Ecological and physiological modelling of mixed stand dynamics

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Abstract. Modelling the dynamics of forest ecosystems is an urgent task, as the volume of publications in the Russian and world press demonstrates. In the proposed work, a new ecological and physiological model of a mixed forest stand has considered. Basically, it proceeds from the ecological and physiological model of a single-breed forest stand, that had obtained from the analysis of the behavior of an open thermodynamic system, which is a forest ecosystem. Four differential equations are required to describe a two-species stand, with the mutual influence of species being expressed both in interspecific competition for a resource and in mutual 'support' in the growth of the trees. The model of mixed stand with two species contains 10 independent parameters that have a clear physical meaning. Six parameters relate to the dynamics of each species, and four ones take into account the interactions of the species during growth. The verification of the model is presented by calculating the biomass dynamics for full two-stage aspen-spruce stands of European part (middle taiga ecoregion) of the first appraisal area. The presented model of the dynamics of forest ecosystems can be used in practical forestry, especially in the transition from an extensive method of forestry to an intensive one.

1. Introduction

At present, a large number of ecological and physiological models are known, so the appearance of any new model requires a separate justification for its using in silvicultural practice. Ecological and physiological models are usually divided into analytical [1-3], imitation [4-7] and analytical-imitation [8-10]. The using of imitational and analytical-imitation models requires the using of a large number of parameters presented in tables, graphs, and elementary mathematical dependences [7] that reduces the generality of the obtained results and requires taking into account the numerous factors affecting the growth of specific stands.

It should be noted that despite the marked progress in the development of mathematical (imitational and analytical-imitational) modeling, the limiting factor in modeling the dynamics of stands of different species composition is the absence of experimental data for the construction of such models [4]. This statement applies in full to analytical models as well. However, analytical models establish a relationship between external factors and the parameters of the modelled forest ecosystems, which is justified by theoretical conclusions and checked with experimental data. Therefore, the results of the analytical models claim a generality that is a consequence of the laws of thermodynamics of open systems operating in the forest ecosystem. Despite the present availability of a sufficiently large number of analytical ecological-physiological models, they cannot fully describe all the features of stand development, particularly the growth dynamics of mixed stands. The construction of such models is
complicated not only by a lack of experimental data, but also by a significant increase in the number of model parameters. This leads not only to an increase in computational difficulties, that is surmountable at today’s level of software development, but also to a partial loss of the ‘physical meaning’ of the model parameters.

In [11], a detailed analysis of existing approaches to modeling the dynamics of mixed stands is given, and quality estimates of various models are proposed there. However, the authors are not aware of the results of calculations for specific models using data on real stands.

The aim of the study is to construct a new ecological-physiological model of mixed stand dynamics, using the model of single-species stand dynamics that we constructed, in which the ‘physical meaning’ of the parameters is preserved and computational difficulties are minimized.

2. Methodology
The following are the main points and statements of the analytical model of the dynamics of a single-species stand.

It is known that at a certain value of time, the plant biomass $M$ reaches a maximum, after that the biomass begins to gradually decrease (this dependence is typical for many plantations (for example, [2,9]).

The biomass of a stand and the number of trees are related by an obvious ratio (1):

$$M = mN,$$  

where $m$ is the average biomass per tree; $N$ is the number of trees per hectare of stands.

It is well known, the Bertalanffy’s model [4] is usually used for describing the behavior of the function $m$. The model consists of one dynamic equation for the biomass of an individual $m$ describing growth due to resource absorption and limitation due to resource consumption (2):

$$\frac{dm}{dt} = fgm^q - rm,$$  

where $f$ is the specific absorption rate of the resource; $r$ is the specific consumption rate of the resource.

In equation (2) and further, the variable $t$ means the age of the stand.

The general solution of equation (2) is well known (for example, [4]) and has the form (3):

$$m(t) = \left( \exp (-r(1-q)t) \left( m_0^{1-q} - \frac{P}{r} \right) + \frac{P}{r} \right)^\frac{1}{1-q},$$  

where $m_0$ is the biomass of the species at the initial point of time $t=0$, $P=fg$.

The starting point of the model is that the biomass of the stand reaches its maximum value at some point of time $t_{\text{max}}$. This means that the biomass growth for this point of time is zero (4):

$$\frac{dM(t_{\text{max}})}{dt} = 0,$$  

or $m \frac{dN}{dt} + N \frac{dm}{dt} = 0$. It follows from this equality (5):

$$\frac{dN(t_{\text{max}})}{dt} = -\frac{1}{m(t_{\text{max}})} \frac{dm(t_{\text{max}})}{dt} N(t_{\text{max}}).$$  

We will suppose that the change in stand abundance will proceed in accordance with equation (4), i.e. equation (4) will describe the dynamics of abundance for any $t$, not only for $t_{\text{max}}$. To determine the analytical form of the dependence of the number of trees on time, the following equation needs to be solved (6):
\[
\frac{dN(t)}{dt} = \left(f_1 g_1 m^{q-1} + r_1\right)N(t),
\]

(6)

where the function \(m(t)\) is defined by relation (3), i.e. it is a general solution of the Bertalanffy's equation. Equations for the number of trees and the biomass coming in per tree will take the form (7) and (8):

\[
m(t) = m_\infty \left(1 + \beta \exp(-\alpha t)\right)^p,
\]

(7)

\[
N(t) = N_0 \frac{(1 + \beta_1) p_1}{(1 + \beta_1 \exp(-a_1 t))^{p_0}}.
\]

(8)

The following symbols are introduced here (9):

\[
c_1 = m_0^{1-q} - \frac{fg}{r}; \quad c_2 = \frac{fg}{r}; \quad c_1 = m_0^{1-q} - c_2;
\]

\[
a = r(1-q); \quad p = \frac{r}{a}; \quad p = \frac{1}{1-q}; \quad c_2 = m_\infty^p;
\]

\[
a_1 = \frac{r_1}{(1-q_1)}; \quad p_1 = \frac{r}{a_1}; \quad p_1 = \frac{1}{1-q_1}.
\]

(9)

The model parameters \(\beta_1\) and \(\beta\) are determined from the initial \((m_0, N_0)\) and final values \((m_\infty, N_\infty)\) by the following formulas (10) and (11):

\[
\beta_1 = \left(\frac{N_\infty}{N_0}\right)^{1-q_1} - 1,
\]

(10)

\[
\beta = \left(\frac{m_\infty}{m_0}\right)^{1-q} - 1.
\]

(11)

For \(t_{\text{max}}\), we have (12):

\[
t_{\text{max}} = \frac{1}{a - a_1} \ln \frac{\beta}{\beta_1}.
\]

(12)

The time determined by formula (12) can either be less than the actual time or more than the time at which the biomass of the stand reaches its maximum value. This fact can be interpreted as follows. In an open system, the stationary regime is not fixed by a strict point in time, it lasts for a certain period of time, and may occur out of sync with the time when the maximum value of biomass is reached, after which it evolves smoothly to the equilibrium state of the open system.

Considering \(q_1 = q + \Delta q\), we get a transcendental equation to determine \(\Delta q\) from relation (12) equation (13):

\[
\left(\frac{m_0}{m_\infty}\right)^{1-q} - \left(\frac{N_\infty}{N_0}\right)^{1-q_1} = t_{\text{max}} \Delta q \left(\frac{m_0}{m_\infty}\right)^{1-q} - 1.
\]

(13)

Therefore, the stand dynamics model has only three independent parameters:

– the time of stationary mode \(t_{\text{max}}\).
– resource consumption rate \( r \);
– a factor \( q \) connecting the area and biomass of an organism.

These parameters can be found by carrying out the optimization procedure accordingly. The limit values of the model \( m_\infty \) and \( N_\infty \) can also be considered as independent parameters.

The object of this research is the structure of forest stands, their interaction with the environment and the interaction of mixed stand species during growth. The main research method is the application of the theory of differential equations and integral calculus to describe the dynamics of stand growth.

The starting points for constructing a mixed stand model are the following two hypotheses:

1) when species grow together, the competition for the available resource for the biomass of the individual tree of the first species is described by the species expression (14):

\[
x_1(t) = \gamma_{11}m_1^{1-q_{22}}m_2^{q_{22}} \frac{1}{1-q_{11}}, \quad (14)
\]

2) when species grow together, competition for the available resource to change the number of trees per 1 ha of the first species is described by an expression of the form (15):

\[
u_1(t) = \gamma_{21}r_2N_2. \quad (15)
\]

The effect of the second species on the dynamics of the first species will be expressed in a similar way to (15) the following equations (16):

\[
x_2(t) = \gamma_{22}m_1^{1-q_{11}}m_2^{q_{11}} \frac{1}{1-q_{22}}, \quad u_2(t) = \gamma_{21}r_1N_1. \quad (16)
\]

The model of mixed stands dynamics will take the following form (17):

\[
\frac{dm_1}{dt} = f_{11}g_{11}m_1^{\eta_{11}} - \eta_1m_1 + \gamma_{11}r_2m_2^{1-q_{22}}m_1^{q_{22}} \frac{1}{1-q_{11}},
\]

\[
\frac{dm_2}{dt} = f_{22}g_{22}m_2^{q_{22}} - r_2m_2 + \gamma_{22}m_1^{1-q_{11}}m_2^{q_{11}} \frac{1}{1-q_{22}},
\]

\[
\frac{dN_1}{dt} = -\left(f_{21}g_{21}m_2^{q_{21}-1} - \eta_2\right)N_1 + \gamma_{21}r_2N_2,
\]

\[
\frac{dN_2}{dt} = -\left(f_{12}g_{12}m_1^{q_{12}-1} - r_2\right)N_2 + \gamma_{12}N_1. \quad (17)
\]

The system of differential equations (17) describes the dynamics of a dual-species stand, where the influence of one species on the other during growth is accounted for by expressions (14), (15) and (16), and parameters \( \gamma_{11}, \gamma_{22}, \gamma_{21}, \gamma_{12} \) indicate the degree of influence of one species on the other. Further we introduce the notations (18):

\[
P_{11} = f_{11}g_{11}, \quad P_{22} = f_{22}g_{22}, \quad P_{21} = f_{21}g_{21}, \quad P_{12} = f_{12}g_{12}. \quad (18)
\]

Let us divide the solution of system (17) into two steps. At the first stage, we find the solution of the first two equations describing the dynamics of the biomass of a single tree. At the second stage, taking into account the found functions \( m_1(t) \) and \( m_2(t) \), we solve the remaining system of two equations with unknown functions \( N_1(t) \) and \( N_2(t) \). To solve the system of the first two equations, we introduce new functions by law (we linearize the system) (19):
By substituting successively (19) into the first two equations (17), we obtain (20):

\[
\frac{dY_1}{dt} = P_1(1 - q_{11}) - \eta_1(1 - q_{11})Y_1 + \gamma_1r_2Y_2,
\]

\[
\frac{dY_2}{dt} = P_2(1 - q_{22}) - r_2(1 - q_{22})Y_2 + \gamma_2\eta_1Y_1.
\]

The system of equations (20) is a system of linear inhomogeneous differential equations of the first order, the algorithm for solving which is well known. The general solution of the system of linear inhomogeneous differential equations of the first order is equal to the general solution of the system of linear corresponding homogeneous differential equations of the first order plus the partial solution of the inhomogeneous system (20). In order to find the general solution of the corresponding homogeneous system, let us form a characteristic equation (21):

\[
S^2 + [r_1(1 - q_{11}) + r_2(1 - q_{22})]S - \gamma_1r_2\gamma_2r_1 = 0.
\]

The equation (21) has two valid roots

\[
S_{1,2} = -0.5\left[\eta_1(1 - q_{11}) + r_2(1 - q_{22})\pm \sqrt{[(1 - q_{11})\eta_1 - (1 - q_{22})r_2]^2 + 4\gamma_1r_2\gamma_2\eta_1}\right].
\]

The functions (22):

\[
Y_1^{0} = A_r \exp(S_r t) \quad \text{and} \quad Y_2^{0} = B_r \exp(S_r t)
\]

form a fundamental system of solutions for the homogeneous system of equations. The values of the quantities \(A_r\) and \(B_r\) are determined by the following equations (23):

\[
A_r[-r_1(1 - q_{11}) - S_r] + \gamma_1r_2B_r = 0,
\]

\[
B_r[-r_2(1 - q_{22}) - S_r] + \gamma_2r_1A_r = 0.
\]

As the system (23) has infinitely many solutions, we choose a solution that satisfies the initial conditions. We find a partial solution of system (20) as follows (24):

\[
Y_{1\text{part.}} = A, \quad Y_{2\text{part.}} = B,
\]

when \(r_1(1 - q_{11})r_2(1 - q_{22}) - \gamma_1r_2\gamma_2r_1 \neq 0\).

Then \(A\) and \(B\) are determined from the following algebraic system of equations (25):

\[
-r_1(1 - q_{11})A + \gamma_1r_2B + P_{11}(1 - q_{11}) = 0,
\]

\[
-r_2(1 - q_{22})B + \gamma_2r_1A + P_{22}(1 - q_{22}) = 0.
\]

The solution to system (25) is (26):

\[
A = \frac{(1 - q_{22})[\gamma_1P_{22} + (1 - q_{11})P_{11}]}{\eta_1[(1 - q_{11})(1 - q_{22}) - \gamma_1r_2\gamma_2]},
\]

\[
B = \frac{\gamma_2[\gamma_1P_{22} + (1 - q_{11})P_{11}]}{r_2[(1 - q_{11})(1 - q_{22}) - \gamma_1r_2\gamma_2]} + \frac{P_{22}}{r_2}.
\]

The result is a solution to system (20) in the form of (27):
\[ Y_1(t) = A_2 \exp(-|S_2| t) + A, \]  
\[ Y_2(t) = B_1 \exp(-|S_1| t) + B, \]  
where \( A \) and \( B \) are defined by equations (26), and \( A_2 \) and \( B_1 \) are selected from the solutions of equations (23), taking into account the initial conditions (28):

\[ Y_1(0) = m_1(0)^{1-q_{11}}, \]  
\[ Y_2(0) = m_2(0)^{1-q_{22}}. \]  

Thus, the solution of the first two equations of system (17) has been obtained, i.e., we have determined the dynamics of the biomass of individual trees in a mixed stand. Next, let us turn to the solution of the following two differential equations determining the dynamics of the number of trees per hectare in a mixed stand (29):

\[ \frac{dN_1}{dt} = -(f_{21}g_{21}m_1^{q_{21}-1} - \eta_1)N_1 + \gamma_{21}r_2 N_2, \]  
\[ \frac{dN_2}{dt} = -(f_{12}g_{12}m_2^{q_{12}-1} - r_2)N_2 + \gamma_{12}r_1 N_1. \]  

We make the following hypothesis. The influence of species in determining the number of trees per hectare is small and the decrease in the number of trees per hectare with age is mainly due to self-thinning processes. Therefore, we assume values of \( \gamma_{21} << 1 \) and \( \gamma_{12} << 1 \). The solutions of the equation will be sought in the form of a series expansion on a small parameter \( \gamma_{21} \) (\( \gamma_{12} \)) (30):

\[ N_1(t) = N_{10}(t) + \gamma_{21}N_{11}(t) + \gamma_{21}^2N_{12}(t) + \cdots, \]  
\[ N_2(t) = N_{20}(t) + \gamma_{12}N_{21}(t) + \gamma_{12}^2N_{22}(t) + \cdots. \]  

By equating the terms at equal degrees of \( \gamma_{21} \) and \( \gamma_{12} \), we have (31), (32), (33) and (34):

\[ \frac{dN_{10}}{dt} = -(P_{21}m_1^{q_{21}-1} - \eta_1)N_{10}, \]  
\[ \frac{dN_{20}}{dt} = -(P_{12}m_2^{q_{12}-1} - r_2)N_{20}, \]  
\[ \frac{dN_{11}}{dt} = -(P_{21}m_1^{q_{21}-1} - \eta_1)N_{11} + \gamma_{21}r_2 N_{20}, \]  
\[ \frac{dN_{21}}{dt} = -(P_{12}m_2^{q_{12}-1} - r_2)N_{21} + \gamma_{12}r_1 N_{10}. \]  

The results of equations (31) and (32) are known because they represent the dynamics of the number of trees per hectare for a single-species stand (relations (8)–(13) of this work). Equations (33) and (34) are linear inhomogeneous differential equations of first order, solutions of which are known also. Let’s write down the general form of the solution of the first order differential equation (35) and (36):

\[ \frac{dy}{dt} + f(t)y = g(t), \]
\[ y = \exp(-F) \left[ \mu + \int_{\xi}^{t} g(t) \exp(F) dt \right], \]

where \( F(t) = \int_{\xi}^{t} f(t) dt \).

For our case we have: \( \xi = 0, \mu = N_{11}(0) \) or \( \mu = N_{21}(0) \). At the initial moment of time there is no mutual influence of species

\[ g(t) = N_{10}(0) \frac{r_2 (1 + \beta_{12})^{r_{12}}}{(1 + \beta_{12} \exp(-a_{12} t))^{r_{12}}} \exp(- |S_2| \beta_{12} + 1) \frac{\eta_2}{|S_2|}. \]

The final result for \( N_{11} \) is (37):

\[ N_{11}(t) = \frac{N_{10}(0) r_2 (1 + \beta_{12})^{r_{12}}}{(1 + \beta_{12} \exp(-a_{12} t))^{r_{12}}} \int_{0}^{t} \left( \exp(- |S_2| \beta_{12} + 1) \frac{\eta_2}{|S_2|} \right) dt. \]

For \( N_{21}(t) \) after similar deductions, we have (38):

\[ N_{21}(t) = \frac{N_{20}(0) r_1 (1 + \beta_{21})^{r_{21}}}{(1 + \beta_{21} \exp(-a_{21} t))^{r_{21}}} \int_{0}^{t} \left( \exp(- |S_1| \beta_{21} + 1) \frac{\eta_1}{|S_1|} \right) dt. \]

For the number of trees in a mixed stand, to within the first-order terms of \( \gamma \), we have (39) and (40):

\[ N_1(t) = N_{10}(t) + \gamma_{21} N_{11}(t), \quad (39) \]
\[ N_2(t) = N_{20}(t) + \gamma_{12} N_{21}(t). \quad (40) \]

Thus, the set of equations of the analytical model for a two-breed stand can be represented as follows:

– the individual tree biomass dynamics of a mixed stand are described by equations (19), (26), (27), (28);

– the dynamics of the number of trees per hectare in a mixed stand are described by equations (39), (40), (37), (38).

Equations (19), (26), (27), (28), (39), (40), (37), (38) will be used for numerical calculations.

The model quality is evaluated by the dimensionless Nash-Sutcliffe efficiency criterion \( ME \) [2], which is traditionally used in environmental models (41):

\[ ME = 1 - \frac{\sum_k (Y_{k,emp} - Y_{k,mod})^2}{\sum_k (Y_{k,emp} - Y_{k,mean})^2}, \]

where \( Y_{k,emp} \) is empirical data for this value from the tables; \( Y_{k,mod} \) is calculated model data for the same time points; \( Y_{k,mean} \) is the average value of the same value.

The value of \( ME \) can be in a wide range \((-\infty, 1)\), and 1 corresponds to the ideal description of the model data, 0 corresponds to the quality of the description that coincides with the average value, \( ME < 0 \) indicates the unsuitability of this model.
To verify the model, we used data for complete two-stage aspen-spruce stands of the European part (ecoregion of the middle taiga zone) of the first bonitet from modal tables of the growth course Shvidenko A Z and others (a link to these tables is contained in [12]). The following data was taken from them:

- number of trees per hectare;
- phytomass of plantings per hectare.

The phytomass of an individual tree \( m \) was obtained by dividing the phytomass of plantations \( M \) by the number of trees \( N \).

The value \( N_\infty \) was selected as an independent parameter, while the corresponding value \( m_\infty \) was determined from the condition

\[
N_\infty = M^*/m_\infty,
\]

where \( M^* \) is value biomass (phytomass) stands for the boundary values to the dynamics of the biological productivity of pine plantations (for aspen and spruce stands, the value of \( M^* \) is chosen at \( t=100 \) years).

The value of the parameter \( q \) for the spruce plantation was equal to \( q=0.7 \). This fact is in agreement with the results of the work [1] mentioned above, as well as with our calculations carried out for the pine plantation. The parameter \( q \) for aspen stands is \( q=0.9 \). This value is consistent with the fact that deciduous trees have a higher area-to-volume ratio than coniferous trees.

The calculations were carried out for the model of single-pedigree stands (model 'a'), which is described by equations (7) and (8), and for the model of mixed stands (model 'b'). The latter includes the relations (19), (26)-(28) to determine the dynamics of the biomass of an individual tree and the ratio (37)-(40) for the number of trees per hectare.

### 3. Results and discussion

The results of calculating the parameters of the model and the Nash-Sutcliffe efficiency criterion ME for complete two-tiered aspen-spruce stands of the European part (ecoregion of the middle taiga zone) of the first bonitet are shown in table 1 and in figures 1-6.

**Table 1.** Results of calculations of the model parameters and the Nash-Sutcliffe ME efficiency criterion for complete two-stage aspen-spruce stands of the European part (ecoregion of the middle taiga zone) of the first bonitet.

| Species | Models | ME | \( m \) | \( N \) | \( M \) | \( \gamma_m \) | \( \gamma_N \) | \( q \) | \( r \) |
|---------|--------|----|------|------|-----|---------|---------|------|-----|
| Aspen   | 'a'    | 0.8966 | 0.9975 | 0.6206 | 0 | 0 | 0.87 | 0.34 |
|         | 'b'    | 0.9967 | 0.9975 | 0.9890 | 0.015 | 0.01 | 0.9 | 0.33 |
| Spruce  | 'a'    | 0.9605 | 0.9578 | 0.9487 | 0 | 0 | 0.7 | 0.031 |
|         | 'b'    | 0.9913 | 0.9674 | 0.9535 | 0.015 | 0.002 | 0.69 | 0.032 |

The specific rate of resource consumption, which is determined by the parameter \( r \), is more than ten times higher for aspen than for spruce. This is quite understandable, since the spruce in this stand grows under the canopy of aspen and access to the resource is limited, although the \( r \) value in order of magnitude is quite consistent with the same value for pine stands, where it has values in the range from 0.038 to 0.052, depending on the bonus. The value of the parameters \( \gamma \), which characterizes the degree of influence of different tree species on each other, fully justifies our assumption of its smallness, although the mutual influence of species has a greater effect on the amount of biomass than on the number of trees per hectare. The value of the Nash-Sutcliffe efficiency criterion ME for model 'b' is higher than for model 'a', which is quite understandable, since the experimental data are given for a mixed stand, in which the mutual influence of tree species occurs during their growth.

The figures show that the reproducibility of the data on biomass per tree is up to 5% for all but the smallest ages; for the number of trees per hectare, the reproducibility for all ages does not exceed 5%.
The situation is slightly worse when total biomass is recalculated, but even in this case the difference from the experiment does not exceed 10-15%.

Figure 1. Dependence of biomass (aspen) $m$ per one tree on time $t$. Index '11' refers to calculated from model 'b'; $m$ is empirical data from [12].

Figure 2. Dependence of biomass (spruce) $m^2$ per one tree on time $t$. Index '122' refers to calculated from model 'b'; $m^2$ is empirical data from [12].

Figure 3. Dependence of number of trees $N$ per hectare (spruce) on time $t$. Index '1t' refers to calculated by model 'b'; $N$ is empirical data from [12].

Figure 4. Dependence of number of trees $N^2$ per hectare (spruce) on time $t$. Index '2t' refers to calculated by model 'b'; $N$ is empirical data from [12].

Figure 5. Dependence of plantation biomass (aspen) $M$ on time $t$. Index '1t' refers to calculated from model 'b'; $M$ is empirical data from [12].

Figure 6. Dependence of plantation biomass (spruce) $M^2$ on time $t$. Index '2t' refers to calculated from model 'b'; $M$ is empirical data from [12].
4. Conclusion
The ecological and physiological model of mixed stand dynamics is used to describe the growth curves of full two-tier aspen-spruce stands in the European part. All parameters of the model have a direct physical interpretation, and six of them are common for both breeds: $\gamma_{11}, \gamma_{22}, \gamma_{21}, \gamma_{12}$ are parameters that take into account the degree of influence of one breed on another during growth, $r$ and $q$ are parameters that show the rate of resource consumption and the allometric parameter, respectively. The remaining four parameters are selected from the initial data on the biomass of the stand and the age of the stationary regime during the growth of the stand.

The data on the efficiency criterion indicate the applicability of the proposed model for forestry practice.

The proposed ecological-physiological model of the growth dynamics of a mixed forest stand is a new step in the development of analytical models. The obtained using this model results have a fairly high accuracy. A small number of parameters and a sufficient simplicity of calculations allow us to speak with a high degree of reliability about good prospects for using this model not only for other bonitets of aspen-spruce stands, but also for other mixed stands, taking into account the multifunctionality and biodiversity of forest ecosystems [13]. From our point of view, there is a fundamental possibility of applying this approach to mixed stands with a large number of species.

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