MATHEMATICAL ANALYSIS OF THE SENSIBILITY AND STABILITY OF PLANT MODELS

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Abstract. The aim of the present article is to report the author's results in the field of analysis and modification of mathematical models of plants. The structural schemes of a plant and the mathematical model applied are presented. The model is presented as a system of differential equations. This model contains 9 state variables, 4 driving variables, and 14 parameters. The model's stability and sensibility are discussed. For the sensibility study the so-called sensibility matrix was calculated in two different time-points. For the stability study of the model the so-called Lyapunov's first method for studying stability in non-linear systems was used. The stability study is carried out using a linearized version of the model. A short description of the results of numerical experiments conducted with our model is also given. At the present stage of research the model fits satisfactorily the theory of plant growth.

Key words: mathematical biology and ecology.

INTRODUCTION

The basic research area in the field of modelling the growth of the plant, not only in Estonia, but also in other countries, has been connected to the modelling of agricultural plants and the coexistence of plants of a single species. Very few studies have been conducted in the area of modelling the coexistence of different plants. This field of study is closely connected with the problems of diversity in nature, environmental protection, pollution, and the rehabilitation of polluted environment.

The most common way of the representation of the growth and coexistence of plants is by using systems of differential equations (Кулль & Кулль, 1989). The models of plants and their coexistence are usually built for studying some special effects which take place in the nature. The present model was built to study light and nitrogen competition in a single plant and in the coexistence of plants.

In modelling the coexistence of large plant communities on the basis of a model of a single plant, there usually occurs the need for some special degree-decreasing methods due to the lack of adequate computer resources. For that reason it is very important to study different qualities of the single plant model (as the model of coexistence is built using

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a model of the single plant), e.g. sensibility, stability, phase planes (Антамонов, 1983a, 1983b; Nagrath & Gopal, 1984), and try to find out possible incorrectness in the model, e.g. linear combinations of state variables (Gill et al., 1991; Stoer & Bulirsch, 1980). In the present work special attention is paid to the single plant model and to methods of the analysis and modification of mathematical models of this type.

METHODS

GUA YTEHSISHITY AND

1. Mathematical model of a plant

The mathematical model of a plant is presented as a system of ordinary differential equations. The model is presented in this article in a laconic way; a more detailed description of basic processes of the model of this kind is given by K. Kull and O. Kull (Кулль & Кулль, 1989). A model which describes the growth of a tree during one vegetation period was presented also by Svirizhev (Свирижев, 1979; see also Глушков et al., 1983).

For better modelling of the growth of a plant the method of dividing a plant into horizontal layers and describing the growth of each layer separately was used in the present project. The model will include only two state variables: the mass of functional nitrogen pool (Nf) and the mass of leaves (Ml) divided into layers. To help understand the method of modelling plant growth using layers a numerical example is given.



Fig. 1. Graphical interpretation of the plant's model.

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Example

The thickness of the layer is 0.5 m. The initial value of the state variable of height (H) will be 0.25 m. When during the numerical experiments the value of H reaches 0.5 m, additional equations of Nf and Ml for layer 2 (the structure of the equations for layer 2 will remain the same as for layer 1) will be formed. 10% of the last values of Nf and Ml in layer 1 will be transformed to layer 2 as initial values for Nf and Ml. Additional equations will again be formed when the value of H reaches 1.0 m, 1.5 m, 2.0 m, etc.

Graphical interpretation of the plant model is shown in Fig. 1.

State variables:

Cl	— mass of the carbon assimilates pool, kg;
Ms	— mass of the trunk and branches, kg;
Mr	— mass of the roots, kg;
Н	— height, m;
Nl	— mass of the moving nitrogen pool, kg;
Nc	- mass of the organic nitrogen pool, kg;
Nm	- mass of the mineral nitrogen pool, kg;
Nf[i]	- mass of the functional nitrogen pool in the <i>i</i> -th layer of
	a plant, kg;
Ml[i]	— mass of the leaves in the <i>i</i> -th layer of a plant, kg.

Driving variables:

$\begin{bmatrix} Cl \end{bmatrix}$	-	concentration of carbon assimilates in the leaves, kg·kg ⁻¹ ;
Ī[i]	-	light radiation in the <i>i</i> -th layer of a plant;
Sl[i]	-	area of leaves in the <i>i</i> -th layer of a plant, m ² ;
p[i]	-	the leaves surface density in the <i>i</i> -th layer of a plant,
		$kg \cdot m^{-2}$.

Notations:

h — number of layers; i — current layer.

Model in the form of ordinary first order differential equations: Growth of the mass of the carbon assimilates pool

$$\frac{\mathrm{d}Cl}{\mathrm{d}t} = k5 \cdot \sum_{i=1}^{h} Nf[i] - k6 \cdot [Cl] \cdot H - k7 \cdot [Cl] \cdot Mr - \sum_{i=1}^{h} k8 \cdot [Cl] \cdot Nf[i] - k9 \cdot [Cl] \cdot Nf[h];$$
(1)

Growth of the mass of the trunk and branches

$$\frac{\mathrm{d}Ms}{\mathrm{d}t} = k6 \cdot [Cl] \cdot H; \tag{2}$$

Growth of the mass of the roots

$$\frac{\mathrm{d}Mr}{\mathrm{d}t} = k7 \cdot [Cl] \cdot Mr - kr \cdot Mr;$$

Growth of the height

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1 3 4

$$\frac{\mathrm{d}H}{\mathrm{d}t} = k9 \cdot [Cl] \cdot \frac{Nf[h]}{Ml[h]};$$

(4)

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(3)



Growth of the mass of the moving nitrogen pool

$$\frac{dNl}{dt} = k4 \cdot Mr \cdot Nm - \sum_{\substack{i=1\\Nl}}^{h} k1 \cdot \frac{kp1 \cdot I[i]}{p[i]} \cdot k8 \times \sum_{\substack{i=1\\Nl}}^{h} Ml[i]; \frac{Nl}{\sum_{\substack{i=1\\i=1}}^{h} Ml[i]};$$
(5)

Growth of the mass of the organic nitrogen pool

$$\frac{\mathrm{d}Nc}{\mathrm{d}t} = k2 \cdot \sum_{i=1}^{h} Nf[i] - k3 \cdot Nc;$$
(6)

Growth of the mass of the mineral nitrogen pool

$$\frac{\mathrm{d}Nm}{\mathrm{d}t} = k3 \cdot Nc - k4 \cdot Mr \cdot Nm; \tag{7}$$

Growth of the mass of the leaves in the *i*-th layer of a plant

$$\frac{\mathrm{d}Ml[i]}{\mathrm{d}t} = k8 \cdot [Cl] \cdot Nf[i] - k2 \cdot Ml[i]; \tag{8}$$

Growth of the mass of the functional nitrogen pool in the i-th layer of a plant

$$\frac{dNf[i]}{dt} = k1 \cdot \frac{kp1 \cdot I[i]}{p[i]} \cdot k8 \cdot [Cl] \cdot Nf[i] \cdot \frac{Nl}{\sum_{i=1}^{h} Ml[i]} - k2 \cdot \sum_{i=1}^{h} Nf[i].$$
(9)

Calculation of driving variables:

Calculation of the concentration of carbon assimilates

$$[Cl] = \frac{Cl}{\sum_{i=1}^{h} Ml[i] + Cl};$$
(10)

Calculation of the light radiation in the *i*-th layer of a plant

$$I[i] = I0 \cdot \exp\left(-ke \cdot \sum_{j=i}^{h} Sl[j]/Sg\right);$$
(11)

Calculation of the area of the leaves in the *i*-th layer of a plant

$$St[i] = Mt[i]/p[i];$$
⁽¹²⁾

Calculation of the leaves surface density in the *i*-th layer of a plant

$$p[i] = kp1 \cdot I[i] + kp2. \tag{13}$$

Parameters:

1.	ke		 light extinction coefficient, none;
2.	Sg		— area of plant, m ² ;
3.	kp1	and kp2	— leaves surface density coefficients, kg \cdot m ⁻² ;
4.	k1		- coefficient of functional nitrogen pool increase,
			day-1;
5.	k2		- coefficient of organic nitrogen pool increase, day-1;

6.	k3	- coefficient of mineral nitrogen pool incre	ase, day-1;
7.	<i>k</i> 4	- coefficient of moving nitrogen pool	increase,
		day ⁻¹ ·kg ⁻¹ ;	
8.	k5	 coefficient of assimilates increase, day⁻¹; 	
9.	<i>k</i> 6	 growth rate coefficient for trunks, kg·m⁻ 	1. day-1;
10.	k7	- growth rate coefficient for roots, day ⁻¹ ;	
11.	k8	- growth rate coefficient for leaves, day-1;	
12.	k9	- growth rate coefficient for tree height, m.	day-1;
13.	kr	- coefficient of root decrease intensity, day	-1.

2. Sensibility study of the plant model

The study of the sensibility of dynamical models poses usually serious difficulties, which are closely connected to problems of the stationary state of systems. Antamonov (Антамонов, 1983b) has discussed these models in biology.

For studying the sensibility of a model the so-called sensibility matrix (Nagrath & Gopal, 1984), which contains sensibility coefficients S_{ij} for two different time-points, must be calculated.

$$S_{ij} = \frac{\Delta y_i / y_i}{\Delta o_i / o_i}$$

where o_j — the value of the *j*-th parameter in this time-point;

 Δo_j — the change of this parameter in this time-point;

 y_i — the value of the *i*-th variable in this time-point;

 Δy_i — the change of this variable in this time-point;

The average absolute values of sensibility are also calculated for each state variable and for each parameter.

For calculating the sensibility coefficients the programming language TurboPascal 5.0, spreadsheet package Microsoft Excel 4.0, and a personal computer with the main processing units Intel 80386 and 80387 were used.

3. Stability study of the plant model

For the stability study of the plant model the so-called Lyapunov's first method of studying stability in non-linear systems (Митропольский, 1977) was used. The most common method for studying stability in nonlinear systems is Lyapunov's second method (Воронов, 1979), but there are great difficulties in applying this method to the models which have a very high degree. Therefore, the study of the stability of our model is performed according to Lyapunov's first method with a linearized version of a system used.

Non-linear system

$$\frac{\mathrm{d}X}{\mathrm{d}t} = F(X),$$

where $X = \{x_1, \ldots, x_n\}$ — vector of the state variables; $F = \{f_1, \ldots, f_n\}$ — vector of functions. Linear system

$$\frac{\mathrm{d}X}{\mathrm{d}t} = A \cdot X,$$

where A is the Jacobian matrix of our non-linear system.

$$A = \begin{bmatrix} \frac{\delta f_1}{\delta x_1} \cdots \frac{\delta f_1}{\delta x_n} \\ \vdots \\ \frac{\delta f_n}{\delta x_1} \cdots \frac{\delta f_n}{\delta x_n} \end{bmatrix}$$

According to Lyapunov and Tsetaev's theorem (Антамонов, 1983a), a linear system is stable, if all the eigenvalues of matrix A have negative real parts (see also Nagrath & Gopal, 1984). A zero eigenvalue means that the system comprises an equation that is a linear combination of some other equations (Gill et al., 1991, ch. 2).

The investigation of stability is also very closely connected with the problems of the idealization of systems (Жаботинский, 1974) and methods of decreasing the degree of a system (Картвелишвили & Галактионов, 1976; see also Глушков, 1983).

The study of stability was carried out on a personal computer (processors 80386/387) using the programming language Microsoft FORTRAN.

4. Numerical experiments with the model

The system of ordinary differential equations was solved by using the Euler method of solving systems of differential equations (Stoer & Bulirsch, 1980). The reason why this method was chosen is that in the present model there could be some equation(s) which is (are) a linear combination of some other equations and therefore the more complex methods may not work properly.

Numerical experiments were done by using a personal microcomputer with the main processing units Intel 80386 and 80387. For building a computer program the programming language TurboPascal 5.0 was used.

A user interface was built. It helps the user who is not familiar with the programming techniques in TurboPascal also to use the program without any difficulties.

RESULTS AND DISCUSSION

1. Numerical experiments performed with the present model

The numerical experiments were made using a personal computer with the main processing units Intel 80386/387 (Table 1).

The graphical representation of the results of the numerical experiment is shown in Figs. 2a-2i,

Table 1

Initial	values	for	numerical	experiments
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1 Mass of the carbon assimilates pool 0.012 kg 2 Mass of the trunk and branches 0.05 kg 3 Mass of the roots 0.05 kg 4 Height 0.25 m 5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the inneral nitrogen pool 0.03 kg 8 Mass of the funcional nitrogen pool 0.03 kg 9 Mass of the leaves (layer 1) 0.1 kg 10 Area of the leaves (layer 1) 0.6 m 11 k1 1 day-1 12 k2 0.03 day-1 13 k3 0.005 day-1 14 k4 0.17 day-1.kg-1 15 k5 3.3 day-1 16 k6 0.0001 kg·m^{-1}.day 19 k9 0.2 m.day-1 20 ke 0.5 - 21 kp1 0.08 kg·m^	No,	Description	Value	Unit
1 Mass of the carbon assimilates pool 0.012 kg 2 Mass of the trunk and branches 0.05 kg 3 Mass of the roots 0.05 kg 4 Height 0.25 m 5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the inneral nitrogen pool 0.03 kg 8 Mass of the funcional nitrogen pool (layer 1) 0.1 kg 9 Mass of the leaves (layer 1) 0.002 kg 10 Area of the leaves (layer 1) 0.03 day ⁻¹ 11 $k1$ 1 day ⁻¹ 12 $k2$ 0.005 day ⁻¹ 13 $k3$ 0.0005 day ⁻¹ 14 $k4$ 0.17 day ⁻¹ kg ⁻¹ 15 $k5$ 3.3 day ⁻¹ 16 $k6$ 0.20011 kg m ⁻¹ day 17 $k7$ 0.4 day ⁻¹ 19 $k9$ 0.2 $m \cdot day^{-1}$			0.010	0.073
2 Mass of the trunk and branches 0.05 kg 3 Mass of the roots 0.05 kg 4 Height 0.25 m 5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the mineral nitrogen pool 0.03 kg 8 Mass of the funcional nitrogen pool (layer 1) 0.1 kg 9 Mass of the leaves (layer 1) 0.002 kg 10 Area of the leaves (layer 1) 0.6 m 11 $k1$ 1 day^{-1} 12 $k2$ 0.03 day^{-1} 13 $k3$ 0.005 day^{-1} 14 $k4$ 0.17 day^{-1} 15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ <tr< th=""><td>1</td><td>Mass of the carbon assimilates pool</td><td>0.012</td><td>kg</td></tr<>	1	Mass of the carbon assimilates pool	0.012	kg
3 Mass of the roots 0.05 kg 4 Height 0.25 m 5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the mineral nitrogen pool 0.03 kg 8 Mass of the functional nitrogen pool (layer 1) 0.1 kg 9 Mass of the leaves (layer 1) 0.002 kg 10 Area of the leaves (layer 1) 0.6 m 11 k1 1 day ⁻¹ 12 k2 0.03 day ⁻¹ 13 k3 0.005 day ⁻¹ 14 k4 0.17 day ⁻¹ ·kg ⁻¹ 15 k5 3.3 day ⁻¹ 16 k6 0.0001 kg·m ⁻¹ ·day 17 k7 0.4 day ⁻¹ 18 k8 6.5 day ⁻¹ 19 k9 0.2 m·day ⁻¹ 20 ke 0.5 — 21 kp1 0.08 kg·m ⁻² 22 kp2 0.02 kg·m ⁻² 23 kr 0.0025 day ⁻¹	2	Mass of the trunk and branches	0.05	kg
4 Height 0.25 m 5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the mineral nitrogen pool 0.03 kg 8 Mass of the funcional nitrogen pool (layer 1) 0.1 kg 9 Mass of the leaves (layer 1) 0.002 kg 10 Area of the leaves (layer 1) 0.6 m 11 $k1$ 1 day^{-1} 12 $k2$ 0.03 day^{-1} 13 $k3$ 0.005 day^{-1} 14 $k4$ 0.17 $day^{-1} \cdot kg^{-1}$ 15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ 21 $kp1$ 0.02 $kg \cdot m^{-2}$ 22 $kp2$ 0.02 $kg \cdot m^{-2}$	3	Mass of the roots	0.05	kg
5 Mass of the moving nitrogen pool 0.004 kg 6 Mass of the organic nitrogen pool 0.05 kg 7 Mass of the mineral nitrogen pool 0.03 kg 8 Mass of the funcional nitrogen pool 0.03 kg 9 Mass of the funcional nitrogen pool 0.03 kg 9 Mass of the leaves (layer 1) 0.1 kg 10 Area of the leaves (layer 1) 0.6 m 11 $k1$ 1 day^{-1} 12 $k2$ 0.03 day^{-1} 13 $k3$ 0.005 day^{-1} 14 $k4$ 0.17 $day^{-1} \cdot kg^{-1}$ 15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ 21 $kp1$ 0.02 $kg \cdot m^{-2}$ 22 $kp2$ 0.022 $kg \cdot m^{-2}$	4	Height	0.25	m
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7Mass of the mineral nitrogen pool 0.03 kg8Mass of the funcional nitrogen pool (layer 1) 0.1 kg9Mass of the leaves (layer 1) 0.002 kg10Area of the leaves (layer 1) 0.6 m11k1 1 day^{-1} 12k2 0.03 day^{-1} 13k3 0.005 day^{-1} 14k4 0.17 $day^{-1} \cdot kg^{-1}$ 15k5 3.3 day^{-1} 16k6 0.0001 $kg \cdot m^{-1} \cdot day^{-1}$ 17k7 0.4 day^{-1} 19k9 0.2 $m \cdot day^{-1}$ 20ke 0.5 $-$ 21kp1 0.08 $kg \cdot m^{-2}$ 22kp2 0.022 $kg \cdot m^{-2}$ 23kr 0.0025 day^{-1}	6	Mass of the organic nitrogen pool	0.05	kg
8 Mass of the functional nitrogen pool (layer 1) 0.1 kg 9 Mass of the leaves (layer 1) 0.002 kg 10 Area of the leaves (layer 1) 0.6 m 11 k1 1 day ⁻¹ 12 k2 0.03 day ⁻¹ 13 k3 0.005 day ⁻¹ 14 k4 0.17 day ⁻¹ kg ⁻¹ 15 k5 3.3 day ⁻¹ 16 k6 0.0001 kg·m ⁻¹ ·day 17 k7 0.4 day ⁻¹ 19 k9 0.2 m·day ⁻¹ 20 ke 0.5 - 21 kp1 0.08 kg·m ⁻² 22 kp2 0.02 kg·m ⁻² 23 kr 0.0025 day ⁻¹	7	Mass of the mineral nitrogen pool	0.03	kg
9Mass of the leaves (layer 1) 0.002 kg10Area of the leaves (layer 1) 0.6 m11k11 day^{-1} 12k2 0.03 day^{-1} 13k3 0.005 day^{-1} 14k4 0.17 $day^{-1} \cdot kg^{-1}$ 15k5 3.3 day^{-1} 16k6 0.0001 $kg \cdot m^{-1} \cdot day$ 17k7 0.4 day^{-1} 18k8 6.5 day^{-1} 20ke 0.5 $-$ 21kp1 0.08 $kg \cdot m^{-2}$ 22kp2 0.022 $kg \cdot m^{-2}$ 23kr 0.0025 day^{-1}	8	Mass of the funcional nitrogen pool (layer 1)	0.1	kg
10Area of the leaves (layer 1) 0.6 m11 $k1$ 1 day^{-1} 12 $k2$ 0.03 day^{-1} 13 $k3$ 0.005 day^{-1} 14 $k4$ 0.17 $day^{-1} \cdot kg^{-1}$ 15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 18 $k8$ 6.5 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ 21 $kp1$ 0.08 $kg \cdot m^{-2}$ 22 $kp2$ 0.022 $kg \cdot m^{-2}$ 23 kr 0.0025 day^{-1}	9	Mass of the leaves (layer 1)	0.002	kg
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13 $k3$ 0.005 day^{-1} 14 $k4$ 0.17 $day^{-1} \cdot kg^{-1}$ 15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 18 $k8$ 6.5 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ 21 $kp1$ 0.08 $kg \cdot m^{-2}$ 22 $kp2$ 0.02 $kg \cdot m^{-2}$ 23 kr 0.0025 day^{-1}	12	k2	0.03	day-1
14, k4 0.17 $day^{-1} \cdot kg^{-1}$ 15, k5 3.3 day^{-1} 16, k6 0.0001 $kg \cdot m^{-1} \cdot day$ 17, k7 0.4 day^{-1} 18, k8 6.5 day^{-1} 19, k9 0.2 $m \cdot day^{-1}$ 20, ke 0.5 $-$ 21, kp1 0.08 $kg \cdot m^{-2}$ 22, kp2 0.02 $kg \cdot m^{-2}$ 23, kr 0.0025 day^{-1}	13	k3	0.005	day-1
15 $k5$ 3.3 day^{-1} 16 $k6$ 0.0001 $kg \cdot m^{-1} \cdot day$ 17 $k7$ 0.4 day^{-1} 18 $k8$ 6.5 day^{-1} 19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.5 $-$ 21 $kp1$ 0.08 $kg \cdot m^{-2}$ 22 $kp2$ 0.02 $kg \cdot m^{-2}$ 23 kr 0.0025 day^{-1}	14	k4	0.17	day-1.kg-1
16 $k6$ 0.0001kg·m ⁻¹ ·day17 $k7$ 0.4day ⁻¹ 18 $k8$ 6.5day ⁻¹ 19 $k9$ 0.2m·day ⁻¹ 20 ke 0.5-21 $kp1$ 0.08kg·m ⁻² 22 $kp2$ 0.02kg·m ⁻² 23 kr 0.0025day ⁻¹	15	k5	3.3	day-1
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19 $k9$ 0.2 $m \cdot day^{-1}$ 20 ke 0.521 $kp1$ 0.08 $kg \cdot m^{-2}$ 22 $kp2$ 0.02 $kg \cdot m^{-2}$ 23 kr 0.0025 day^{-1}	18	k8	6.5	day-1
20ke 0.5 $-$ 21kp1 0.08 kg·m ⁻² 22kp2 0.02 kg·m ⁻² 23kr 0.0025 day ⁻¹	19	k9	0.2	m·day-1
21 $kp1$ 0.08 $kg \cdot m^{-2}$ 22 $kp2$ 0.02 $kg \cdot m^{-2}$ 23 kr 0.0025 day^{-1}	20	ke	0.5	-
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	21	kp1	0.08	kg⋅m ⁻²
23 kr 0.0025 day ⁻¹	22	kp2	0.02	kg⋅m ⁻²
	23	kr	0.0025	day-1
24 dt-iteration step $0.1 dav^{-1}$	24	dt-iteration step	0.1	dav-1
25 Number of iterations 32000 —	25	Number of iterations	32000	_
26 /0	26	10	1	

2. Sensibility study

The sensibility matrix was calculated for two different time-points (t1=150 and t2=320 days). The calculated sensibility coefficients at time-point t1=320 days are presented in Table 2.

The average for the sum of the mass of the leaves is 2.8333 and that of the mass of functional nitrogen pool is 2.95962.

According to the results, the most sensible state variables are the mass of the functional nitrogen pool and the mass of the leaves in layers. The parameter which affected the development of the plant the most strongly is k2 (the coefficient of the organic nitrogen pool increase). It describes the process where the mass of the functional nitrogen pool (which is divided into layers) changes into the mass of the organic nitrogen pool (which is not divided into layers). The state variable Nc (organic nitrogen pool) has, according to the results, the lowest absolute average of sensibility coefficients. The parameter which affects the development of the plant the least is k6, the growth rate coefficient for trunks.

Comparing the study of the sensibility of the model PUU-1 carried out by K. Kull and O. Kull (Кулль & Кулль, 1989, pp. 115—118 and 147—155) with the results of the present sensibility study, we can see that the most



layer,

Table 2

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Calculated sensibility coefficients at time-point t1=320 days

Average	0.7895	4.2592	0 1600	2.1000	1.1875	3.5902	0.0423	1.1740	1.0797	0.9785	3.3481	2.6656	0.2721	1.3394		
Nf[4]	1.6193	-14 8113	9 2746	0.7140	2.0347	3.7308	-0.0118	-2.6770	1.3677	2.8855	3.6149	-9.3958	-0.4115	1.0984		3.6179
Nf[3]	0.3700	9 4064	1 6110	0140	0.3821	1.9223	-0.0002	0.5061	0.2196	-0.1829	1.6871	2.1064	-0.1369	-0.4296	20	0.9203
Nf[2]	-1 1838	4 6169	0110 0	-3.2140	-2.1372	-5.6958	0.0086	1.8518	-1.7273	-2.0576	-6.1563	3.7434	0.4295	-2 2870		2.7007
Nf[1]	-1 9933	4 8810	00000	-0.8032	-3.5235	-13.4137	0.0118	2.2620	-3.5323	-1.5420	-13.9003	4.1210	0.9021	-2 8475		4.5996
<i>Mi</i> [4]	1 5943	6000 06	7010.07	3.33/9	2.1747	3.8948	-0.0133	-3.5303	1.7307	2.8985	3.5738	-9.9335	-0.4102	1 7479		4.2908
MI[3]	0 4469	2022.0		1.7494	0.7533	2.5233	-0.0027	-0.1557	0.8437	-0.0592	1.8445	1.8308	-0.1608	0 6094	1700.0	0.8694
MI[2]	_11187	101111	4077.4	-2.9568	-1.6104	-3.6669	0.0063	1.4260	-0.8323	-2.0612	-5.6900	3.6712	0.4140	0 0002	0706.0-	2.1988
[1] <i>IW</i>	1 0084	100001	4.1008	-6.5512	-2.8928	-10.0664	0.0354	1.9194	-2.3809	-1.5382	-13.2740	4.0836	0.9157	01001	0100.1-	0.3974
Nm	0 0010	2100.0	0.130/	0.0097	-0.3167	-0.8945	0.0015	-0.6137	0.4658	-0.0148	0.0058	-0.0244	-0.0011	1 00000	1.0320	0.3368
Nc	0 0050	0077.0	0.0394	-0.3731	0.0725	0.2201	-0.0003	0.1972	-0.1621	0.0043	-0.0442	0 1967	-0.0419			0.2058
IN	00000	-0.8838	-2.0212	0.8485	0.1687	0.4187	6000.0-	0.1102	-0.0324	-0.0016	0.1664	-0 4774	0 1644		1014.0-	0.4443
Н	10000	0.0300	0.6310	0.0874	0.0453	0.1198	-0.0002	-0.0424	-1 0643	0.9261	0.0995	-0 0869	00003	0,000	0.0342	0.2442
Mr .		0.2238	0.6915	0.6952	-0.7942	0.9473	-0.0018	0 7949	-0 6913	0.0187	-0.0487	0 1509	-0.0403	001000	-3.9842	0.6933
Ms		0.0206	0.2191	0.0511	0 1649	4 5473	0.5344	-0 3079	-0.8578	0.4410	0.0375	0.0065	0.001	1100.0	0.3877	0.5848
CI		0.2177	0.1619	0.6855	0.7419	1 7918	-0 0059	-1 9869	-0 9879	-0.0458	-0.0783	0 2050	0.0200	6600.0	1.5187	0.5343
Par- ameter	tst	kl	k2	k3	<i>k</i> 4	k5	k6	67	68	p.a.	oq	bul	1 day	742	Rr	Averag

sensible state variables in the present models are those that were divided into layers (Ml and Nf). In the present case the mass of roots comes next. In the sensibility study of the model PUU-1 the most sensible state variables were connected with roots (the mass of roots and the mass of carbon assimilates in roots). The least sensible state variables in the present model are the mass of the organic nitrogen pool and the plant height. In the model PUU-1 the least sensible state variables were the overall mass of the nitrogen pool (in this model only the overall sum of the nitrogen pools in a plant was investigated as state variable) and the height.

The above facts indicate that in a model where some state variables are divided into layers those state variables may become the most sensible ones.

At the present stage of research fundamental conclusions cannot be made on the basis of those two sensibility studies of plant models, as the studies were carried out in different time-points using different methods of computing and different computer environments, which all affect the final results.

3. Stability study

The eigenvalues of the linearized system of ordinary non-linear differential equations were calculated for two typical situations: (1) for the model where dH/dt=0, e.g. the dimension of the system is not changing; and (2) for the model where the dimension is changing, here the eigenvalues were calculated for two layers.

- (1.1) Calculated eigenvalues at the point t=0: 0.0; -0.3379; $+0.01358\pm0.03509$; 0.007944; -0.01573; -0.0001107; -0.0028; -0.005955.
- (1.2) Calculated eigenvalues in the neighbourhood of the stable point (t=3200 days) (the neighbourhood was found by numerical experiments as stated above):

0.0; -111; -1.165; $-0.004899 \pm 0.02914i$; -0.01301; -0.004601; -0.0003307; 0.00001534.

The eigenvalues indicate that one of our equations is a linear combination of some others (one eigenvalue equals zero). It is not difficult to find out such dependence, as a more thorough investigation of the model shows that there exists a precondition according to which the sum of all nitrogen pools stays constant:

$$Nm + Nc + Nl + \sum_{i=1}^{h} Nf[i] = N_{\text{total}} = \text{const};$$

$$\frac{dNm}{dt} + \frac{dNc}{dt} + \frac{dNl}{dt} + \sum_{i=1}^{h} \frac{dNf[i]}{dt} = 0.$$

This kind of dependency can be easily removed if N_{total} occurs in t=0 as an input variable and one of the equations of nitrogen (for example Nm) is replaced by an equation of subtraction

$$Nm = N_{\text{total}} - Nc - Nl - \sum_{i=1}^{h} Nf[i].$$

After this modification of the model a new Jacobian matrix and new eigenvalues must be calculated, because there can be more incorrectnesses in the model and the linear combination can be more complex than stated above.

As it can be seen in t=0, there is an eigenvalue whose real part is positive. This means that there exists a trajectory from this point which leads the system to an unstable state. The absolute values of eigenvalues are very small, which also means that the system is very "far" from the state of stability.

All the calculated eigenvalues in the possible neighbourhood of the stability point t=3200 (days) have negative values, which means that the system is moving toward a state of stability and it is much closer to stability as the absolute values of the eigenvalues are relatively big (-111; -1.165, etc.).

- (2.1) Calculated eigenvalues at the beginning of the first layer:
 0.0; -0.2774; -0.006657±0.01877i; -0.01698; 0.009908; -0.005628;
 -0.0000278±0.0002654i;
- (2.2) Calculated eigenvalues before the creation of the second layer:
 0.0; 0.1167; -0.08445; -0.02163±0.007881i; -0.009962;
 -0.000006757; -0.005748; -0.002632;
- (2.3) Calculated eigenvalues after the creation of the second layer: 0.0; 0.0; 0.0; -0.09877; 0.0; -0.005; -0.1481; 0.2133 E-17; -0.05261±0.007619i; -0.03;
- (2.4) Calculated eigenvalues in the middle of the second layer:
 0.0; 0.0; 0.0; -0.01107; 0.0; -0.005; -0.1427; -0.05213±0.007824i;
 -0.9291 E-18; -0.03;
- (2.5) Calculated eigenvalues before the creation of the third layer: 0.0; 0.0; 0.0; -0.01163; 0.0; -0.005; -0.1478; 0.7502 E-18; -0.05322±0.007419i; -0.03.

As it can be seen, when the degree of the model increases, there are now four equations in the model which are linear combinations of the others. One of these equations is, as stated above, one of the equations of nitrogen. The other two zero eigenvalues come from two similar equations which we obtained from dividing the plant into layers. The fourth zero eigenvalue requires a deeper investigation of the applied modelling process as there could be one more equation which is a linear combination of some others. It could occur for example in the modelling of the growth of the mass of the carbon assimilates pool or the growth of the mass of leaves, trunks, and roots. (Among the eigenvalues calculated in Section 1 there was a relatively small eigenvalue, which could occur due to computation errors. This proves that there can be an equation which is a linear combination of others.)

There are also some eigenvalues which have a positive real part, but their absolute value is relatively small compared to those eigenvalues which have a negative real part. The reason why there are eigenvalues with a positive real part could be a calculation error, as a computer operates only with real numbers with a fixed degree. In general it may be stated that our model seems to fit the stability conditions, but in the points considered here it is very "far" from the point of stability. The model probably reaches the stable equilibrium point at a certain degree.

IDEAS ABOUT FURTHER WORK

The following is a presentation of an idea of a method which could be useful in analysing mathematical models of a plant and plants' coexistence. It has not yet been applied to the present model.

A system of differential equations $dx_i/dt = f_i(a, b, c, d, ..., x_i)$, which describes the growth of the plant (where x_i — state variables; a, b, c, d... — parameters of the system).

We will search for a combination of parameters, when the given point $\{x_i\}$ in a state space is a steady point. As the coordinates of the steady point are given it is easy to calculate the values of dx_i/dt in this point.

As there are usually very many parameters, then some of them could be left constant and combinations of other nonconstant parameters could be searched. (For example, in the model presented above, all the parameters will be left constant except for parameters k7, k8, kr, and ke. What are the values of the growth rate coefficient for roots, growth rate coefficient for tree height, root decrease intensity coefficient, and light extension coefficient, provided all the other coefficients which describe our model stay constant, at which this possible steady point is steady?)

Assuming only two coefficients a and b are changing, then, in order to

$$\mathbf{D}_{xi}^{a0} = \frac{\mathrm{d}x_i}{\mathrm{d}t} \quad a = a0,$$

we will give to a instead of value a0 the value a1 ($\Delta a = a1 - a0$) and calculate all the values of D_{xi}^{a1} . If we do the same with the coefficient **b** we will get D_{xi}^{b1} . Now we can write

 $\Delta D_{xi} \stackrel{x_i}{=} (D_{xi}^{a_1} - D_{xi}^{a_0}) \Delta a + (D_{xi}^{b_1} - D_{xi}^{b_0}) \Delta b; \quad i = 1, \dots, n,$ where $D_{xi}^{a_0} = D_{xi}^{b_0} = D_{xi}^{0}$ is the difference in the starting point. As $\Delta D_{xi} = D_{xi} - D_{xi}^{0}$ and in dividing D_{xi} by D_{xi}^{0} we will get

$$D_{xi}/D_{xi}^{0} - 1 = (D_{xi}^{a1}/D_{xi}^{a0} - 1) \Delta a + (D_{xi}^{b1}/D_{xi}^{b0} - 1) \Delta b;$$

$$i = 1, \dots, n.$$

Assuming that the overall result of the change of the difference should be zero, we will get the following system of equations 0

$$= (D_{xi}^{a1}/D_{xi}^{a0}-1)\Delta a + (D_{xi}^{b1}/D_{xi}^{b0}-1)\Delta b;$$

$$i=1,\ldots,n$$

By solving this system of equations we will get the linear approximation to the change of a and b.

It is obvious that in the case our model consists of two parameters and four state variables, there can be no solution. A non-zero solution can occur when there are more parameters than state variables, but then the number of solutions will be infinite. In reality the linear approximation is never accurate. Therefore it is reasonable to require that the decrease of the change of the difference should be 2 or 3 times. In this way we will get a solvable system:

$$V = \mathbf{D} \cdot \begin{bmatrix} \Delta a \\ \Delta b \end{bmatrix},$$

where V — given vector of decrease coefficients; D — matrix $[D_{xi}/D_{xi}^0 - 1]$, which has *n* rows and 2 columns.

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