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TRENDS IN THE TRANSFORMATION OF PLANT ONTOGENESIS UNDER GLOBAL CLIMATE WARMING

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ABSTRACT. Observations of the process of ontogenesis in a group of woody plants and forest grass in the phytocenoses of the Ukrainian Polesie of Sumy region with their division into boreal and nemoral species were done. Found that in the last two decades, nemoral plant species begin vegetation earlier and pass the first phases of the ontogenetic cycle faster than boreal species. Changes in plant ontogenesis, in turn, lead to changes in the population characteristics of plant species: the number of individuals in the population, the size and configuration of the population field and the ontogenetic and vital spectra of populations changed. There has been a tendency to regular changes in the ontogenetic spectra of both nemoral and boreal plant species, but their nature was different. In nemoral plant species, the proportion of juvenile and immature individuals in the ontogenetic spectra increased and populations acquired the character of invasive, reflecting the process of progressive strengthening of their position in phytocenoses. In populations of boreal species, on the contrary, the ageing process accelerated – the proportion of old generative, senile and subsenile individuals increased.

Introduction

Global climate warming in different regions of the planet is manifested to a different extent. On the territory of Ukraine, according to meteorological observations, it is expressed quite clearly. Since 1991, each subsequent decade has been warmer than the previous one: 1991–2000 – by 0.5 °C, 2001–2010 – by 1.2 °C, 2011–2020 – by 1.7 °C. In the north–eastern part of the Sumy region, the average annual temperature in the last decades of the twentieth century was 8.2°C, and in the period 2015–2020, it was steadily maintained at 10 °C.

In recent years, summer maximum temperatures have increased that significantly affecting the vital state of plants. Over the past three years, they have risen in the summer months (Table 1).

Table 1. Maximum summer temperatures (°C) for the last three years

Month	2019	2020	2021
June	33	34	37
July	33	36	35

On the contrary, the number of days with severe frosts in winter has decreased. The duration of the growing season for plants has changed: it has begun to start earlier and ends later.

In the eastern part of the Ukrainian Polesie, the average annual precipitation tended to increase. During the period from 1940 to 2010, it increased on average from 550 to 660 mm, in contrast to the south and centre of Ukraine, where the climate became drier (Kovalenko, 2012; Semenova, Polovyi, 2020; Polevoi *et al.*, 2019). But over the past decade, the tendency to decrease precipitation has also manifested itself in this region (Fig. 1). Sharp fluctuations in the amount of precipitation falling in adjacent years have become characteristic: it varies from 344 to 729 mm per year, which creates tension in the water balance of perennial plants.

Global climate warming in its effect on the habitat of plants is diverse. In recent decades, the concentration of carbon dioxide in the air has increased as a result of warming (Saxe *et al.*, 2001; Sytnik, Bagniuk, 2006; Seidl *et al.*, 2017). There are certain trends in the properties of the soil: the height of the groundwater, the amount of humus and the content of nitrogen, potassium and other biogenic minerals in the soil are noticeably changing.

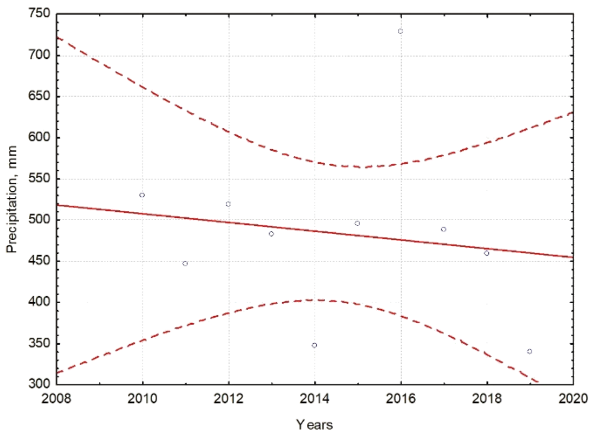

Figure 1. Annual precipitation in Sumy region for the period 2010–2020 (according to Meteo Farm)

In the aggregate final impact, environmental changes caused by global climate warming have a significant effect on photosynthesis and the production process of plants, on metabolism, in general, and ultimately on their size. Changes in the composition of the forest entomofauna of pollinators affect the reproduction of entomophilic forest plants (Pureswaran *et al.*, 2018; Polevoi *et al.*, 2019; Sereda, 2011). All these changes have a multidirectional character. They are favourable for thermophilous plants and not favourable for boreal plants (Kolomyc, 2006).

Global climate warming leads to the transformation of all types of natural ecosystems (Malhi *et al.*, 2020). In Ukraine, the borders of climatic zones are shifting towards the north: steppe, forest-steppe and forest zones.

In the Ukrainian Polesie, there was a tendency to change the species composition of forests with more thermophilous invasive plant species being introduced into them.

Changes in forest vegetation under the influence of global climate warming and its aridization are of a chain character (Fig. 2). They begin with the transformation of the grass-subshrub layer of forest ecosystems. It changes the relationship between the abundance of plant species, new species appear, some fall out completely, which ultimately changes the nature of the regeneration niches for tree species. And changes in the nature of regeneration transform the composition of the tree tier. Thus, the key to understanding the processes which take place in the forests of the Ukrainian Polesie, under the influence of global climate warming processes, is in the grass-subshrub layer of forests of the Ukrainian Polesie.

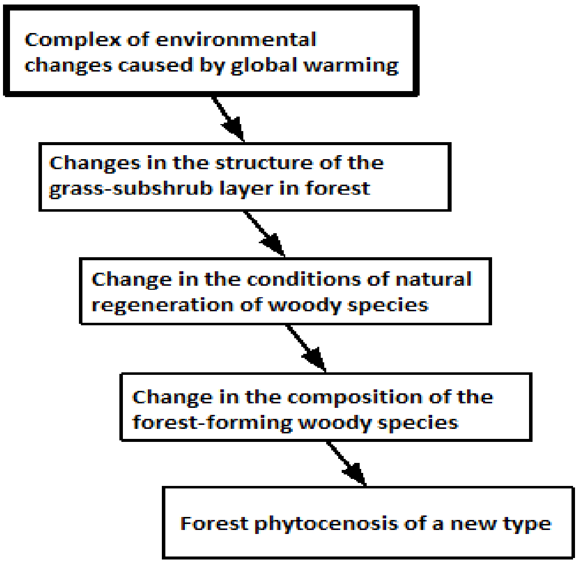

Figure 2. Diagram illustrating the chain nature of the transformation of forest ecosystems under the influence of global warming

In the complex transformations that occur in the living ground cover of forest ecosystems, in turn, one should distinguish primary and secondary processes. The primary ones are changes in the state of plant individuals – their ontogenesis, and the secondary ones are changes in the populations and, at the final stage, the phytocenoses that they are part of (Fig. 3).

Plant individuals act as a primary acceptor of the perception of parameters of the ecological habitat. Changes in their vitality and the ontogenetic spectrum of populations under the influence of unfavourable environmental conditions lead to a change in the number of individuals and a decrease in the size of their population fields. And this, in turn, causes the transformation of forest phytocenoses and forest ecosystems as a whole.

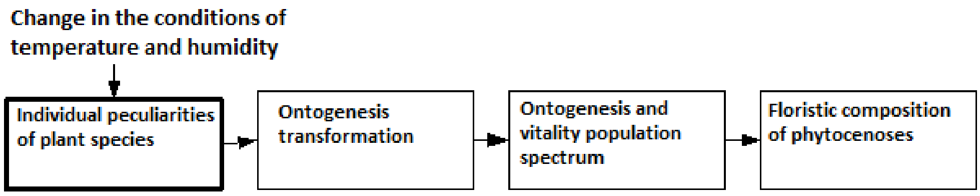

Figure 3. A sequence of processes carried out when the state and viability of plant individuals change, as primary acceptors of the changing ecological environment

Materials and Methods

To identify the stability of forest plants and the transformation of their ontogenesis in the period 2000–2021, we conducted observations of the process of ontogenesis in a group of woody plants and forest grass in the phytocenoses of the Ukrainian Polesie of Sumy region with their division into boreal and nemoral species based on the generally accepted criteria (Zozulin, 1955; Popadiuk *et al*., 1994).

The group of boreal species included: *Vaccinium myrtillus L., Majanthemum bifolium L., Oxalis acetosella L., Trientalis europaea L., Circaea alpine L., Paris quadifolia L.* The group of immoral forest grasses included *Lathyrus vernus (L.) Bernh., Aegopodium podagraria L., Carex pilosa Scop., Asarum europaeum L., Convallaria majalis L., Viola riviniana Rchb., Stellaria holostea L.*

The two groups of forest–forming tree species were identified similarly. The group of boreal species included: *Pinus sylvestris L., Picea abies (L.) H. Karst., Populus tremula L., Betula pendula Roth., Betula pubescens Ehrh., Alnus incana (L.) Moench., Alnus glutinosa (L.) Gaertn., Salix pentandra L.* The group of nemoral species consisted of: *Quercus robur L., Tilia cordata Mill., Acer negunda L., Acer platanoides L., Pyrus communis L., Fraxinus excelsior L., Ulmus glabra Huds.*

To determine the growth parameters of plants, the method of morphometric analysis was used (Zlobin *et al*., 2022), with the help of which metric parameters (plant height, phytomass *etc*.) were determined first, and then allometric parameters (absolute growth rate, relative growth rate).

Evaluation of ecological amplitudes of plants of each group was carried out using the ecological scales of Didukh (2011) according to the generally accepted methodology.

Ontogenetic analysis of populations was carried out according to generally accepted methods (Zlobin *et al*., 2022). In each species, within the population, the number of plants of different ontogenetic states was determined – from seedlings (p) to subsenile (ss) and senile (s) plants. Based on these data, the percentage of plants in each ontogenetic state within the population was determined and the ontogenetic spectra of the populations were determined.

Results

The assessment of the ecological amplitudes of plants of these two groups according to ecological scales (Didukh, 2011) has shown that with species individuality, nemoral species of forest grasses are on average more thermophilic (average amplitude 4.86–12.00 *vs.* 3.83–11.3) and less demanding of the humidification regime (5.71–10.57 *vs.* 6.00–11.34 in boreal species) (Table 2).

Table 2. Ecological amplitudes of boreal and nemoral forest herbaceous plants

Plant species	Thermal regime	Humidity	Soil water regime
Boreal plant species			
Vaccinium myrtillus	2–9	7–12	8–16
Majanthemum bifolium	4–11	7–11	8–16
Oxalis acetosella	4–13	5–11	8–16
Trientalis europaea	3–10	7–12	8–16
Circaea alpina	6–13	5–11	10–17
Paris quadifolia	4–12	5–11	9–15
Average	3.83–11.33	6.00–11.34	8.5–16.0
Optimum	7.58	8.67	12.25
Nemoral plant species			
Lathyrus vernus	4–13	5–10	8–15
Aegopodium podagraria	5–12	5–12	9–17
Carex pillosa	6–11	6–13	8–15
Asarum europaeum	6–12	7–9	9–15
Convallaria majalis	5–12	7–11	8–16
Viola riviniana	4–12	5–11	8–15
Stellaria holostea	4–12	5–11	8–16
Average	4.86–12.00	5.71–10.57	8.29–15.57
Optimum	8.43	8.14	11.93

*values are in Celsius.

A similar analysis carried out for boreal and nemorale species of woody plants (Table. 3) has shown that nemoral species are characterized by the optimal thermal regime, which is 1.6 °C higher than the boreal ones. According to the scales of climate humidity and soil water regime, ecological optima and amplitudes of non-moral species are shifted towards aridity. In general, these types of woody plants are more adapted to changes in the forest-growing conditions resulting from global climate warming. They are better able to tolerate high summer temperatures and summer droughts, which gives them competitive advantages in the conditions of increasing global warming.

The expansion of nemoral plant species to the north is also facilitated by such a feature of their ontogenesis as a high growth rate of phytomass.

Several nemoral tree species have an advantage over boreal ones in terms of growth rate. Thus, according to the classification accepted in dendrology, such a nemoral species as *Acer platanoides* refers to very fast-growing tree species with an annual increase of two or more meters, and *Fraxinus excelsior* and *Ulmus glabra*

– to fast-growing with an average increase of at least 1 meter per year. It differs in the speed of growth and undergrowth of nemoral tree species.

Table 3. Ecological amplitudes of boreal and nemoral forest trees

Plant species	Thermal regime	Humidity	Soil water regime
Boreal plant species			
Pinus sylvestris	7–12	7–11	8–20
Picea abies	5–10	7–10	10–18
Populus tremula	4–12	6–11	9–19
Betula pendula	4–12	6–11	9–19
Betula pubescens	3–10	7–11	10–20
Alnus incana	3–10	7–10	11–19
Alnus glutinosa	4–11	6–11	11–19
Salix pentandra	4–12	4–11	13–19
Average	4.25–11.13	6.25–10.75	10.13–19.12
Optimum	7.69	8.5	14.63
Nemoral plant species			
Quercus robur	6–12	6–11	8–17
Tilia cordata	6–12	6–11	9–18
Acer negunda	7–15	6–11	9–15
Acer platanoides	6–11	6–10	9–17
Pyrus communis	6–13	10–15	7–15
Fraxinus excelsior	8–13	10–16	8–17
Ulmus glabra	7–11	9–14	9–17
Average	6.57–12.14	7.57–12.57	8.43–16.57
Optimum	9.36	10.07	12.50

*values are in Celsius.

The study of annual tree rings throughout the boreal zone shows that a decrease in the growth rate of the boreal group of tree species has been observed in many areas of Eurasia since the 1900s and is associated with an increase in the average annual temperature. This is observed in many areas throughout the boreal zone among a wide range of coniferous species studied. A decrease in growth rates is more often observed in warmer areas and indirectly confirms that this is a reaction to warming and aridization of the climate (Olsson, 2011; Gauthier *et al.*, 2015).

Currently, successful natural regeneration of maple, linden, elm and ash is registered in the forests of Left-Bank Ukraine (Rumiantsev *et al.*, 2016). In the future, oak, maple, elm and other broad-leaved species will replace the disappearing conifers.

Pine is a tree species with a fairly wide ecological amplitude, but even its natural renewal under the canopy of forests is best carried out in fresh forests and sub-forests (Sendonin, Bilous, 2013, and climate aridization is unfavourable for the sustainable existence of pine forests.

For the last decades, it is characteristic that poor natural renewal of spruce is recorded along the southern border of the forest zone in birch-aspen-spruce stands. The vitality of spruce undergrowth is deteriorating (Pukinskaia, 2021) and as a result, mixed forests with spruce are replaced by lime-maple forests. The cenotic optimum for small undergrowth of another boreal species *Pinus sylvestris* covers only the conditions of several phytocenoses of *Pineta (sylvestris) hylocomiosa* and *Pineta (sylvestris) franguloso (alni)-vacciniosa (myrtilli)* association group (Skliar, 2015). On the contrary, the undergrowth of the nemoral tree species *Acer platanoides* is characterized by wide habitat versatility and accumulates in large quantities in forest phytocenoses of different types (Skliar, 2012).

Nemoral species of herbaceous plants have an advantage over boreal species of herbs in terms of growth rate and accumulation of phytomass. We have evaluated and compared the absolute growth rate (AGR) and relative growth rate (RGR) in the boreal species such as *Vaccinium myrtillus* in the five associations: I – *Pinetum myrtilloso-hylocomiosum*; II – *Pinetum molinioso-myrtillo-sum*; III – *Querceto-Pinetum myrtillosum*; IV – *Betuletum molinioso-myrtillosum*; V – *Betuleto-Pinetum franguloso-myrtillosum* with corresponding indicators of the nemoral species *Aegopodium podagraria* in the three associations: I – *Quercetum coryloso-aegopodiosum*; II – *Querceto-Pinetum coryloso-aegopo-diosum;* III – *Betuleto-Pinetum coryloso-aegopodiosum* (Table 4).

Table 4. Absolute (AGR) and relative growth rate (RGR) of such boreal species as *Vaccinium myrtillus* and such nemorale species as *Aegopodium podagraria*

Association	AGR, g day^{-1}	RGR, g g^{-1} day^{-1}
Vaccinium myrtillus		
I	0.013 ± 0.02	0.01 ± 0.003
II	0.06 ± 0.018	0.007 ± 0.002
III	0.021 ± 0.006	0.012 ± 0.005
IV	0.045 ± 0.015	0.013 ± 0.006
V	0.047 ± 0.03	0.009 ± 0.003
Aegopodium podagraria		
I	0.027 ± 0.01	0.020 ± 0.008
II	0.070 ± 0.03	0.028 ± 0.006
III	0.039 ± 0.01	0.023 ± 0.011

It can be seen that in the boreal species such as *Vaccinium myrtillus*, under the most favourable conditions (association V), the absolute growth rate is 0.047 g day^{-1}, and the relative growth rate is at most 0.013 g day^{-1}. Whereas in such nemoral species as *Aegopodium podagraria*, these indicators in the most favourable ecological and phytocenotic environment (association II) are respectively equal to 0.070 g day^{-1} and 0.028 g g^{-1} day^{-1}, *i.e.* more than two times higher. Such difference in the conditions of climate warming gives nemoral species significant competitive advantages and enables them to displace boreal species from phytocenoses.

Phenological observations have shown that in the last two decades, nemoral plant species begin vegetation earlier and pass the first phases of the ontogenetic cycle faster than boreal species. The germination of seeds and the growth of ramets in nemoral plant species in spring is also carried out more actively and faster.

The competitive advantages of nemoral species in the conditions of earlier spring warming are also determined by the fact that, by their initial biological nature, they belong either to the group of early spring plants (*Asarum europaeum*) or to spring-summer plants (*Aegopodium podagraria*). Boreal species mostly belong to the group of summer or even summer-autumn species (*Oxalis acetosella, Paris quadrifolia*).

Phenological changes in boreal species of flowering plants caused by global warming turn out to be incompatible with the life cycles of pollinating insects, which leads to the loss of both types of organisms from forest ecosystems (Heller, Zavaleta, 2009; Patyka, Patyka, 2014).

In recent decades, in the forest communities of Polesie, there has been a tendency to regular changes in the ontogenetic spectra of both nemoral and boreal plant species (Table 5). But their nature is different. In nemoral plant species, the proportion of juvenile and immature individuals in the ontogenetic spectra increases and populations acquire the character of invasive, reflecting the process of progressive strengthening of their position in phytocenoses. In populations of boreal species, on the contrary, the ageing process accelerates – the proportion of old generative, senile and sub-senile individuals increases in them. The phytocenotic position of this group of species is weakening under the influence of global climate warming in the forests of the north of Sumy region.

Table 5. Changes in the ontogenetic spectra of plants of the grass-subshrub layer during 2000–2020

Plant species and years of observations		Ontogenetic states, %							
		j	im	v	g1	g2	g3	ss	s
Boreal	2000–2005	7	6	15	23	25	18		6
	2015–2020	4	4	14	11	26	27	3	11
Nemoral	2000–2005	1	12	14	25	21	13	11	3
	2015–2020	9	17	20	24	16	10		4

j – juvenile, im – immature, v – virginile, g1 – young generative, g2 – middle aged generative, g3 – old generative, ss – subsenile, s – senile.

Discussion

Thus, the reactions of boreal and nemoral plant species of forest phytocenoses in the north Sumy region to climate change are opposed. Depending on their genetically determined properties, the vital state of individuals changes to one degree or another, which in turn affects the passage of the plant stages of ontogenesis. Its phases may shorten or lengthen, at the stages of germination – juvenile individuals, an increase or decrease in survival is observed.

Changes in plant ontogenesis, in turn, lead to changes in the population characteristics of plant species: the number of individuals in the population, the size and configuration of the population field and the ontogenetic and vital spectra of populations change. Such trends in population processes play a key role in the dynamics of forest ecosystems (Zlobin, 2009).

The variation of the ontogenetic spectra of populations is due to the conditions in which the ontogenesis of individual individuals forming the phytopopulation takes place. Therefore, the ontogenetic spectra of populations carry important information on the course of the processes of renewal and extinction of individuals, about the rate of generational change in populations and, therefore, enable to assess and predict the dynamic processes in phytocenoses that are formed by these populations. The ontogenetic spectra of plant populations have independent significance, they almost do not correlate with the population density and the number of plants in it.

The changes that have begun in the ontogenetic processes of plant individuals give impetus to other transformations of populations of boreal and nemoral plant species. If the complex of environmental impacts for a particular boreal plant species is negative, then the population field is insularized, that is. its dismemberment into separate parts. The process completes with the loss of a plant species from the phytocenosis with the appearance of free ecological niches into which other plant species are introduced. As a result, the phytocenosis is transformed, and its syntaxonomic status changes.

At the same time, the emergence of free ecological niches strengthens the phytocenotic positions of nemoral species and opens the way for the introduction of invasive plant species into the forests of Polesie. Indeed, 126 invasive species have been registered in the Desniansk-Starogut National Nature Park and their share in the flora is 16% (Panchenko, Kutiavin, 2011; Burda *et al.*, 2015). Invasive ephemerophytes such as *Callistephus chinensis (L.) Nees, Nicotiana rustica L., Lupinus luteus L., Aronia melanocarpa (Michx.)* Elliot and xerophytes *Epilobium pseudorubescens* and *Axyris amaranthoides L.* have been identified in the flora of this park.

Climate warming is a global process that manifests itself in many ways and its manifestations have been recorded and noted in various ecosystems of the world for a long time by many researchers. Thus, under the conditions of global climate changes, changes in the floristic and syntaxonomic composition, the course of phenological phenomena, as well as the coenopopulation structure of meadow ecosystems were noted during the population-ontogenetic studies of the dominant species of floodplain meadows of the Sozh River within the Vetkiv district of the Gomel region (Daineko *et al.*, 2022).

According to the results of four-year research Danko (2022) of the cenopopulation of *Cyperus michelianus* (L.) Link., a characteristic representative of pioneer psammophyte communities formed on alluvial sands, changes in the density of individuals within the population, changes in the ontogenetic spectrum, and an increase in the density of generative individuals in drought conditions were found.

Populations of rare plant species, as a critical component of biodiversity, are primarily affected by such a global factor as climate change, which leads to their degradation and extinction. According to Klymenko (2022), who analyzed threats to the sustainable existence of populations of rare plant species in the Sumy region (Ukraine), the process of degradation and extinction occurs as follows: there is a successive decrease in the vitality of individuals and, in particular, indicators of reproduction, a decrease in the number of individuals in the population, fragmentation of the population into separate loci and, finally, its complete extinction.

Dmytrakh (2019) studied the impact of climate change on the population of herbaceous plant species in the modern conditions of the Ukrainian Carpathian highlands, noted the increase in the activity of successional demutation processes. The main reason for the changes in the structure of populations is the inability to compete in the conditions of the invasion of tree-shrub species and to adapt to the changed environmental conditions. It was noted that in some cases, dynamic trends in populations are accompanied by an increase in the number of individuals and the expansion of their borders, while in others the changes are opposite, which is associated with a decrease in the number and their fragmentation.

Specialists of the World Wildlife Fund (WWF) singled out climate change as one of the five groups of main ecological factors that cause the global impoverishment of biodiversity (Ivaniuta *et al.*, 2020). Most researchers believe that the impact of climate change on changes in biodiversity is underestimated.

In general, as a result of climate change, the species composition and population structure of plant communities is undergoing restructuring (Didukh, 2009).

Conclusion

The analysis has shown that the initial manifestation of environmental changes caused by climate warming is recorded primarily at the level of plant individuals and occurs at the pace of the first phases of ontogenesis. Forest ecosystems are characterized by two processes: change in the floral composition of plant species that form the grass-subshrub layer and change in the composition of forest-forming tree species. The first of these processes is primary, the second is completely conditioned by it. As a result of these processes, against the background of the loss of competitive advantages, a trend of general nemoralization of forest phytocenoses of Polesie with changes in their floral composition is formed in the group of boreal species.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publications of this paper.

Author contributions

IK – study conception and design, drafting of the manuscript;
SB – performed the literature data analysis and discussion of the results;
AZ – analysis and interpretation of data and is the corresponding author;
IP – author of the idea, critical revision and approval of the final manuscript, guided the research;
OA – acquisition of data, drafting of the manuscript;
HK – performed the literature data analysis, critical revision and approval of the final manuscript, guided the research.
All authors read and approved the final manuscript.

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