



Change in the general aboveground phytomass as a basis for modeling dynamics of recovery of vegetative cover

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Our study was focused on changes in the general aboveground phytomass during restoration of the vegetative cover. The objective was to analyze changes in the aboveground phytomass as an indicator of autogenic ecosystem dynamics. Therefore, we set the following goals: to detect changes that occurred in the amount of aboveground phytomass while the natural vegetation recovered; develop a mathematical model that would describe the process of dynamics of aboveground phytomass during progressive autogenic successions; develop a parameter of natural ecosystem dynamics based on changes in the aboveground phytomass during recovery of natural vegetation. To achieve our goals, we conducted a series of eight stationary experiments that lasted from 2005 to 2014 in the territory of central Polissia. Also, we carried out geobotanical studies, measuring phytomass outside the stationary plots. As vegetation in the disturbed areas recovered, the amount of aboveground phytomass naturally increased. Function of the natural logarithm is a mathematical model of change in the aboveground phytomass. In this model, regression coefficient “a” represents the initial conditions of when recovery started. For secondary ecological successions, regression coefficient “a” was higher than for the initial one. Regression coefficient “b” indicated the rates of production of aboveground phytomass. With time, a predicted trend of change in the aboveground phytomass becomes more likely to deviate. Increase in the aboveground phytomass in most cases accompanies autogenic succession, and its decline, except in rare cases, accompanies/homogenic succession. Accumulation of maximum possible phytomass and its storage for a maximum time interval corresponds to the state of energy (climatic) climax, while stopping its production at lower values – to catastrophic climax. The mathematical model of change in the general aboveground phytomass is the basis for further development of an integral theory of ecosystem dynamics. Prediction algorithms that have been developed based on the proposed mathematical model can be useful during environmental audit or decision making in nature protection when assessing whether an area requires a strict protection regime.

Keywords: autogenic succession; prediction algorithms; energy climax; catastrophic climax.

Introduction

The Earth’s biosphere is a dynamic system that undergoes changes triggered by anthropogenic and natural (cosmic and terrestrial) influences. The ability to predict changes in the biosphere is the basis of humankind’s survival (Ord, 2020). Such predictions are possible only in the case of high ability to determine accurate parameters of changes within particular ecosystems. Such predictions could only be made if changes in particular ecosystems are measured with high accuracy. First of all, those are trend and rates of their dynamics (O’Sullivan et al., 2021). According to Eugene Odum, there are three main types of ecosystem dynamics: evolution, succession, and fluctuations (Odum & Barrett, 1971). Studies of evolutionary changes in ecosystems most often are of purely theoretical interest. Only in recent years, has it started to become practically significant due to the global climate changes and recently studied cosmic threats of planetary scale (Anyomi et al., 2022). At the same time, we try to predict outcomes of formation of new ecosystems and how they will affect the stability of the biosphere and wellbeing of the humanity (Berglund & Kuuluvainen, 2021). New ecosystems result from long evolution of certain species that are important for their functioning, and also as a result of a new combination of species, especially invasive transformer species that travel outside their ranges (Zavialova et al., 2021). Such processes pose serious threat to

biodiversity, because newly formed ecosystems often spread fast, leaving no place for many native species’ niches (Khomiak et al., 2024). Identification of the seriousness of threats to native species or the invasive status of an alien species requires long-term studies, because ecosystems may undergo short-term changes, and quickly recover to the previous state afterwards. This type of dynamics is called fluctuating. The consensus among ecosystem scientists and geobotanists is that the minimum time necessary for biota surveillance is 12 years (Rampino et al., 2021). This is associated with effect of solar-activity cycle on the natural ecosystems.

Since evolution is a very long and hard-to-predict process, and fluctuations end on their own by an ecosystem recovering to the previous state, successions are of the greatest interest for applicable modeling of dynamics. Their course indicates balance between the process of self-organizing and ruining external impacts. For example, we may observe it when vegetative cover is ruining or is naturally recovering.

The process of succession best describes the human impact on the environment and ecological recovery over the medium term. Such an approach is a necessary statutorily mandated procedure for assessing effects on the environment, a planned, legally established activity. Characteristics of the ecosystem dynamics are the basis for such modeling and prediction of state of the environment under anthropogenic pressure. Modeling can predict implications of exploiting natural resources, effects of particular

kinds of human activity on the local ecosystems and extent of their anthropogenic transformation, and help decision making in nature protection.

Modeling successions in ecosystems has been a subject of intense discussions since first reports by F. Clements (Xu & Trugman, 2021). The greatest interest is related to recording particular stages of dynamics (van Breugel et al., 2022). Changes that accompany successive processes can be a set of indicators of ecosystem dynamics, of which the most effective, informative, and objective should be chosen. This way, we can make a step forward to developing a theory of the ecosystem dynamics and apply this theory to practice (Hanusch et al., 2022). Many such indicators can be distinguished. Attempts to include them in an integral model are not only a technologically complex task, but also a low-effective approach. Any algorithm, even if using modern powerful super computers, will be overwhelmed by mountains of secondary information.

As of now, researchers propose several approaches to choosing the most important parameters characterizing the ecosystems and their dynamics. In the history of ecology, there has long been a struggle between two approaches to describing ecosystems—polycentric and monocentric. In the first case, all blocks of ecosystem and all changes are considered equally significant (Rasigraf & Wagner, 2022). This approach was dominant in the ecological schools related closely to geography and zoology. In the second case, the center of any model is anthropogenic block. This approach has been prevalent in classic ecological schools and schools associated with geobotany. Followers of the second approach presented arguments that certain narrow-specialized geotrophs are able to trigger drastic changes in the ecosystems only in individual cases, while the essential role in most is played by autotrophs. First of all, the latter have stronger relationship with the environment and a certain area where ecosystem is located. Secondly, their primary production determines quantitative and qualitative characteristics of other elements of the ecosystem's trophic network (Yi et al., 2022). Thirdly, their presence is the best indicator of type and state of the ecosystem.

The idea to monitor vegetation for effective indicators of successive processes became popular in the 1990s. Scientists propose various approaches, first of all, floristic. For instance, Didukh & Pliuta (1994) propose using variations of ratios of families of higher vascular plants. For example, they recommend using the ratios of representatives of the families Asteraceae and Brassicaceae to Rosacea or Fabaceae and Coryophylaceae to Cyperaceae. Also, they discussed the possibility of using the ratio between species and different plant life forms, strategies or carriers of certain anatomic specifics. In practice, this method is applicable only to large units of classifications of ecosystems and cannot be employed to characterize a particular local area of the Earth's surface. Representatives of the family are able to adapt to assemblies at different stages of ecological succession, including those where most other representatives of this family do not live (Backhaus et al., 2022). Thus, a local ecosystem that has a low number of species will either contain a non-typical representative of a family proposed by the authors or include no species of those families at all.

An original approach to identifying dynamics is analysis of parameters of detritus in natural ecosystems (Khodyn & Chornobrov, 2021). However, this parameter represents absence of a specialized anthropogenic impact that would remove it rather than the course of autogenic succession itself, because in many known cases detritus accumulated in the conditions of a catastrophic climax. For example, in subtropical and tropical grasslands – due to moisture deficit, seasonality of its deposition and activity of ruminants – deposition of dead remains in soil occurs regularly. At the same time, amount of formed humus reflects both the stage of succession and duration of catastrophic climax. In oligotrophic wetlands, a similar situation occurs with accumulation of peat. Its amount can serve an indicator of succession only at its early stages. Later, a more important aspect will be the presence of loose sedimentary rocks. The peat thickness only indicates how long it has been accumulating. At the same time, in the climax old-growth forests, accumulation of detritus will be the highest and stable. Therefore, by contrast to other ecosystems, presence of a certain amount of it in pre-climax and climax forest ecosystems can be an indicator of its dynamics.

Already in the 1940s, researchers started to shift their focus from individual signs of dynamics to changes in the general state of ecosystem. Raymond Linderman (1942) noted ecosystems accumulating energy re-

serves as biomass during autogenic successions or when approaching the state of climax. The idea of change in the energy balance in ecosystems during progressive autogenic successions was developed further by Howard and Eugene Odum. To model energy currents, Howard Odum suggested using analogies with electronic network. He compared electric current to the flow of nutrients and energy in ecosystems, and also compared condensers to its reserves (Odum & Barrett, 1971).

Interest in the relationship between change in ecosystems' energy exchange and its dynamics rose in the twenty first century with the establishment of better and more available methods of computer modeling (Skene, 2024). Scientists have been making numerous attempts to explain the energy of ecosystem dynamics using general thermodynamic theories (Nielsen et al., 2020). Oftentimes, attempts were limited to theoretical reviews because of the complexity of accurately assessing energy balance in ecosystems and finding ecological analogues for fundamental thermodynamics concepts (Didukh & Lysenko 2010). Models for such studies are often anthropogenically disturbed territories – quarries, fallows, post-military objects, and abandoned settlements and their outskirts (Didukh, et al., 2023).

The objective of our studies was to analyze changes in the general aboveground phytomass as an indicator of autogenic dynamics of ecosystems. Therefore, our goals were as follows:

- identify change in the amount of general aboveground phytomass during recovery of natural vegetation;
- develop a mathematical model that would describe the process of dynamics of the general aboveground phytomass during progressive autogenic successions;
- develop a parameter of natural ecosystem dynamics based on changes in the general aboveground phytomass that occurred in the natural vegetation during natural recovery.

Materials and methods

Materials of the study were standard geobotanical relevés, conducted in the territory of the central Polissia in the period from 2004 to 2023, and measurements of the aboveground phytomass taken between 2005 and 2015. In the period from 2005 to 2014, stationary studies were conducted in areas where – other than standard geobotanical relevés – the number and age of aboveground phytomass were identified. Eight examined stationary plots were located in the central Polissia.

The stationary plots were established in the form of 8 x 20 m rectangles, stretching in a latitudinal direction. Parameters of edaphic and orographic factors of all stationaries were similar. Deviations of the environmental factors such as content of available nitrogen and general saline regime were no higher than 8% and 2%, respectively. The rest of the parameters ranged less than 4%. At the beginning of the stationary studies (2005), those areas were fallows for the first year after soil treatment. Each stationary plot was divided into ten 16 m² areas. Each year, the aboveground phytomass from one of the abovementioned areas was removed and weighed. Phytomass was removed manually and mechanically (Partner B347B trimmer, Poland) at the end of mass vegetation (from July 15 to August 1). The first to undergo removal was the southwest part of the stationary plot. Further removal of phytomass was carried out from west eastward, starting from its southern part. Phytomass reserves were weighed on Adler AD 8151b mechanical scales (Poland) with 1 kg measurement accuracy.

Outside the stationary research areas, aboveground phytomass was measured using a combination of methods of forest taxation with the earlier indicated method of measuring phytomass of herbaceous and shrub vegetation. The research areas outside the stationary plots were 4 m² plots for herbaceous vegetation, 100 m² for shrubs, and 200 m² for forests. Vegetation located band-like was studied on rectangular plots of 2 m length for herbaceous vegetation, 5–10 m for shrubs, and 10–20 m for forest vegetation. Phytomass was sampled from center of geobotanical releve in 4 x 4 m areas (Levchenko et al., 2021). The age of perennials was identified using the methods of dendrochronology (Frank et al., 2022).

Classification of vegetal groups was performed using the principles of ecologic-flouristic school of Braun-Blanquet. The distinguished phytoce-

noses were identified using Prodrum of Vegetation of Ukraine (Dubyna et al., 2019). To process and save the phytocenotic data, we used the Turboveg software for Windows (Czech Republic, 2001) (Hennekens, 2009). Parameters of environmental factors were determined using the methods of synphytoindication (Didukh & Pliuta, 1994). For this purpose, we used two phytoindication scales: the Didukh-Pliuta scale for the main abiotic factors (Didukh & Pliuta, 1994) and the Didukh-Khomiak scale for anthropogenic factor (Khomiak et al., 2020). The data base for phytoindication characteristics of plant species were the EcoDBase5e base of the Laboratory of Theory of Ecosystems at the Ivan Franko Zhytomyr State University. The analysis was carried out using the Simargl 1.12 program.

Determination coefficient as a parameter of dependence of variation of dependent variable on an independent was calculated using the formula:

$$R^2 = 1 - \frac{\sigma^2}{\sigma_y^2}$$

where σ^2 – conditional dispersion of dependent value (dispersion of model error), σ_y^2 – dispersion of random value.

Table 1

Value of aboveground phytomass at experimental plots (t/ha)

Names of stationary study plots	Time periods (years)									
	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Budivelyk 1	8.3±0.01	10.0±0.01	13.8±0.01	15.6±0.02	18.9±0.02	20.2±0.02	20.6±0.02	21.2±0.02	21.4±0.02	21.5±0.02
Budivelyk 2	5.7±0.01	9.1±0.01	15.2±0.02	18.1±0.02	25.9±0.03	33.7±0.03	37.5±0.04	44.3±0.04	46.7±0.05	48.0±0.05
Soniachne 1	9.2±0.01	11.2±0.01	18.1±0.02	18.8±0.02	20.3±0.02	20.4±0.02	24.8±0.03	28.0±0.03	28.4±0.03	31.7±0.04
Soniachne 2	8.7±0.01	11.2±0.01	20.2±0.02	21.5±0.02	40.5±0.04	42.7±0.04	45.4±0.05	46.6±0.05	53.4±0.05	55.3±0.06
Novopil 1	6.2±0.01	15.5±0.02	19.9±0.02	20.6±0.02	26.8±0.03	28.0±0.03	29.2±0.03	36.0±0.04	36.2±0.04	36.5±0.04
Novopil 2	8.2±0.01	14.8±0.02	18.0±0.02	19.8±0.02	19.9±0.02	21.5±0.02	21.5±0.02	21.5±0.02	21.8±0.02	21.5±0.02
Kamianohirska	12.9±0.01	16.5±0.02	23.1±0.02	23.8±0.02	33.3±0.03	41.0±0.03	45.1±0.05	48.0±0.05	48.0±0.05	48.3±0.05
Pishchanka	5.5±0.01	15.6±0.02	16.8±0.02	19.3±0.02	21.4±0.02	38.8±0.03	42.6±0.04	45.4±0.05	47.3±0.05	50.9±0.05

In the Ukrainian Polissia, climatic parameters were observed to undergo several changes in the longitudinal and latitudinal directions. According to the literature data, in the northern and western directions, precipitation amounts increase and continentality and frigidty decrease due to the proximity of the ocean and its warm North-Atlantic current. Distance between the stationary plots equaled 114 km from north to south, and 30 km from west to east. The northern- and westernmost area Kamianohirska had relatively high rates of aboveground-phytomass production and its amount at the end of experiment. Already in the first year of recovery of natural vegetation, its aboveground phytomass reached the greatest result of 12.9 t/ha. Over ten years, it grew to 48.3 t/ha. At the same time, some areas farther south and east exhibited higher values (55.3 t/ha at the Soniachne 2 plot and 50.8 t/ha at the Pishchanka plot), although in the first year of the experiment their aboveground phytomass was lower (8.7 and

Dynamics of the ecosystems was modeled in Python (USA, 1991) using the Visual Studio 2022 software (USA, 2022).

Results

During the stationary field studies, we observed increase in the general aboveground phytomass at all the plots (Table 1). Rates of phytomass production and its end amount across the plots varied. In the first year of studies, the aboveground phytomass accounted for the average of 8.1 t/ha. Among plots, it ranged 5.5 to 12.9 t/ha. Thus, there were areas where the initial production of aboveground phytomass was 4.8 t/ha above the average or, by contrast, 2.6 t/ha behind. With time, not only the mean value of aboveground phytomass increased, but also difference between the lowest and highest parameters. Being 7.4 t/ha in the first year, it reached 33.8 t/ha at the end of the study. Because edaphic and orographic conditions of the environment were almost identical, the hypothetical causes of such a deviation could have been climatic factors, external influences of partial stochastic nature, and unpredictability of the dynamics process.

5.5 t/ha, respectively). Such parameters disprove the likelihood of a notable effect of climatic differences in the territories of certain stationary plots on the production of aboveground of phytomass within the studied area. The main difference of the Kamianohirska plot is that it is surrounded by thorough forests on three sides. Therefore, it had a great amount of seeds of phanerophytes in the soil and their powerful seed diaspora from neighboring areas. Those seeds germinated en masse in the first years after active soil treatment had stopped. To a certain degree, such a situation reminds one of vegetation recovery after cutting forests. Production of phanerophytes in forests and areas neighboring with forest gave two-three times the amount of aboveground phytomass in classic fallows. Therefore, the starting conditions of recovery of natural vegetation after disturbance notably affected the presence or bringing of seeds of certain plant life forms from outside.

Table 2

Parameters of anthropogenic impact on study plots (in points according to the Didukh-Khomiak scale)

Names of stationary study plots	Time periods (years)									
	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Budivelyk 1	11.1±0.33	11.0±0.33	10.9±0.33	10.5±0.32	10.3±0.31	9.7±0.29	9.7±0.29	9.5±0.29	9.4±0.28	9.5±0.29
Budivelyk 2	11.0±0.33	7.6±0.23	10.9±0.33	10.4±0.31	9.4±0.28	9.2±0.28	8.9±0.27	8.7±0.26	8.4±0.25	8.3±0.25
Soniachne 1	11.2±0.34	11.1±0.33	10.1±0.30	10.1±0.30	10.0±0.30	9.1±0.27	8.9±0.27	9.0±0.27	9.1±0.27	9.1±0.27
Soniachne 2	11.0±0.33	10.7±0.32	10.1±0.30	10.0±0.30	9.4±0.28	8.5±0.26	8.4±0.25	8.2±0.25	8.1±0.24	7.9±0.24
Novopil 1	11.5±0.35	10.4±0.31	9.9±0.30	10.0±0.30	9.8±0.29	9.1±0.27	9.0±0.27	8.6±0.26	8.6±0.26	8.5±0.26
Novopil 2	11.1±0.33	10.0±0.30	10.1±0.30	10.0±0.30	9.5±0.29	9.8±0.29	9.9±0.30	9.7±0.29	7.5±0.23	9.6±0.29
Kamianohirska	11.0±0.33	10.1±0.30	10.3±0.31	10.3±0.31	9.3±0.28	9.0±0.27	9.3±0.28	8.6±0.26	7.8±0.23	8.9±0.27
Pishchanka	11.5±0.35	10.0±0.30	7.2±0.22	9.9±0.30	9.1±0.27	9.3±0.28	8.8±0.26	8.3±0.25	8.1±0.24	7.6±0.23

Differences in production of aboveground phytomass among other plots could be attributed to other external influences, first of all, multifaceted anthropogenic impact. So as to identify whether or not those areas had been subject to an anthropogenic loading, we conducted synphytoindication (Table 2). In the first year of the experiment, the parameters of anthropogenic transformation were approximately even, but in the following years they changed asynchronous at various plots.

The lowest parameters of anthropogenic transformation were seen at the end of the experiment at the plots Pishchanka, Soniachne 2, and Budivelyk 2, measuring respectively 7.6, 7.9, and 8.3 points according to the

Didukh-Khomiak's scale. This corresponds to locations with plants tolerant to high anthropogenic impact, according to classification of anthropogenic-impact tolerance of Blume and Sukopp. Aboveground phytomass in those areas was high as well, amounting to 50.9, 55.3, and 48.3 t/ha. Those values are in the best four results of the all eight areas. An exception was the abovementioned plot Kamianohirska, which concentrated 48.3 t/ha of phytomass against the background of anthropogenic impact equaling 8.9 points (the boundary between plants that are tolerant to average and high anthropogenic impact). At the same time, at the plots Novopil 2, Budivelyk 1, and Soniachne 1, the phytomass parameters were the lo-

west (21.5 t/ha at Novopil 2 and Budivelnik 1 and 31.7 t/ha at Soniachne 1). Their level of anthropogenic transformation reached 9.6, 9.3, and 9.1 points, respectively, according to the Didukh-Khomiak scale. This corresponded to habitat tolerant to average anthropogenic impact, at the boundary with locations that are able to withstand high anthropogenic impact. Such a level indicates a notable presence of human impact. In those areas, we observed signs of regular recreational activities and grazing of animals. Not only had domestic animals (*Capra hircus* L.) eaten herbaceous plants, but they had also damaged young phanerophytes and their undergrowth. Another factor in those areas, coming both from domestic animals and humans, was tramping. This downgraded the meadow vegetation from more productive groups into less productive with numerous small ruderal elements. They included *Plantago major* L., *Poa annua* L., *Prunella vulgaris* L., *Taraxacum officinalis* Webb. ex Wigg., and *Trifolium repens* L. This suggests that anthropogenic loading in our experiment was the main factor hindering the accumulation of aboveground phytomass. The level of anthropogenic transformation and

amount of aboveground phytomass were observed to have an inverse linear correlation, with the correlation parameter of 0.77.

External factors can influence growth of aboveground phytomass, making an accurate prediction of its amount after a certain moment of time impossible without their consideration. Those factors are, first of all, human activity, presence of a seed bank in the soil, or its introduction in the form of seed diaspora from neighboring territories. If those factors are absent, then ecosystems will develop naturally in the same starting conditions at similar rates, and also follow a similar scenario. However, due to external effects, the likelihood and degree of deviations from a predicted parameter are high (Fig. 1). Thus, in approximately the same edaphic conditions of one geobotanical zone, recovery of vegetation in fallows in the first year of the research had only 7.3 t/ha difference in the production of phytomass across the plots. In ten years, this difference grew to 33.8 t/ha. Therefore, an accurate multi-year prediction requires factoring in the probability of external factors shaping the production of aboveground phytomass, for example, anthropogenic effect.

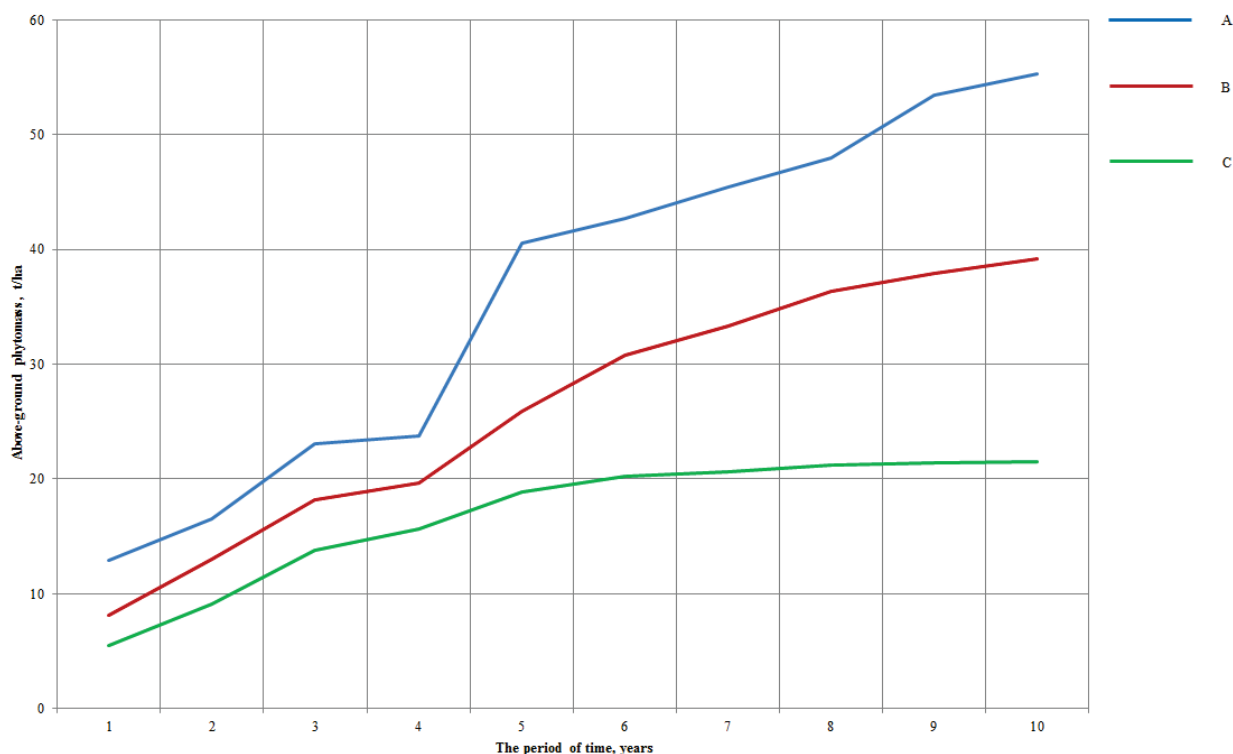


Fig. 1. Dynamics of aboveground phytomass. Legend:

A – maximum values of phytomass, B – average values of phytomass, C – minimum values of phytomass

By approximating statistical data, we can obtain a mathematical model that corresponds to the logarithmic correlation of increase in aboveground mass with time:

$$m_p = a + b \ln t$$

where m_p – amount of aboveground phytomass, t – time, “ a ” and “ b ” – regression coefficients.

For the overall result of our experiment, this formula looks as follows

$$m_p = 4.1 + 14.6 \ln t$$

At the same time, the model dynamics of the aboveground phytomass at each stationary plot, and also changes in the mean, minimum, and maximum parameters vary (Table 3). This difference will be relevant mostly for the value of regression coefficients “ a ” and “ b ”. Only at two plots, will the sign for the first of them be altered. Regression coefficients “ a ” at different plots will differ 12.9, and the “ b ” coefficients will differ 15.0. Regression coefficient “ a ” can point to the initial favorability of the environmental conditions for the beginning of autogenic succession with aboveground-phytomass production or the so called progressive autogenic succession. Those conditions include presence of a complete seed bank or seed diaspora from beyond the plot and susceptibility of an edaphotope’s endoecogenesis-susceptibility. In other words, the value of regression parameter “ a ” will decrease as the area approaches the initial succession, and increase when it nears the secondary succession. In our models, its lowest

values were observed at the plots Budivelnik 2 and Pishchanka. This also manifested in the lowest amounts of aboveground phytomass in the first year of recovery of natural vegetation – 5.7 and 5.5 t/ha. At the same time, the mean parameter at all the stationary plots in the first year of the experiment was 8.1 t/ha. Therefore, the conditions in those areas were closer to the first succession than in the others. High parameters of the regression coefficient “ a ” at the plot Novopil 2 were due to the fact that despite high anthropogenic loading, the starting conditions were quite favorable, which allowed the phytomass to grow above the average value – to 8.2 t/ha.

Regression coefficient “ b ” reflects the rates at which aboveground phytomass grew. Its highest values were observed for the models of dynamics at the plots Soniachne 2 (22.6), Pishchanka (20.6), and Budivelnik 2 (20.5). At the end of the experiment, those plots concentrated the highest amount of aboveground phytomass – 55.3, 50.9, and 48 t/ha, respectively. An exception was the Kamianohirska plot, where the end values of aboveground phytomass were high (48.3 t/ha), but the regression coefficient “ b ” was somewhat lower – 18.1. This was due to high aboveground phytomass at the start of the study (12.9 t/ha), and therefore lower rate of its production. Also, naturally, regression coefficient “ b ” was quite high for all the plots in total – 20.3. In all the studies, including outside the stationary plots, regression coefficient “ b ” for the progressive autogenic succession attained positive values.

Table 3

Linear and logarithmic models of dynamics of aboveground phytomass and their determination coefficients

Names of stationary study plots and statistical parameters	Linear mathematical model	Determination coefficient of linear function (r^2)	Logarithmic mathematical model	Determination coefficient of logarithmic function (r^2)
Budivelnyk 1	$m_p = 1.5t + 8.8$	0.87	$m_p = 7.2 + 6.6 \ln t$	0.96
Budivelnyk 2	$m_p = 5.2t - 0.1$	0.98	$m_p = -2.6 + 20.5 \ln t$	0.90
Soniachne 1	$m_p = 2.4t + 8.1$	0.96	$m_p = 6.6 + 9.6 \ln t$	0.92
Soniachne 2	$m_p = 5.6t + 3.9$	0.94	$m_p = 0.4 + 22.6 \ln t$	0.90
Novopil 1	$m_p = 3.2t + 7.9$	0.93	$m_p = 5.3 + 13.4 \ln t$	0.97
Novopil 2	$m_p = 1.2t + 12.4$	0.67	$m_p = 10.3 + 5.6 \ln t$	0.91
Kamianohirska	$m_p = 4.5t + 9.5$	0.94	$m_p = 6.6 + 18.1 \ln t$	0.91
Pishchanka	$m_p = 5.2t + 1.6$	0.94	$m_p = -0.9 + 20.6 \ln t$	0.87
Average	$m_p = 3.9t + 6.2$	0.97	$m_p = 3.7 + 15.8 \ln t$	0.95
Maximum	$m_p = 5.0 + 8.4$	0.95	$m_p = 5.5 + 20.3 \ln t$	0.90
Minimum	$m_p = 1.7t + 8.3$	0.76	$m_p = 5.9 + 7.7 \ln t$	0.94

For outside the stationary plots, such models were harder to develop due to variety of edaphic and orographic environmental conditions influencing the production of phytomass in different ways. Another problem is obtaining information about the history of old anthropogenic effects that can lead to catastrophic decrease of phytomass. For example, when studying a forest, we want to develop a model using time parameter from the moment of forest planting or start of its recovery after cutting or fire. We cannot be sure that over decades or even hundreds of years, the ecosystem has been developing at minimum anthropogenic loading or without natural disasters. Furthermore, developing an accurate model is hindered by absence of a sufficient number of areas that have been preserved well for a long period of time, where autogenic succession would have been occurring subject to minimum external effects for hundreds and more years. This could produce a relatively accurate model based on the statistical processing of a large amount of data. Therefore, the only significant models that we can use today are those obtained in studies similar to ours.

The highest parameters of aboveground phytomass in our study outside the stationary plots were recorded in the State Forest Reserve Poiaskivskiy Lis, known as the Korabel Tract. The reserve is located in the Poiaskivske Forestland of Bilokorovytskyi State Forest Holding. Since 1929, any activity but research (surveillance without direct intervention) is prohibited in its territory. Exceptions were the times of WW2, when a small partisan unit was based in the reserve, and 2009, when attempts at illegal cutting of several trees were made. At the moment of study, in 2012–2013, the aboveground phytomass of the oldest area of the Poiaskivskiy Lis (17th quarter of the Poiaskivske Forest) accounted for 377.9 t/ha. The basis of the tree stand comprised *Quercus robur* L., aged 250 to 400–450 years. Its mass was 83% of the total (313 t/ha). Such a forest, aged couple of centuries, can later be an etalon site for developing an integral model of ecosystem dynamics in Polissia.

Discussion

Modern studies confirm the similarity of models of changes in amount of aboveground phytomass during recovery of disturbed vegetative cover. They point to the presence of a mathematical model that is a function of a natural logarithm. However, they vary in regression parameters. For example, Khaurdinova (2014) provided such model for a pine forest in the Chomobyl area. The objects of her studies were hundred-years-old forests. Regression coefficients in her equation equaled 3.8 (a) and 93.1 (b). Similarity of the first coefficient to the average of the same parameter at other stationary plots (4.1) indicated similarity in the starting conditions. The five plots she sampled and the control plot were in fallow lands with sod-podzolized soils in the area of the Kopachi village (the Chomobyl Exclusion Zone). The plots were 10-, 24-, 58-, and 100-years-old planted pine forests and fallow lands. Based on the study, the author drew conclusions about the production of aboveground phytomass over a hundred years. Our data of stationary and expedition studies are somewhat different due to the fact that the stationary plots have existed for only 10 years, while biota outside them have been developing in individual cases as primary succession, reaching the age of 250 and more years. The etalon plot of the State Forest Reserve Poiarskyi Lis, starting from

2014, had been impacted by illegal amber mining nearby (Kovalevskii et al., 2021). Unfortunately, it is now impossible to identify whether such parameters of aboveground phytomass are the highest possible for the central Polissia. In order to obtain an etalon ancient forest, one should use extraordinary measures to protect the lowland areas of the reserves Tryhirskiy, Denyshivskiy, Bilokorovytskyi, and Olevskiy. Since tree stands in those locations are on average 100–130 years-old, such a regime should last at least 400–500 years.

Normal production of aboveground phytomass in land ecosystems during natural recovery of vegetation has several explanations. First of all, competition among species leads to formation of multi-strata vegetation. Species in higher strata naturally have higher parameters of aboveground phytomass (Yi et al., 2022). However, emergence of first scattered phanerophytes does not necessarily have a needed effect (Anyomi et al., 2022). In our case, indicative are situations at the plots Novopil 2 and Kamianohirska. The first phanerophytes emerged four years after the start of the experiment. Those were single individuals of *Pyrus communis* L. at Novopil 2. That year, the level of aboveground phytomass reached only 19.8 t/ha. At the same time, the Kamianohirska plot was still covered with high herbs with *Calamagrostis epigeios* (L.) Roth dominating (up to 70%). However, at the last plot, the aboveground phytomass accounted for 23.8 t/ha. The first phanerophytes emerged already in the next year. Those were undergrowth of *Pinus sylvestris*. Only on the tenth year, did there form a complete young regrowth forest with participation of *Betula pendula* Roth., *Pinus sylvestris* L., *Pyrus communis*, and *Salix caprea* L. The herbaceous cover in that forest was comprised of *Calamagrostis epigeios* (up to 60%) and *Rubus caesius* L. (25%), the meadow species *Poa pratensis* L. (20%), *Fragaria vesca* L. (up to 5%), *Achillea submillefolium* Klok. et Krzyzka (1%), and *Veronica officinalis* L. (1%). At the same time, the aboveground phytomass reached 48.3 t/ha. At the sixth plot, there were no new phanerophytes. At the end of the experiment, there were only few wild pear *Pyrus communis*, and the mass only reached 21.5 t/ha. Therefore, competition between plants for solar energy, expressed in formation of multi-strata vegetation, leads to increase in a group's aboveground phytomass. A similar situation was observed in the Chomobyl Zone by a number of researchers of the M. H. Holodnyi Institute of Botany of NAS of Ukraine (Didukh et al., 2023). In the case we studied, *Calamagrostis epigeios* outcompeted other species of herbaceous cover and – thanks to better adaptability to the environmental conditions and allelopathic abilities – continued to dominate even thirty years after the recovery of natural vegetation had started. This was especially pronounced at the plots that had been subjected to pyrogenic factor. Groups formed by *Calamagrostis epigeios* (association *Calamagrostis epigeios* Juraszek 1928 of class *Epilobietea angustifolii* Tx. et Preising ex von Rochow 1951) are often found at forest-fire-affected sites. Even after becoming a regrowth forest of association *Salicetum capreae* Schreier 1955 (class *Robinietaea Jurco* ex Hadac et Sofron 1980), such an ecosystem contains a large amount of *Calamagrostis epigeios*. Thus, deviations from the predicted results could be attributed to external influences or specifics of the primary producers. Ecosystems in such cases can develop following both divergent and convergent patterns (Backhaus et al., 2022). Taking into account phytomass in predictions of ecological succession produces more

accurate results. If the external factors are insignificant and growth of phytomass is normal, the next link can be different from the predicted according to the traditional knowledge of the dynamics of ecosystems or compared to observations in other circumstances. In some cases of an invasion of a species with powerful competitive abilities, especially invasive alien species, the rates of phytomass accumulation can decline.

Another explanation of natural increase in aboveground phytomass is some aspects of support of energy balance of the ecosystem. On the other hand, this can be provision of energy of primary producers for increasing the number of branches of the trophic network. There occurs a gradual increase in complexity of contents of niches, thereby enhancing the conditional stability of the system. This, in turn, causes increase in the number of species and general number of individuals that need larger amounts of energy. Primary producers can harness and store energy reserves, which they can use during their lifetime and also retain for use after their death (Khodyn & Chomobrov, 2021). That is why some researchers believe that accumulation of detritus is one of the features of autogenic succession. On the other hand, the amount of energy of primary producers accumulated in the ecosystem can be a sign of stability from the standpoint of thermal dynamics. Such an approach was considered by Didukh & Lysenko (2010). They tried using the classic notions borrowed from thermodynamics for this purpose. Actually, in ecosystems as open systems where numerous biochemical and biophysical transformations occur, the main laws of thermodynamics govern their functioning (Svirezhev & Jørgensen, 2004). According to the first law of thermodynamics, an ecosystem can function using only the energy stored within its biota (Rahmonov et al., 2021). This is first of all the primary production that is the source of functioning for all living organisms. While thermal or light energy is used as additional, the primary source for phototrophic ecosystems is the light energy and such for chemotrophic ecosystems is chemical energy. This is where the second law of thermodynamics applies. It indicates changes in entropy in ecosystems. In all abiotic systems, entropy increases, but biotic systems are different from them because are self-organized. Regulation of energy currents and processes that is oriented at reducing entropy is one the main signs of life.

Entropy in inanimate nature directly correlates with the amount of energy that flows into the system and inversely correlates with its temperature. In other words, temperature rise is a reaction of the system to increasing amount of energy, leading to decline in entropy. However, uncontrolled rise in temperature leads to ruination of biosystems. Thus, a paradox occurs, when the ecosystem should accumulate energy to increase its stability, but cannot increase temperature to reduce entropy. The evolutionary solution to this problem became concentration of energy in biomass of primary producers. In the case of the main land ecosystems, those are aboveground phytomass. Thus, ecosystems amass energy and at the same time withdraw it from active circulation, which results in entropy decrease. Another aspect of stability of ecosystems with high reserves of phytomass is fluctuation or certain catastrophic events. Presence of those reserves increase chances of the ecosystem and its biota to survive in critical conditions, depending on amount of energy accumulated in it. When the external energy flow temporarily declines, ecosystems can function for a certain time on the existing reserves.

Energy changes that accompany accumulation of aboveground phytomass allow us to look at ecosystem dynamics in another way. Since processes of internal self-organization in natural ecosystems lead to storage of energy in aboveground phytomass, it can be the basis for development of a universal dynamics parameter. Since phytomass forms and exists for a long time, measuring it requires – besides its amount – consideration of its age. The more time biomass has been forming within the ecosystem, the longer the successful processes of recovery of natural vegetation take. In other words, such an ecosystem is at a more advanced stage of natural development. Thus, the total sum of the product of phytomass of certain age groups of individuals and its age can be used as an indicator of natural dynamics. Using the age of phytomass is also important when assemblies are formed of species that have various types of photosynthesis. For example, some ruderal or water-edge-aquatic groups of plants with C_4 photosynthesis can produce a large phytomass (up to 10 t/ha), but are able hold only its part for no more than two years. As is known, shrub groups that have a similar amount of phytomass are at

more advanced stages of ecosystem natural development. Considering this, their phytomass remains for several years, which allows a more accurate identification of their positions in successive series.

The abovementioned approaches to identification of natural dynamics require looking at ecological succession and climax theory in a different way. The classic knowledge of succession as a series of different-vector changes that occur subject to internal or external factors and climax as a condition when those changes ended does not completely correlate with the energy characteristics of ecosystem dynamics. From the standpoint of energy in ecosystems, a progressive autogenic succession is a natural process accompanied by a significant change in the series of groups with increase in amount of aboveground phytomass and its age.

Homogenic succession is most often the reverse process. However, such definition cannot be absolutized. In certain cases, homogenic successions can be progressive and boost phytomass production, because its maximum production rate is possible only in specific edaphic conditions that are optimal for creating a most productive group of a particular natural zone. In our case, those were gray forest soils on loess, with multiyear water regime in the range of 11.8–11.9 points and the general saline regime in the range of 6.2–6.5 points according to the scale of Didukh-Pliuta. Such conditions can be called a climax optimum of soil (Khomiak, 2024). It is also important that soil contains a seed bank of plants that are necessary for all following succession stages in which there is a potential for seeds to be introduced from outside the ecosystem. In conditions that are deviant from those parameters, any external effect that brings the territory closer to a climax edaphotope optimum will foster rates of phytomass accumulation, for example, detritus can be carried away during a flood onto a sandy above-river terrace with poor sod-podzolized soils. Human activities are often the primary drivers of favorable conditions for phytomass accumulation. For instance, planting species that thrive in nutrient-rich soils or introducing organic matter and mineral fertilizers to areas with poor soil quality can significantly enhance phytomass growth. Additionally, regular irrigation in areas with low water availability can also support phytomass accumulation. In the rest of cases, external effects only hinder the process of accumulation of aboveground phytomass.

Each natural zone or geobotanical subprovince has a potential for formation of a certain plant group that is able to concentrate maximum aboveground phytomass and hold it in a relatively unaltered state for a long time. Such a group will be an autotrophic block of the ecosystem in state of energy (climatic) climax. It will be an attractant of autogenic dynamics of aboveground phytomass in our model. All vectors of dynamics are directed to it, and at the same time graphically correspond not to linear but logarithmic function. Currently, we do not know accurate parameters of such a group in the territory of Polissia. The existing mature oak forests in optimal environmental conditions, exposed to minimum external pressure, have not yet reached its energy maximum. Quarter 17 of the Poiaskivske Forestland that we considered etalon did not correspond to the abovementioned conditions entirely. Most representatives of its tree stand (*Quercus robur*) have not reached the maximum physiological age, and soil conditions are not optimal. Therefore, our empirical model developed based on studies outside the stationary plots is quite reliable and provides accurate predictions (Khomiak et al., 2019).

Accumulation of aboveground phytomass can slow down or completely stop, having not reached the predicted maximum. Such a stop is catastrophic climax (Odum, 1971). Phytomass production can be slowed by external or internal effects on the ecosystem. An external effect can be any action that reduces its amount at rates higher than the rates of its natural production, for example, mowing hay, grazing, excessive recreational loading, regular cutting of phanerophytes, infiltration of invasive species on the role of “edifiers” (plants with high habitat-forming ability, to a certain degree determining species composition of the phytocenosis) (Khomiak, 2024). In our experiment, such a situation was observed at the plots Novopil 2, Budivelnik 1, and Soniachne 1. For example, at Novopil 2, phytomass increased to 21.5 t/ha on the fifth year and practically did not change until the end of study. If regulated grazing of domestic animals had continued, we could state formation of catastrophic-climax state at this plot.

Internal reasons of slowed production of phytomass is blocking of endocogenesis and absence of necessary species in the soil seed bank. For

example, in the area of the town of Hoshcha (Rivne Oblast), the shrubs at the stage of autogenic succession have not transitioned into regrowth forest due to absence of sources of seeds and its edificers nearby. Endoecogenesis is blocked due to inability of soil substrate to transition into climax edaphic optimum. Most often, it occurs due to sizes of particles of mineral component of soil. For example, monolithic vertical outcrops of crystalline rocks stop the succession at the stage of crutose lichen for a historically significant time period. During our study, the highest rate of endoecogenesis outside the stationary plots was seen in loess substrate and gray forest soils based on it (Harbar et al., 2021). Its internal structure had perfect conditions for the functioning of the capillary system and storing humin complexes. The largest substrates have good drainage, while the smallest are hard-to-access for water, therefore undergoing endoecogenesis much slower (Harbar et al., 2023).

At the stationary plots and outside of them, we observed significant annual production of the aboveground phytomass, independent of external influences or state of edaphotope. During the first years, recovery of vegetation went fast, but then gradually slowed. Such a situation was mostly typical for secondary successions where they had not been delayed by the need of endoecogenesis or seed diaspora. This is due to the strategy of certain species of plants that are adapted to domination at certain stages of ecosystem dynamics. This is well noticeable during formation of shrub groups or young regrowth forests. Edifiers of those groups are able to grow relatively fast. Those are mostly representatives of the genera *Salix*, *Betula*, and *Populus*. In the first 2–3 years, they can – in favorable conditions – grow two-meter tall, forming phytomass of over 15 t/ha. Later, the rates began notably decrease. Most species of the *Salix* genus stopped growing above 4–5 m. The dominant species in the tree stand typically begin to disappear after 20–30 years, allowing slower-growing but longer-living species like *Fraxinus excelsior* L. and *Fagus sylvatica* L. to take over. Representatives of some *Betula* and *Populus* plants undergo this change in 50–100 years. In many cases, they are replaced by *Pinus sylvestris* L., which lives up to 150 years. Later on, the dominating species became *Quercus robur*, which is the longest-living tree in the Polissia. Subdominants became *Acer platanoides* L., *Carpinus betulus* L., and *Tilia cordata* Mill., which occupy areas after the oak's departure from the tree stand, which is a result of its local disappearance. Such forest ecosystem reaches the state of dynamic balance in which its aboveground phytomass ranges around a certain potentially maximum value.

Our mathematical model of change in aboveground phytomass during natural recovery of natural vegetation should be elucidated and corrected by future researches, first of all, multiyear monitoring and experiments in various edaphic conditions and in conditions of multifaceted external influence. This allows one to obtain a series of models of ecosystem dynamics that could be used to develop algorithms to predict local environmental changes. Such an approach allows one to predict – with an acceptable accuracy – consequences of human activity for the environment and spontaneous changes in it due to other factors. This would protect us from underestimating such an impact, a mistake quite common those days. Those algorithms will have a broad application, both for ecological auditing (for example, when reporting assessment of impact on environment and for nature protection (for example, when assessing practicability of implementation of strict protection regime in a certain area).

Conclusions

During natural recovery of vegetation in disturbed territories, the amount of aboveground phytomass naturally increased. The mathematical model of change in the aboveground phytomass is the function of a natural algorithm. In this model, regression coefficient “a” indicates starting conditions of the recovery process. For the secondary ecological successions, regression coefficient “a” was higher than for the initial one. Regression coefficient “b” refers to the rates of production of aboveground phytomass. With time, deviation from a predicted trend of the change of aboveground phytomass becomes more likely. Production of aboveground phytomass in most cases was accompanied by autogenic successions, and its decline, except rare exceptions, – by homogenic ones. Accumulation of the maximum possible phytomass and maintaining it for a longest possible time corresponds to the state of energy (climatic) climax, while

production stop at lower values – to catastrophic climax. Mathematical model of change in aboveground phytomass is the groundwork for further studies focusing on structure of the integral theory of ecosystem dynamics. Practically, it can be used to predict implications of human activity for the natural ecosystems.

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