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ECOLOGICAL STRATEGIES OF PLANTS IN THE PROCESS OF RESTORATION OF DISRUPTED NATURAL ECOSYSTEMS OF UKRAINIAN POLISSIA

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Tasks related to the restoration of disturbed natural ecosystems are of theoretical and practical importance. Traditional approaches to remediation are often utilitarian. We often observe that the natural processes of ecosystem restoration occur faster and with better quality than those carried out by humans under similar conditions. The purpose of our work is to investigate the role of plants that have different ecological strategies during the process of restoration of disturbed ecosystems. The following tasks were outlined to achieve this goal: to identify groups of plants with different ecological strategies involved in the restoration of natural vegetation; develop models of vegetation restoration using plants with different ecological strategies. The materials of our research are standard geobotanical descriptions made on the territory of Ukrainian Polissia in the period from 2004 to 2023. We consider environmental strategies more broadly than R. Whittaker, L. H. Ramensky, J. Grim and E. Pianki in their classic works. The ecological strategies of plants differ in the way of spreading and reproduction, as well as in the signs of fixation on the soil; by methods of energy reservation; changing the environment around itself. The rate of restoration of natural ecosystems, as well as their characteristics, depend on the configuration of the disturbed area, the substrate of its surface, and the adaptive strategies of the plants that fall on it. The classification of adaptive strategies of species that affect the process of restoration of natural ecosystems is formed on the basis of the variety of methods of reproduction and distribution of fruits and seeds of autotrophs, as well as the peculiarities of their energy distribution in the reproduction process. The change in ecological strategies of species is because ecosystems are dynamic systems,

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therefore, during primary successions; disturbed ecotopes are most successfully populated by patient species, and during secondary ones by explerent species and violent species. Plants penetrate the primary substrate with the help of seeds, spores, or vegetative organs (most often rhizomes). In the early stages of primary succession, the seeds and spores of patient species are the most successful – those with low competitiveness and can achieve reproductive and vegetative success outside the communities. The balance of the amount of energy of Polissia pioneer patients is often shifted from supporting the vegetative part of the body to its seeds. Species that spread to pioneer substrates using rhizomes do not have such a limitation because they share a common distribution of matter and energy with the pioneer part of the community. Those species on the primary substrate, having no competitors, actively photosynthesize and share carbohydrates, while those on the formed substrate and have many competitors for solar energy share water and mineral nutrients. Global climate changes, which lead to xerophytization of Polissia and warm winters with little snow, are becoming an obstacle to the rapid natural restoration of pine forest ecosystems in large areas of disturbed areas.

Key words: adaptation, reclamation, succession, modelling of vegetation dynamics

ЕКОЛОГІЧНІ СТРАТЕГІЇ РОСЛИН У ПРОЦЕСІ ВІДНОВЛЕННЯ ПОРУШЕНИХ ПРИРОДНИХ ЕКОСИСТЕМ УКРАЇНСЬКОГО ПОЛІССЯ

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Завдання, пов'язані із відновленням порушених природних екосистем мають теоретичне та практичне значення. Традиційні підходи до відновлення порушень частіше за все проявляють утилітарний підхід. Часто доводиться спостерігати за природними процесами відновлення екосистем, які відбуваються швидше і якісніше ніж ті, що здійснюються людиною в аналогічних умовах. Метою роботи є дослідження ролі рослин із різними екологічними стратегіями в процесах відновлення порушених екосистем. Для досягнення поставленої мети були окреслені наступні завдання: визначити групи видів із різними екологічними стратегіями, які беруть участь у відновленні природної рослинності; розробити моделі відновлення рослинного покриву із використанням рослин із різними екологічними стратегіями. Матеріалами дослідження є стандартні геоботанічні описи, зроблені на території Українського Полісся в період із 2004 по 2023 роки. Ми розглядаємо екологічні стратегії ширше, ніж це подається в класичних роботах Р. Віттекера, Л. Г. Раменського, Дж. Грайма та Е. Піанки. Вони відрізняються за способом поширення та розмноження, а також за ознаками фіксації на ґрунті; за способами резервування енергії; за зміною середовища в районі фітополя. Темпи відновлення природних екосистем, а також їхні характеристики залежать від конфігурації порушеної території, субстрату її поверхні та адаптивних стратегій рослин, які на неї потрапляють. Класифікація адаптивних стратегій видів, які впливають на процес відновлення природних екосистем, формується на основі різноманітності способів розмноження та поширення плодів і насіння автотрофів, а також особливостей їхнього розподілу енергії в процесі репродукції. Зміна екологічних стратегій видів обумовлена тим, що екосистеми є динамічними системами, тому під час первинних сукцесій порушені екотопи найбільш успішно заселяють види-патієнти, а під час вторинних види-експлеренти та види-віоленти. На первинний субстрат рослини проникають за допомогою насіння, спор або вегетативних органів (частіше за все кореневищ). На ранніх стадіях первинної сукцесії найбільший успіх має насіння та спори патієнтів – тих, які мають низьку конкурентоздатність та спроможні досягати репродуктивного і вегетативного успіху за межами угруповання. Баланс кількості енергії поліських піонерних патієнтів часто зміщений від підтримки вегетативної частини організму до його насіння. Види, які поширюються на піонерні субстрати за допомогою кореневищ, не мають такого зміщення, тому що мають спільний розподіл речовини та енергії із піонерною частиною спільноти. Види на первинному субстраті, не маючи конкурентів, активно фотосинтезують і діляться вуглеводами, а ті що знаходяться на сформованому субстраті і мають багато конкурентів за сонячну енергію діляться водою та мінеральними елементами живлення. Глобальні зміни клімату, які призводять до ксерофітизації Полісся та малосніжних теплих зим, стають на перешкоді швидкому природному відновленню екосистем соснових лісів на великих за площею порушених ділянках.

Ключові слова: *адаптація, рекультивація, сукцесія, моделювання динаміки рослинності.*

Introduction

The process of harmonizing relations between mankind and the environment is multifaceted and includes many different aspects. In some cases, we have theoretical problems that are related to the natural youth of the science of ecology. In other cases, we have application problems. Applied problems arise when we have not yet found algorithms the practical application for known theoretical propositions. However, there are such problems of human relations with the environment, during the solution of which we will receive new ecological theories and technologies. Tasks related to the restoration of disturbed natural ecosystems belong to this group of problems (Bell et al., 1997). Since violations occur both under the influence of human activity and without it, the comparison of these two processes is of great interest to science (Khomiak, 2022).

The restoration of ecosystems is a natural process that is present at all stages of the development of life on our planet and beyond. The spread of organisms on the surface of the planet began at the moment of their emergence. Thus, natural ecosystems were formed on lifeless landscapes. When, as a result of lithospheric, atmospheric, or cosmic factors, ecosystems were partially or completely destroyed, the settlement process began again. In addition, even established ecosystems that are close to each other are constantly competing for territory, trying to displace each other. Their struggle cannot be directly compared to the competition at the species level. The exception is cases when invasive transformers species are edifiers of newly formed ecosystems. And also, we observe several processes of dynamics, as a result of which one ecosystem replaces another. Thus, research and modeling of the processes of restoration of natural ecosystems after disturbances is an excellent tool for developing a theory of their dynamics (Hobbs, 2004).

Anthropogenic impact on ecosystems often resembles catastrophic natural processes. Here we are talking, first of all, about activities that lead to the destruction of the soil cover, as well as to the destruction or reduction of living organisms in a certain area. The study of the mechanisms of the impact of human activity on the environment and the elimination of its consequences has not only been theoretical but also applied importance (Yu, 1999).

Traditional approaches to restoration of ecosystems after disturbances are most often utilitarian. We are talking about the use of reclamation to restore the fertility of the soil (arable land) or forest plantations (sources of commercial timber). In many cases, such a procedure is not only irrational but also impossible. For example, when it comes to long-term open mining of construction raw materials. It is mostly impossible to close such quarries with overburden and waste rock and soil from dumps and restore them as arable land or forests with commercial timber (Zhang et al., 2018). However, these artificially created landscapes have the potential to recreate quite rare and ecologically valuable habitats (Bren et al., 2022). In this case, restoration of natural ecosystems will have more promising advantages than classical reclamation, because they will correspond to the characteristics of landscapes (Khomiak et al., 2021).

The effectiveness of our restoration or reclamation efforts is another aspect of this problem (Cherniaieva et al., 2022). We often have to observe when the natural self-recovery of ecosystems occurs faster and better than what is done by humans (Asr et al., 2019). Consequently, our efforts often result in significant expenditure of resources and time, but have low reliability and efficiency (Cristea et al., 1990). We do not pay attention to this because of our egocentrism and "earthly chauvinism". We hear enthusiastic stories about successful projects and never hear about the numerous failures of similar approaches in conversations with proponents of various ecosystem restoration methods (Baasc et al., 2012). Often imperfect methods of restoration and reclamation are successful because their success is made possible by the autonomous natural process of ecosystem formation that occurs simultaneously with human intervention (Leshchenko & Khomiak, 2021).

Nature compensates for imperfect methods when human actions prove ineffective or fail. This creates the illusion of successful human activity. In fact, it's wasted time, effort, and resources that could be used elsewhere (Zolenko & Khomiak, 2021) We need to create models of their settlement by autotrophs in order to increase the efficiency of the process of restoration and reclamation of disturbed ecosystems. A main characteristic of autotrophs for such models will be their ecological strategy (Guo et al., 2018; Bondar & Khomiak, 2021).

The purpose of the article: to investigate the role of plants with different ecological strategies in the processes of restoration of disturbed ecosystems.

In accordance with the goal, the following tasks were set:

• Identify groups of species with different ecological strategies involved in the restoration of natural ecosystems

• Develop ecosystem restoration models using plants with different ecological strategies.

Research material and methods.

The research materials are standard geobotanical descriptions made and the territory of the Ukrainian Polissia in the period from 2004 to 2023. We made geobotanical descriptions on abandoned fields, mines and quarries (Khomiak, 2022). The materials were collected using route-expedition, semi-stationary and stationary methods.

Geobotanical descriptions were analyzed using Turboveg for Windows (Hennekens & Schaminée, 2001). After the transformation of the general array of data, we divided it into separate classes according to the deductive principle on the basis of defined blocks of diagnostic species. Each class resulting from this division is divided into phytocenones (Braun-Blanquet, 1964). Phytocenones are elementary homogeneous units of vegetation. For the development of the syntaxonomic scheme, we used the "Vegetation Prodrome of Ukraine" (2019). The synphytoindicative analysis was carried out according to the principles laid down by J.P. Didukh and P.G. Plyuta (Didukh & Pliuta, 1994; Didukh & Khomiak, 2007) using the Simargl 1.12 program (Khomiak, 2018). Synphytoindication was carried out using the "EcoDBase 5d" database of the "Theory of Ecosystems" laboratory of Zhytomyr State University named after I. Franko (Khomiak, 2018; Khomiak et al., 2020).

Research results.

We consider environmental strategies more broadly than Robert Whittaker, L.G Ramensky, J. Grime, and Eric Pianki in their classic works (Pianka, 2011; Grime & Pierce, 2012). We consider not only the competition between species for the distribution of resources within a specific ecotope, but also the specific methods of their competitive struggle. One of the biggest problems with the classic strategic triad is that it ignores ecosystem dynamics. On the one hand, at different stages of succession, the species playing the roles of violent, exploiters and patients change. On the other hand, the same species, even the same individual, of different ages and in different places in the successional series of ecosystems, can play different strategic roles (Table 1).

Table 1.
Distribution of species with different ecological strategies on abandoned fields on loess substrates of well-lit gentle slopes of the Central Polissia.

A type of ecological strategy	Stages of overgrowth of abandoned fields						
	Primary seed	Primary rhizome	Meadows	Meadows - Chamaephytes	Bushes	Derivative forests	Native forests
Violents	-	*Elymus repens* (L.) Gould.	*Agrostis capillaris* L.	*Genista tinctoria* L.	*Salix caprea* L.	*Betula pendula* Roth.	*Quercus robur* L.
Explerents	-	*Scleranthus annuus*	*Elymus repens* (L.) Gould. *Agrostis capillaris* L. *Quercus robur* L. *Scleranthus annuus*	*Agrostis capillaris* L. *Agrostis capillaris* L. *Quercus robur* L. *Elymus repens* (L.) Gould. *Scleranthus annuus*	*Agrostis capillaris* L. *Quercus robur* L. *Genista tinctoria* L. *Elymus repens* (L.) Gould. *Betula pendula* Roth. *Polytrichum commune* Hedw	*Agrostis capillaris* L. *Quercus robur* L. *Genista tinctoria* L. *Elymus repens* (L.) Gould. *Salix caprea* L. *Polytrichum commune* Hedw	*Betula pendula* Roth. *Polytrichum commune* Hedw
Patients	*Elymus repens* (L.) Gould. *Polytrichum commune* Hedw. *Scleranthus annuus*	*Polytrichum commune* Hedw	-	-	*Parmelia sp.*	*Parmelia sp.*	*Parmelia sp.*

Since ecosystems are dynamic systems where syngenesis and endoecogenesis are constantly taking place, this causes a change in the ecological strategies of species. These environmental changes lead to changes in the roles of species in phytocenosis (Khomiak et al., 2023). There is one environment here before the plant species entered here and another environment after the plant species entered here. For example, the characteristics of the edaphotope have a very strong influence on the environment. During secondary successions, the edaphotope is already formed and has a supply of the necessary seeds. During primary successions, the substrate lacks necessary elements, and not all environmental indicators (edaphic factors) are in the optimum zone. Therefore, patient species most successfully populate the territory during primary successions of disturbed ecotopes. Other species, the seeds or vegetative parts of which fall into such conditions, die or are in a depressed state until the moment before the environmental conditions change. Here, the monolith of the substrate and its exposure has the greatest influence on the direction of ecosystem restoration (Table 2). We can divide such substrates into several groups conditionally. Vertical and well-lit monoliths are the least favorable for endoechogenesis. Ecosystems with an autotrophic block in the form of terrestrial algae and lichens form here (Kapets et al., 2019). Here, the restoration of the natural vegetation of the climactic type occurs so slowly that it is customary to consider the state of such ecosystems as a catastrophic climax. On the horizontal outcrops of loess, on the contrary, the restoration of ecosystems occurs very quickly. Seeds or vegetative parts of plants located in neighboring areas, penetrating the loes substrate, form natural ecosystems without waiting for the completion of the endoecogenesis process. As a rule, these are the first stages of overgrowth of fallows: meadows and meadow-shrubs with isolated sparse undergrowth of trees and shrubs. An exception is the rapid formation of native forests, if the disturbed area is located on the edges of forests and meadows within the phytofield of ecosystem engineer species.

Table 2.

Examples of plant species adapted for living on different types of primary substrates.

Types of primary substrates	Examples of plant species	
	Slope 45-90°	Slope 0-45°
Monolith	*Candelariella vitellina* (Ehrh.) Müll.Arg.	*Polytrichum commune* Hedw
Gravel	*Ceratodon purpureus* (Hedw.) Brid.	*Carex hirta* L.
Sand	*Polytrichum piliferum* Hedw	*Elytrigia intermedia* (Host) Nevski
Loes	*Asplenium trichomanes* L.	*Elymus repens* (L.) Gould.
Clay	*Hylocomium splendens* (Hedw.) W.P. Schimp	*Populus tremula* L.

Plants penetrate the primary substrate with the help of seeds or vegetative organs (most often rhizomes) (Table 3). These two methods use completely different strategic approaches. In the early stages of primary succession, the seeds of patients are the most successful – those plants that have low competitive indicators but are able to achieve reproductive and vegetative success outside the grouping. The seeds of these plants are able to germinate in conditions of limited resources. Outside Polissia, these can be species that produce a small number of fruits and seeds with large reserves of nutrients. For example, coconut palms, whose fruits are able to germinate on disturbed sands of ocean beaches. No such cases were recorded in the studied area.

Fruits transferred zoochorically have few chances during primary successions. In the process of secondary successions, this transfer occurs constantly. We can observe in the early stages of abandoned fields the presence of individual trees from the later stages of succession (for example, *Quercus robur* L.). Most of the species, the seeds of which penetrate the primary substrate, have small sizes of vegetative organs and numerous adaptations for extreme environmental conditions. They produce different numbers of seeds. When we talk about betting on the number of seeds, we mean not their number, but the balance between energies. It is the balance of the energy that the organism spends on maintaining its existence and the energy that the organism spends on producing and dispersing fruit.

Rhizome species have no such limitations. Rhizome species operate according to the corporate principle. Individuals of plants on the primary substrate, having no competitors, actively photosynthesize, transferring carbohydrates through the common rhizome system. Individuals of plants that are combined with them, but are in a formed group, have many competitors for solar energy. However, they have a better supply of water and mineral nutrients. They share them with the pioneering part of their superorganism (Cherniaieva & Khomiak, 2021; Khomiak & Shamonina, 2021).

Table 3.

The plant species examples with different ways of spreading to disturbed ecotopes.

Types of plant species by distribution method	Subtypes of plant species distribution	Examples of plant species
Rhizome species	Rhizome species	*Carex hirta* L., *Elytrigia intermedia* (Host) Nevski, *Elymus repens* (L.) Gould.
Seed species	Small-seeded species	*Populus alba* L., *Populus nigra* L., *Salix fragilis* L.
	A multi-seeded species	*Stellaria media* (L.) Vill., *Echinochloa crusgalli* (L.) Beauv.

Once a species enters an area devoid of vegetation and becomes part of a successional series, it uses various ways to adapt to environmental conditions and increase its reproductive success. These methods differ in the method of fixation on the soil (stem-rooted and taproot-rooted); by methods of energy reserve (rhizome, rhizome, bulb); by change of the environment in the phytofield area (turf, allelopathic) (Table 4). Plants use two approaches for fixation on the soil surface: to sink with one powerful root as deep as possible into the substrate or to fix themselves on it with numerous small roots. This choice is influenced by a large number of other factors: from the hydration of the substrate to the size of the organism itself.

The manner in which stored energy is handled is an equally important influence on the ecological strategy of pioneer plants. Some species of plants try to immediately realize the energy accumulated during one vegetative season as much as possible in seeds. Other species of plants, with its help, strengthen their ability to resist environmental pressure. Some use an intermediate option - the first year they accumulate underground phytomass, and in the second year they turn it into numerous seeds. Some species of plants accumulate energy in bulbs and use it to generate the next season in conditions of sharp fluctuations in environmental indicators caused by seasonal dynamics. In temperate climates, this most often applies to spring ephemeroids. Most of them try to store energy in early spring, while competition for sunlight is low. At different stages of restoration of natural ecosystems, there is a change in the ratio of species with different approaches to energy use. In the earliest stages of ecosystem restoration, most plants located here channel energy into seeds. Later, the maximum number of species appears, which make its short-term reserves in the underground parts. Species that use energy for individual resilience dominate the final stages of recovery after disturbances.

Some plants actively change the environment for their needs when they adapt to it. In this case, we are talking not only about the classic competition for light using different biomorphs. Due to the release of special substances into the soil (allelopathy), plants suppress the growth of competitors, and due to the formation of sod, plants block the path for the penetration of seeds of other species of plants.

Table 4.

Examples of plant species with different types of adaptation strategies.

Survival strategies on a new substrate	Examples of plant species
Rhizomatous	*Elymus repens* (L.) Gould.
Seminal	*Stenactis annua* Nees
Taproot	*Betula pendula* Roth.
Fibrous-root	*Festuca pratensis* Huds.
Bulbous	*Allium oleraceum* L.
Rhizomatous-stallon	*Daucus carota* L.
Allelopathic	*Solidago canadensis* L.
Sodden	*Dactylis glomerata* L.

In the early stages of the restoration of natural ecosystems, the pace of changes and the quality composition of the autotrophic block depends on the method of seed transfer. The transfer of seeds can occur through the air (anemochory), on the surface of the soil or snow, with the help of water (hydrochory), animals (zoochory), and gravity. Since the adaptations to spread in different species differ, we observe its annual transfer of seeds to different distances. If the disturbed site occupies a large area, then its settlement by such species occurs unevenly. Its periphery is populated much more densely and earlier than the parts remote from the edges. Some species spread their seeds exclusively within their phytofield, while others are able to do so over considerable distances.

A special situation with the distribution of Pinus sylvestris L. on disturbed soils. There is a relationship between the presence of snow cover in the second half of winter and the spread of pine seeds. In winters with little or no snow, pine seeds spread only a few meters from the mother tree. In other cases, several seeds spread a few hundred meters. Global climate changes, which lead to xerophytization of Polissia and warm winters with little snow, are becoming an obstacle to the rapid natural restoration of ecosystems on large areas. For example, according to the forecast of 2015, to the southeast of the village of Novoselytsia (Zhytomyr district, Central Polissia), multi-aged pine forests of association *Dicrano-Pinetum* Preising et Knapp ex Oberdorfer 1957 (class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939) and and mesoxerophytic meadows of the union *Agrostion vinealis* Sipaylova, Mirk., Shelyag et V.Sl. 1985 (class *Molinio-Arrhenatheretea* R.Tx 1937) should have formed on the fallows.

However, during the survey in 2023, we observe a predominance of Nardus swards of the association *Calluno-Nardetum* Hrync 1959 (*Nardetea* *strictae* Rivas Goday et Borja Carbonell in Rivas Goday et Mayor López.1966), between which there are islands of pine forests of the association *Cladonio-Pinetum* Juraszek 1927, with pine trees over 15 years old. This is due to xerophytization processes that have dominated this area for the past 12-15 years. The spread of pine has practically stopped, so we see 1-3 year old growth only near the mother trees. Since these are sod-podzolic soils with a well-drained sandy base, the irregularity of precipitation and high summer temperatures led to a decrease in the long-term moisture regime. That is why psammophytic patient plants prevail here instead of meso-xerophytic explerants and violents.

Conclusions.

The rate of restoration of natural ecosystems, as well as their characteristics, depend on the configuration of the disturbed area, the substrate of its surface, and the adaptive strategies of the plants that fall on it.

The classification of adaptive strategies of species that affect the process of restoration of natural ecosystems is formed on the basis of the variety of methods of reproduction and distribution of fruits and seeds of autotrophs, as well as the peculiarities of their energy distribution in the reproduction process.

The change in ecological strategies of species is because ecosystems are dynamic systems, therefore, during primary successions; disturbed ecotopes are most successfully populated by patient species, and during secondary ones by explerent species and violent species.

Plants penetrate the primary substrate with the help of seeds, spores, or vegetative organs (most often rhizomes). In the early stages of primary succession, the seeds and spores of patient species are the most successful – those with low competitiveness and can achieve reproductive and vegetative success outside the communities. The balance of the amount of energy of Polissia pioneer patients is often shifted from supporting the vegetative part of the body to its seeds. Species that spread to pioneer substrates using rhizomes do not have such a limitation because they share a common distribution of matter and energy with the pioneer part of the community. Those species on the primary substrate, having no competitors, actively photosynthesize and share carbohydrates, while those on the formed substrate and have many competitors for solar energy share water and mineral nutrients.

Global climate changes, which lead to xerophytization of Polissia and warm winters with little snow, are becoming an obstacle to the rapid natural restoration of ecosystems in large areas of disturbed areas.

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