Model adaptation mechanisms of cultivated plants in extreme conditions

E N Anikieva\textsuperscript{1} and A A Anikiev\textsuperscript{2}

\textsuperscript{1}Michurinsk State Agrarian University, 101, International st., Michurinsk, 393760, Russia
\textsuperscript{2}Bauman Moscow State Technical University, 2-ya Baumanskaya line, 5, Moscow, 105005, Russia

E-mail: korol_0909@mail.ru

Abstract. This study presents a new mathematical model of the physiology of the plant open system development in the conditions far from equilibrium. Unlike existing approaches, our model is based on the equations describing competition for the substrate between the three main compartments of cultivated plants - the root, stem and leaf system in extreme conditions. Exchange with the external environment occurs through two channels - through the leaves and the root system. The internal control channel is defined as a function of limiting the plant biomass through the biomass of the individual structural parts. The model viability was tested on the example of physiological model of tomato development. The system’s behavior was studied under two varieties of extreme conditions - a lack of nutrients in the soil and a low level or lack of solar radiation. In the first case, the model shows the restructuring of the system after several levels of vibrations to a stable state with a low consumption of substrate and a redistribution of the leaves, stem and root masses. In the second case, the calculations show a significant suppression of leaf cover biomass and mass redistribution in favor of the stem and root. However, even in this case, after a period of instability, the system comes to a stable state with the mass of the stem exceeding the mass of other structures. For each case, phase trajectories of the biomass and substrates behavior are constructed.

1. Introduction
In the process of the plant organism development, we see the passage of several generalized phases of vegetation: growth, flowering, fruiting. In the case of perennials or fruit trees, this cycle can be repeat many times throughout life. The transition from one phase to another is associated with various morphogens, whose activation happens due to the activation and inhibition of the corresponding enzymes \cite{1, 2}. A plant organism cannot increase the mass endlessly even in the case of an unlimited amount of nutrient substrate and ideal conditions. There are regulatory mechanisms that limit the flow of matter and energy in the system and thereby preserve fracture resistance of the system. The evolution of a physical system, the structure of which is determined by the forces of interaction between micro-particles, is entirely related to external control parameters, while the biological system owes its development to an internal control function, having an inverse relationship with the parameters of the external environment. Time is the governing parameter of morphogenesis \cite{3–5}.

The stability of a biological system will be understood as the process of preserving its functional properties and parameters in the presence of external subcritical disturbances. From this point of view,
the system will be called stable if, under the influence of an external disturbance not exceeding the critical one, the system, having exited the equilibrium state after a certain period of time, returns to the equilibrium state again [6]. The general equation of the evolution of the system can be written as:

\[
\frac{dx}{dt} = F_{in}(x, \Lambda) + F_{ext}(x, \Lambda) + F_{cf}(x(\Lambda)).
\] (1.1)

Here \(x\) is the column vector of system parameters, \(\Lambda\) is the set of external parameters acting on the system, \(F_{in}(x, \Lambda)\) is the function characterizing the internal flows and forces in the system, \(F_{ext}(x, \Lambda)\) is the function characterizing the external flows and forces, which the system exchanges with the external environment, \(F_{cf}(x(\Lambda))\) is the internal control function. The first two functions on the right side of equation (1) determine the evolution of any inanimate system. The last term in the right-hand side of equation (1), the control function, is only characteristic for biological systems and is determined by gene expression, a process that is individual for each biological object and both transmits hereditary information, and controls the system’s development.

In this paper, we consider a generalized model of the plant organism’s development with allowance for its own control function.

2. System model

In a biotic or abiotic stress situation, specific defense mechanisms are activated in plants, which transfer the plant to another level of physiological state or level of resistance [7-11]. If the external influence exceeds the level permissible for a given plant, mechanisms are activated at the physiological, morphological, biochemical and molecular levels. At the same time, there is an interaction between these levels that ensures the plant remains in a new stable state. After the end of the action of the stressor, the plant can return to its original state, restoring homeostasis and preserving the memory of the stress experienced in DNA packaging [11-14].

It is known [15, 16] that the intensity of growth processes is one of the functions of plants that most fully reflect the aggregate of metabolic changes under any type of stress. The growth rate (biomass build-up) to a large extent and quickly reacts to changes in environmental conditions, therefore, many diagnostic methods are based on this indicator when determining the degree of resistance of a plant organism. In addition, the facts of the competitive relationship between various structural organs of plants for physiologically active and nutrient substances during periods of stress are widely known. So, for example, in the inflorescences of cultivated cereals and in the crowns of fruit trees in abnormal climatic and weather conditions, more than half of the established ovaries can fall off. During the period of stress, the processes of aging and shedding of the lower leaves are accelerated, while there is a redistribution of nutrients in favor of younger leaves, in particular from the lower to the apical ones.

Thus, under extreme conditions, the model of development of a plant organism should be based to a greater extent on the competitive relationship between plant organs for a substrate. During the period of stress, new mechanisms of interaction of organs at the organismal level are added to the cellular adaptation mechanisms [17, 18].

We will consider a model of evolution of a structured plant system, tracking one of the parameters. In the case of a plant, we have three macro-compartments: leaves, stem and root. For fruit trees, a four-compartment model can be considered: leaves, branches (shoots), trunk and root system.

One of the possible extreme situations may be a decrease in the function of the root system, that is caused, for example, by a large amount of resistance during substrate transport (mechanical damage), or soil contamination, a lack of the most necessary substances, or water excess, in other words, impaired membrane permeability at the cellular level of the root system. In this case, the system has a certain time margin for adaptation to changed external conditions, even if the duration of the disturbance exceeds the time of the plant’s active life.

In contrast to existing biological models [1-3], we will consider the individual structural parts of the plant as competing with each other for the substrate. We will not divide the total biomass into structural and stocked parts, assuming that the changes in these parts are taken into account in the
coefficient of the problem, and the masses of the individual structural parts of the plant are normalized to the total biomass. In addition, we take into account the substrate transportation between the individual structural parts, and the restrictions on the maximum mass value — that is specified by the genotype, affects the evolution of the parts’ masses through the interaction between them. Then the system of equations for the mass of leaves, stem and root \( m_1, m_2, m_3 \) with the corresponding equations for the substrates \( s_1, s_2, s_3 \) will look like:

\[
\begin{align*}
\frac{dm_1(t)}{dt} &= \frac{\mu s_1(t)}{k+s_1(t)} \cdot m_1 - a \cdot m_1 \cdot (b_2 - m_2)^2 - \gamma \cdot m_1 \cdot m_2 \\
\frac{ds_1(t)}{dt} &= \left[ v_1 - \frac{\mu s_1(t)}{k+s_1(t)} \cdot m_1(t) - \frac{s_1-s_2}{r_1} \beta \right] \frac{1}{\tau} \\
\frac{dm_2(t)}{dt} &= \frac{\mu s_2(t)}{k+s_2(t)} \cdot m_2 - a \cdot m_2 \cdot (b_1 - m_1) \cdot (b_3 - m_3) - \gamma \cdot m_1 \cdot m_2 \cdot m_3 \\
\frac{ds_2(t)}{dt} &= \left[ s_1-s_2 \cdot \frac{\mu s_2(t)}{k+s_2(t)} \cdot m_2(t) - \frac{s_2-s_3}{r_2} \beta \right] \frac{1}{\tau} \\
\frac{dm_3(t)}{dt} &= \frac{\mu s_3(t)}{k+s_3(t)} \cdot m_3 - a \cdot m_3 \cdot (b_2 - m_2)^2 - \gamma \cdot m_3 \cdot m_2 \\
\frac{ds_3(t)}{dt} &= \left[ v_2 + \frac{s_1-s_3}{r_2} \beta - \frac{\mu s_3(t)}{k+s_3(t)} \cdot m_3(t) \right] \frac{1}{\tau}
\end{align*}
\]  

(2.1)

In these equations, \( \mu \) is the specific growth rate, which is assumed to be the same for all structural parts. It was taken into account that this quantity decreases as the substrate \( s_1 \) is exhausted. Coefficient \( k \) is the substrate - binding constant. The first term on the right side shows that the biomass growth rate is proportional to the biomass. The second term is the restriction on the decrease (increase) in biomass due to the restriction in the growth of the stem (trunk). The third term indicates the decrease in biomass due to the competition from the side of the stem (trunk). In the second equation for the rate of the substrate change in the leaves, the first term on the right side is the growth of the substrate due to the supply of photosynthesis products, the second term is the rate of utilization of the substrate by the leaves, the third term is the removal of the substrate into the stem due to the difference in their concentrations with the specific velocity \( \beta \) and the transport resistance \( r_1 \). We leave the relaxation time of the substrate evolution process (\( \tau \)) the same for all substrates of the problem in order to avoid a large number of parameters.

The growth rate of the trunk (stem) biomass is given by the third equation. It is proportional to the biomass itself, taking into account the decrease in the rate of substrate consumption as it is exhausted. The speed limit is due to the leaf and root reaching the biomass limit values \( b_1 \) and \( b_3 \) — the values are specified by the genome and the loss is associated with stem competition with leaves and root for the substrate at the decrease rate \( \gamma \). The fourth equation describes the change rate of the stem substrate. Sources of the stem substrate are the transport of the substrate from the leaves and the root, and the decrease is associated with the utilization of the substrate by the stem at a speed proportional to the stem mass. The fifth and sixth equations describe the rate of change of the root mass and substrate. Here \( v_2 \) is the source of the substrate after processing minerals obtained from the soil with a given efficiency.

3. Results and discussion

First, we consider a situation where for some unknown reason substrate transportation between the stem and the root is difficult. In this case, the interaction between these two structures affects the specific rates of biomass decrease and we actually have two connected systems of the deciduous mass and stem and the autonomous existence of the root. We solve system (1) with the initial conditions \( m_1(0) = 0.1, m_2(0) = 0.1, s_1(0) = 0, s_2(0) = 0 \). We take the dimensionless parameters of the problem in the form: \( \mu = 1, k = 1, a = -0.2, b_1 = 2.6, b_2 = 2.4, \tau = 0.8, v_1 = 1.4 \).
The stationary solution of the first four equations shows the existence of two stable states of the system. The system exhibits the greatest sensitivity with respect to the maximum possible values of the stem and leaves biomass. Figure 1a shows the temporal evolution of the leaf and stem biomass; (Fig. 1 b) substrates in the leaves and the stem.

![Figure 1](image1.png)

Figure 1. (a). Temporal dependence of the leaf and stem biomass. (b) Temporal dependence of the substrates in the leaf and stem. The solid curves are the leaf biomass and substrate; the dotted line is the stem biomass and substrate.

As can be seen from the figure the system after initial significant fluctuations adapts gradually to a stable state with a different biomass of leaves and stem. However, an insignificant change in the parameters $b_1$ and $b_2$ leads to a trigger regime — a transfer of the system to a new equilibrium position with inverse values of the leaf and stem masses. Such a situation is depicted in Figure 2 a, b.
Figure 2. (a) - Evolution of biomass with time and (b) - substrate with time. With a slight variation in the maximum permissible of the stem mass, the system passes through a significant interval of the unstable state and adapts to new conditions with the excess of the stem mass over the leaves mass. The dashed line is the mass and substrate of the stem, the solid line is the mass and substrate of the leaves.

Figure 3 shows the phase trajectories of the leaf and stem masses corresponding to the solution shown in Figure 1. As can be seen from the figures that there is a stable focus with the values $m_1 = 7.02$ and $m_2 = 0.2$ for these masses. At the same time, the values of the substrates are close and have the values $s_1 = 0.23$, $s_2 = 0.18$. 
Figure 3. Phase trajectories of the leaf and stem masses. A stable focus corresponds to the reduced masses $m_1 = 7.02$ and $m_2 = 0.2$. At the top figure (a) – the phase trajectory of the leaf masses, and in the bottom picture – the stem (b).

The phase trajectories of the substrates are shown in Figure 4.
Figure 4. Phase trajectories of the substrates evolution. The trajectory of the leaf substrate is shown at the top (a), and the stem substrate shown in the bottom figure (b). The trajectory of the curve is wrapping around a stable focus, the initial value of the curve is $s_1(0) = 0, s_2(0) = 0$.

We suppose that all three systems work without impaired substrate transport and we have two sources of substrate — photosynthesis and the entry of substances through the root system. However, there is a lack of solar radiation. Setting parameter $\nu_1 = 0.2$ is eight times less than necessary, and leaving the remaining parameters unchanged ($\nu_2 = 1.8, \gamma = 0.9$), we obtain the result shown in Figure 5 as a solution to the system of six equations (1).

Figure 5. Temporal evolution of leaf, stem and root biomass. There are three periods of plant adaptation to changing conditions.

As can be seen from the figure, leaf biomass is suppressed significantly, tending to a minimum value. At the same time, the stem - and root biomass increases to a maximum value of 2, moreover, for a stem with a delay in relation to the leaves and root masses. Then the root mass decreases sharply to a minimum along with the leaves mass. The mass of the stem decreases slowly and tends to a minimum value.

The greatest delay shows the change in the biomass of the stem. Adaptation of the root system has three periods correlated with changes in substrate concentration. Despite the fact that the source of the
root substrate differs from value zero, its activity is suppressed simultaneously with the activity of the leaves.

4. Conclusion
The conditions and parameters of the model, describing the modes of the cultivated plant adaptation to changing external conditions and also taking into account internal limitations, are considered. The system evolution was studied under the influence of two external factors: 1) a deficiency of nutrients or moisture in the soil and 2) a low level or lack of solar radiation. The substrate deficiency coming from the root system leads to a redistribution the deciduous cover, stem and root masses and a gradual transition of the system to a stable state with reduced substrate consumption after a certain period of instability. With a sharp decrease in the level of solar radiation, leaves biomass is suppressed significantly and biomass is distributed in favor of the stem and root. However, in this case, after a period of instability that is significant compared with the first extreme factor, the system stabilizes with the stem mass exceeding the mass of other structures. A high sensitivity of the model and periods of adaptation to the size of the constraints set by the genome on the maximum possible masses of the plants structural parts and the whole plant, providing long periods of sustainable development, was found.

References
[1] Shchukin R A, Bogdanov O E, Zavoloka I P, Ryazanov G S and Kruglov N M 2020 Biotechnological basis for application of growth regulators for rooting of green cuttings of trees and shrubs in a greenhouse with a misting system BIO Web of Conferences 23 01009
[2] Kuzin A, Solovchenko A, Stepanstsova L and Pugachev G 2020 Soil fertility management in apple orchard with microbial biofertilizers E3S Web of Conferences 222 3020
[3] Kartechina N V, Bobrovich L V, Nikonorova L I, Plchelineva N V and Abaluev R N 2020 Practical application of variance analysis of four-factor experience data as a technology of scientific research IOP Conference Series: Materials Science and Engineering 919(5) 052030. doi:10.1088/1757-899X/919/5/052030
[4] Tarova Z N, Churikova N L, Dubrovsky M L, Kruzikhov A V and Savelyeva N N 2020 Agrobiological evaluation of new apple clonal rootstocks of the Michurinski State Agrarian University selection using different breeding methods BIO Web of Conferences 23 01002
[5] Tarova Z N, Bobrovich L V, Krivolapov I P, Astapov A Yu, Korotkov A A and Grechushkina K S 2020 Analysis of taxation assessment results and development of a method for applying digital technologies in the assessment of garden agroecoses stability Journal of Physics: Conference Series 1679(2) 022101
[6] Papikhin R V and Dubrovsky M L 2018 Cytological features of male gametophyte formation from distant hybrids pyrus X Malus and ribes X Grossularia Journal of Pharmaceutical Sciences and Research 10(10) 2524-2527
[7] E Lamalakshmi Devi, Sudhir Kumar, T Basanta Singh, Susheel K Sharma, Aruna Beemrote, Chingakham Premabati Devi et al 2017 Adaptation Strategies and Defence Mechanisms of Plants During Environmental Stress, in: Mansour Ghorbanpour Ajit Varma (ed) Medicinal Plants and Environmental Challenges (Springer International Publishing AG) pp 359-413
[8] 2017 Metabolic Responses of Medicinal Plants to Global Warming, Temperature and Heat Stress, in: Mansour Ghorbanpour Ajit Varma (ed) Medicinal Plants and Environmental Challenges (Springer International Publishing AG) pp 69-80
[9] Potters G, Pasternak T P, Guisez Y, Palme K J and Jansen M A K 2007 Stress-induced morphogenic responses: growing out of trouble? Trends Plant Sci. 12 98-105
[10] Jaleel C A, Manivannan P, Wahid A, Farooq M, Somasundaram R and Panneerselvam R 2009 Drought stress in plants: a review on morphological characteristics and pigments composition Int. J. Agr. Biol. 11 100-105
[11] Parvaiz Ahmad, Mohd Rafiq Wani (eds) 2014 *Physiological Mechanisms and Adaptation Strategies in Plants under Changing Environment* (New York: Springer)

[12] Bartoli G, Forino L M C, Tagliasacchi A M, Bernardi R and Durante M 2010 Ozone damage and tolerance in leaves of two poplar genotypes *Caryologia* **63** 422-435

[13] Bulgakov V P, Hui-Chen Wu and Tsung-Luo Jinn 2019 Coordination of ABA and Chaperone Signaling in Plant Stress Responses *Trends Plant Sci.* **25**. DOI: 10.1016/j.tplants.2019.04.004

[14] Avramova Z 2015 Transcriptional ‘memory’ of a stress: transient chromatin and memory (epigenetic) marks at stress response genes *Plant J.* **83** 149–159

[15] Udovenko G V 1979 *Physiology and biochemistry of cultivated plants* **11(2)** 99-107

[16] Goncharova E A 2011 *Sel'skokhozyaistvennaya biologiya* **1** 24-31

[17] Lykova N A 2009 *Prevegetation effect. Environmental aftereffects* (St Petersburg: Nauka) 311 p

[18] Kosulina L G, Lutchenko E K and Aksenova V A 1993 *Physiology of plant resistance to adverse environmental factors* (Rostov University Publishing) 121 p