B_F)^\gamma / (1 + c_G(1 - \kappa(T))) \quad (\text{A6})$$

The biomass is transformed into phytomass at a rate of

$$dP/dT = B(T)/\tau_M \quad (\text{A7})$$

A sense of the elements of expressions (A3-7) is as follows: $\kappa(T)$ shows a level of provision of a plant with limiting resource, αB^k – expenses for maintenance of biomass ($k < 1$), the multiplier $f_1(B/B_F)$ is essential for re-growth of a plant and γ – parameter (Galitskii 1984), c_G – coefficient of respiration of growth (Makela and Hari 1986), τ_M^{-1} – specific intensity of transformation of a biomass in phytomass.

An analysis of system (A1-6) shows that at $A(T)/A_F(T) \geq 1$ a plant is free-growing ($B(T) = B_F(T)$), and at $A(T)/A_F(T) < 1$ the biomass of a plant begins to decrease and when

$$B(T) < \varepsilon_M B_F(T), 0 < \varepsilon_M < 1 \quad (\text{A8})$$

a plant is considered as dead.

The model of dynamics of a community represents the joint dynamics of plants in a territory. The size $A(T)$ (in expression (A4)) is the territory accessible to a plant in a community, and S_{pl} is the area of the appropriate polygon of the Voronoi mosaic, ($A(T) = S_{pl}$) constructed for system of points in the territory of a plant community.

When a plant dies according to a condition (A8) the Voronoi polygon occupied by the dead plant is released and polygon is re-partitioned among its live neighbors (re-partitioning of a resource is an act of competition between the plants neighboring a dead plant. Of possible variants of re-partitioning (Galitskii 2003) the so-called central way of local re-building of Voronoi mosaic around the dead plant has been used.

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