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Forecasting post-fire dynamics of vegetation recovery in natural ecosystems

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ABSTRACT

The study investigates the patterns and ecological consequences of vegetation succession in areas affected by ground fires within the Roztochya region of Ukraine. The objective was to identify key stages and drivers of post-pyrogenic vegetation recovery and assess the role of dominant species in ecosystem stabilization. Field surveys were conducted in burned and control sites using geobotanical methods, Braun-Blanquet cover-abundance scales, and Ellenberg indicator values. Species richness, vegetation structure, and environmental indicators were analyzed to determine successional dynamics. The results revealed that post-fire communities demonstrate clear differentiation in floristic composition and soil-vegetation relationships compared to unburned areas. Pioneer species with high ecological plasticity dominated the early successional stages, while later phases showed a gradual restoration of native species. The findings contribute to understanding post-fire regeneration processes and provide a foundation for managing pyrogenic landscapes and implementing nature-based solutions in fire-prone ecosystems. The study emphasizes the need for long-term monitoring and ecosystem-based management strategies in regions exposed to increasing fire risks under climate change.

Keywords: dry meadow, ecotope, fire, post-pyrogenic succession, complex environmental gradient, multidimensional vegetation ordination, mathematical modelling, environmental safety

INTRODUCTION

The impact of fires in natural ecosystems on vegetation is extremely diverse. Fire partially or completely destroys tree, shrub and grass layers, lichen and moss cover, and litter, activating erosion processes. The geochemical parameters of the soil also change: there are changes in the pH value towards an alkaline reaction, the content of soluble forms of nitrogen, phosphorus, and potassium increases (Buts & Nekos, 2013). The direct and indirect impact of fires on the soil cover causes changes in edaphic conditions and determines the further specificity of vegetation development after fires. Notably, fires in natural ecosystems cause significant harm to the human body due to the ingestion of combustion products into the respiratory and visual organs (Serhiyenko & Serhiyenko, 2022).

Worldwide, numerous studies are being conducted on post-fire succession and vegetation regeneration at fire sites. The influence of location of the site on species diversity was revealed (Capitanio & Carcaillet, 2008). The dynamics observed after the fire demonstrates a gradual transition between three stages, from the initial, through the transitional to the mature one. Each stage is characterised by a different relative species density.

Furthermore, several plant species can be classified as early, intermediate, or late successional species based on their densities at different times after burning.

Succession is largely dependent on the regeneration strategies and dispersal ability of the species found in the burned area. Spontaneous plant communities occur only at the first stage of succession, when competition for resources is low. This process can be called the 'race for territory occupation'. The second stage, when competition for resources becomes increasingly important, can be called 'efforts to preserve space' (Ghermandi et al., 2004).

On burnt areas, the regeneration of the vegetation cover with age is carried out by *Melastoma malabathricum, Eupatorium inulaefolium, Ficus* sp., *Vitex pinnata* L., but these species were rare in the secondary regeneration. Structure had a strong influence on regeneration: soils with more than 50% sand had slower development towards secondary regeneration. In more sandy soils, the number of species was lower. The latter showed a stronger increase in *Pteridium aquilinum* L. over time, which slows down the next stage of vegetation development (Yassir et al., 2010).

Cistaceae seedlings (mainly *Cistus albidus* and *Helianthemum marifolium*) were the most abundant after the fire (63% of total germination), while *Fabaceae* species (including *U. parviflorus* and *Ononis fruticosa*) accounted for 25% and *Lamiaceae* (limited to *Rosmarinus officinalis*) accounted for only 3% of total occurrence. After the fire, the biomass of *Fabaceae* decreased from 78.7% to 13.1%, while *Cistaceae* increased from 8% to 83.4%. Considering that the frequency, intensity or severity of fires is partly controlled by the composition and structure of the plant community, changes in the population of key species may affect future fire regimes and, in turn, affect the hydrological, ecological and economic role of large areas of forest and sparse woodland in western Mediterranean ecosystems (De Luis et al., 2006).

Evergreen shrubs and semi-deciduous sage scrub were studied for five years after fires to assess hypothetical determinants of post-fire recovery and succession. Residual species existing in the environment immediately after the fire dominated the early succession. In the fifth year after the fire, approximately half of the species were colonisers that were not present in the first year, but they accounted for only 7–14% of the cover. Strong 'ecological filter' effects were observed in the landscape, resulting in complex patterns of post-fire recovery and succession between riparian and inland associations of both vegetation types (Keeley et al., 2005).

In 1981, a particularly devastating fire in the São Carlos region of São Paulo state (Brazil) destroyed the above-ground vegetation and litter (Yassir et al., 2010; Soares et al., 2006). There were three successive phases in the succession process: the species foundation; intraspecific competition due to the restructuring of individuals per species; and interspecific competition with the displacement of some species from the plots (Soares et al., 2006).

The results of the floristic survey show that most species have been present since the beginning of succession and suggest that *Pinus brutia* forests of the eastern Mediterranean basin are recovering by autosuccession. However, changes in species richness and β-diversity indicate successional changes, and therefore the authors cannot fully support the theory of direct regeneration (Kavgacı et al. 2010.

The dynamic process of post-fire vegetation succession was determined for forest types A and B (Liu et al., 2009). The post-fire 80-year succession trend of the Type A forest is a mixed forest of *B. platyphylla* and *Larix gmelinii*. Its shrub layer is mainly made up of *Corylus heterophylla* and *Vaccinium uliginosum*, and the herb layer is dominated by *Carex tristachya*, *Athyrium multidentatum* and *Pyrola incarnate*; while the 80-year post-fire succession trend of the B-type forest is a mixed forest of *Q. mongolica* and *B. davurica*.

In the drier stands of old-growth yellow pine, relatively little change has occurred even after more than a century without fire. Reconstructing historical forest densities in productive mixed coniferous forests suggests that these areas were historically linked to the wider dry forest landscape structure through frequent fire and should be a priority for restoration (Johnston, 2017).

In the first four years after the fire, annual species were the largest floristic group, but herbaceous perennials and shrubs were the main contributors to community biomass. Nitrogen-fixing species and exotic species contributed significantly to the early community structure after the fire. Although general trends in post-fire succession are clear in terms of temporal changes in the relative proportions of different plant groups, environmental changes and the nature of the plant life history of constituent species, especially dominant species, can significantly alter such trends (Guo, 2001).

The results presented in (Dawe et al., 2022) show that the 2014 wildfires in Canada, being particularly large and severe, also increased landscape heterogeneity. At the same time, these wildfires caused changes at the stand level in the predominance of tree species and associated plant communities.

It was found that fires in natural ecosystems affect the migration of heavy metals and radionuclides in soil genetic horizons (Popovych et al., 2021). Acute and chronic illnesses are caused by heavy metal concentrations that exceed the permissible limits set by several national and international organisations. They can range from non-fatal, such as muscle and physical weakness, to fatal, such as brain, nervous system, and even cancer (Serhiyenko & Serhiyenko, 2022). Among others, genotoxic biomarkers such as micronucleus frequency may provide insights into long-term health effects of environmental stress (Nersesyan et al., 2021).

Fires in natural ecosystems have a significant impact on the development of micromycete colonies. Soil samples from burned and unburned forests were analysed for ectomycorrhizal fungi (EcM) using bioassays. The number of EcM species was significantly lower in samples from recently (2-5 years) burned areas than in unburned forests, and increased over time as the fire reached the level of adjacent forests after 15–18 years. The community composition changed after the fire, but did not approach the composition of unburned plots within 18 years. Only *Rhizopogon roseolus* and *Cenococcum geophilum* were distributed both in the burned areas and in the adjacent forests. The data indicate fire resistance of some EcM fungal species, as well as rapid persistence of species numbers, but not species composition (Kipfer et al., 2011).

The quantity, composition and diversity of fungi at four soil depths (0–5 cm, 6–10 cm, 11–15 cm, 16–20 cm) during a low- and high-intensity fire in a subtropical peatland in the southeastern United States were assessed. It was found that a small fire significantly increased the diversity of fungi (by Shannon) and saprotrophic fungi in the 0–5 cm soil layer immediately after the fire, and then disappeared within 2 years. This pattern was not observed in soils below 5 cm. The dominant class of fungi, *Archaeorhizomycetes*, initially decreased and then returned to pre-fire levels at 0-5 cm depth. The diversity of fungi could not be restored to the unburned state even 30 years after a severe fire, especially in the 6–20 cm soil layers (Tian et al., 2021).

Numerous studies confirm the global relevance of post-fire succession across different ecosystems – from the grasslands of Indonesia (Yassir et al., 2010) and Brazilian cerrado (Soares et al., 2006) to subtropical peatlands, where fungal communities reveal distinct patterns of recovery (Tian et al., 2021). In the context of the Ukrainian Roztochya, local botanical diversity and phytocenotic dynamics are comprehensively described by Soroka (2008), whose findings provide a valuable ecological background for interpreting post-pyrogenic processes in the region.

Moreover, digital analysis of forest environments and vegetation dynamics through intelligent data tools is gaining relevance for post-disturbance assessments (Skrobala, 2010). From a health and bioindication perspective, biochemical and physiological changes related to environmental stress, including metabolic and cardiovascular responses, may serve as complementary indicators of ecosystem disturbance (Serhiyenko, 2014; Serhiyenko & Serhiyenko, 2023; Nersesyan et al., 2021).

At the same time, fires in natural ecosystems regulate the development of living organisms and their reproduction. In particular, terrestrial spiders were studied using booby traps 3–4 months after a forest fire, and then for three post-fire years (Koponen, 2005). The burned area in a pine forest in Finland was dominated by *Lycosidae*, while the control area was dominated by *Linyphiidae*. *Linyphiidae* dominated both sites in terms of species abundance, while *Lycosidae*, *Gnaphosidae* and *Theridiidae* were more abundant in the burned site than in the control site. The spider community at the burned site was clearly different from the control group during the three years after the fire, mainly due to the abundance of *Gnaphosidae* and *Lycosidae*.

MATERIALS AND METHODS

The environmental regularities of post-pyrogenic succession of dry meadow in the Ukrainian Roztochya were studied using data mining methods. Data mining is the process of analytical research of large amounts of information in order to identify certain patterns and dependencies between variables (hidden knowledge) that can be applied to new data sets and reliable forecasting of processes and phenomena (Kantardzic, 2020). The research included three main stages: studying the structure of the mutual arrangement of plant associations in the multidimensional space of environmental parameters, mathematical modelling of the structure and verification of the model (Skrobala, 2010; Skrobala et al., 2020).

The geobotanical information is based on data on the environmental parameters of more than 500 plant communities representing meadow, ruderal and forest vegetation, based on six parameters: L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content, pts (Ellenberg et al., 1991; Adamenko et al., 2017). This approach is in line with ecological quality assessments of protected hydroecosystems, where territorial norms are often used as a reference (Adamenko et al., 2017).

Mathematical modelling was performed by establishing systematic relationships between the environmental parameters of vegetation habitats (Skrobala et al., 2020; Pukish et al., 2024). Each plant community can be represented as a point in a multidimensional feature space, the coordinates of which correspond to the parameters of environmental regimes. In this case, the similarity of plant communities by a set of environmental parameters can be determined based on the distances between the points. The essence of the subsequent mathematical procedure is to identify complex environmental gradients and build typological schemes of vegetation based on discriminant analysis. The mathematical model was verified by a comparative assessment of the position of the post-pyrogenic succession plant community and vegetation associations on the axes of maximum variation (multidimensional ordination) with the results of geobotanical studies and literature data (Soroka, 2008).

RESULTS AND DISCUSSION

After a fire, the herbaceous and shrubby cover, depending on the growing conditions, is transformed mainly in four directions: prairiefication, steppification, waterlogging and the appearance of wastelands. The process of vegetation recovery can take decades. But already at the initial stage of succession, the floristic composition of the plant community allows predicting the direction of its dynamics. For example, the floristic composition of a post-fire dry meadow in the 3rd year after the fire includes meadow, segetal, ruderal and forest species (Table 1).

These vegetation types (classes *Molinio-Arrhenatheretea, Artemisietea vulgaris, Agropyretea intermedio-repentis and Querco-Fagetea*) are the most likely to develop in the plant community. However, the type of human activity should also be taken into account. If no crops are to be grown on the slope, then the segetal vegetation of the *Secalietea class (Stellarietea mediae)* will not develop there. According to the syntaxonomic

Table 1. System of ecological and cenotic groups of species of the post-fire succession plant community

Ecological and cenotic group (group of vegetation classes, vegetation class)	Common representatives of flora
3. Disturbed and secondary vegetation	
3.3. Chenopodietea community with domination of ruderal annual plants of restorative stable succession on disturbed ecotopes	*Sonchus oleraceus* L. – 1 species
3.4. Secalietea Agrophytocenoses of cereals and row crops	*Anagallis arvensis* L. – 1 species
3.5. Artemisietea Ruderal communities of tall biennial and perennial species	*Daucus carota* L., *Stenactis annua* – 2 species
3.6. Agropyretea Ruderal and semi-ruderal hemicryptophyte communities on dry anthropogenic or natural ecotopes with compacted soils	*Elytrigia repens* (L.) Nevski, *Convolvulus arvensis* – 2 species
5. Anthropo-zoogenous heath, grasslands and pastures	
5.3. Festuco-Brometea Steppe communities	*Erigeron acris* L. – 1 species
5.4. Molinio-Arrhenatheretea Meadow communities (except for wet meadows)	*Achillea submillefolium* Klok. et Krytzka, *Bellis perennis* L., *Leucanthemum vulgare* Lam., – 3 species
8. Broadleaved forests and woodlands	
8.4. Quereo-Fagetea Broadleaved forest communities on nutrient-rich soils	*Galium odoratum* (L.) Scop. – 1 species

classification of the vegetation of the Ukrainian Roztochya, the *Chenopodietea* class is considered to be part of the *Stellarietea mediae class* (Soroka, 2008). The restoration of the herbaceous cover in the study area also depends on the biological characteristics of species, in particular their ability to reproduce by rhizomes. First of all, it is couch grass (*Elytrigia repens*) and sweet woodruff (*Galium odoratum*).

Typically, vegetation succession is studied by comparing the floristic composition of communities at different stages of its recovery. But this process requires a long time of research. Therefore, in our work we used a completely different approach, which consists in comparing the environmental parameters of habitats (Table 2). Their analysis was based on the phytoindicative assessment according to the ecological scales of Ellenberg (1991):

- Illumination scale (L), pts: 3 – shade-loving plants; 5 – shade-tolerant plants; 7 – light-loving plants; 9 – very light-loving plants.
- Temperature scale (T), pts: 5 – temperate (moderately warm) climate; 6 – moderately warm to warm; 7 – warm climate.
- Continentality scale (K), pts: 3 – oceanic to sub-oceanic (mainly Central European species); 4 – sub-oceanic (Central European and Eastern European species); 5 – intermediate (slightly sub-oceanic to slightly subcontinental); 6 – subcontinental (East-Central European and Eastern European species).
- Soil moisture scale (F), pts: 3 – dry habitats; 5 – fresh habitats (medium-moist); 7 – moist habitats.
- Soil acidity scale (R), pts: 3 – acidic soils; 5 – moderately acidic soils; 7 – slightly acidic to slightly alkaline soils.
- Nitrogen richness scale (N), pts: 3 – nitrogen-poor habitats; 4 – poor to moderately nitrogen-rich habitats; 5 – moderately nitrogen-rich habitats; 6 – moderately nitrogen-rich to rich habitats; 7 – nitrogen-rich habitats.

To find out which environmental factors determine the dynamics of vegetation cover within the specified vegetation classes (Table 2), a one-factor analysis of variance was performed. This analysis is based on the calculation of Fisher's criterion, which is the ratio of intergroup and intragroup variances. The analysis revealed that the maximum value of Fisher's F criterion is inherent in the environmental parameters of illumination (F = 686.7, significance level p < 0.001), soil acidity (F = 260.3, p < 0.001) and nitrogen content (F = 204.6, p < 0.001), less so continentality (F = 81.8, p < 0.001) and thermal regime (F = 73.5, p < 0.001). These factors are the basis for the ecological differentiation of meadow, ruderal and forest vegetation. The environmental parameter of soil moisture is characterised by the minimum value of Fisher's criterion (F = 35.3, p < 0.001), the differences between the studied vegetation classes by this factor are not significant.

The analysis of the relationship between the environmental parameters of more than 500 vegetation habitats indicates the presence of a reliable relationship between individual variables. Thus, for soil acidity and nitrogen content, the correlation coefficient is r = 0.80; for temperature and soil acidity, r = 0.55; for temperature and soil moisture, r = -0.51. Thus, the multidimensional ordination of the vegetation of the Ukrainian Roztochya is characterised by a certain degree of orderly structure, which provides for a mathematical procedure for reducing the dimensionality of the ecological and phytocoenotic space and building a typological scheme.

The idea of our further research was to mathematically model the structure of phytocoenoses in the hyperspace of features. Since it is impossible to visually recognise the structure in a multidimensional space, we focused on multidimensional ordination methods. Since the environmental parameters of habitats are correlated with each other, the observed data can be explained by a small number of new variables that are not directly measured but can be obtained through a linear combination of the original data. It allows to reduce the dimensionality of the observation space. Graphically, the calculation procedure is reduced to moving the origin to the centre of the data and rotating the coordinate axes so that the abscissa goes in the direction of the maximum variance of the data set.

Mathematical model 1 reflects the most general typological scheme of vegetation cover at the level of vegetation classes. The results of mathematical modelling (Table 3, Fig. 1) can be represented by the following equations:

$$\mathbf{Root}_1 = 1.805\times L - 0.156\times T - 0.183\times K + 0.189\times F + 0.220\times R + 0.535\times N - 15.157,\ l_1=7.83;$$

$$\mathbf{Root}_2 = -0.834\times L + 0.310\times T + 0.560\times K + 0.026\times F + 0.814\times R + 0.281\times N - 5.307,\ l_2=1.76;$$

Table 2. Ecological parameters of vegetation habitats in the Ukrainian Roztochya

No.*	Association	Environmental parameters, pts.					
		L	T	K	F	R	N
	class *Querco-Fagetea*						
14	*Potentillo albae-Quercetum*	4.93	5.45	4.06	4.73	5.49	4.31
16	*Stellario nemorum-Alnetum glutinosae*	4.19	5.13	3.59	6.52	5.80	6.23
17	*Dentario glandulosae-Fagetum*	3.44	5.36	3.61	5.39	6.15	5.69
20	*Carici pilosae-Fagetum*	3.93	5.97	4.22	5.13	5.21	5.21
27	*Tilio cordatae-Carpinetum betuli*	3.83	5.27	3.54	5.61	6.48	6.04
	class *Vaccinio-Piceetea*						
35	*Cladonio-Pinetum*	6.49	5.32	3.56	4.18	3.53	2.19
37	*Leucobryo-Pinetum*	5.31	4.97	4.21	4.64	2.89	2.61
39	*Festuco ovinae-Pinetum*	6.38	5.40	3.73	4.38	3.73	2.29
40	*Querco roboris-Pinetum*	4.54	5.29	3.93	5.03	4.50	3.87
	class *Molinio-Arrhenatheretea*						
102	*Lolio-Polygonetum arenastri*	7.30	5.91	3.58	5.14	6.64	6.39
104	*Bryo-Saginetum procumbentis*	7.19	5.90	3.37	5.06	7.00	6.36
105	*Prunello-Plantaginetum*	7.16	5.93	3.90	5.37	6.14	6.31
106	*Poetum annuae*	7.04	5.97	4.58	5.55	5.92	7.45
107	*Polygonetum avicularis*	7.20	5.98	4.45	4.80	6.81	6.91
108	*Lolio-Potentilletum anserinae*	7.06	5.92	3.61	5.57	6.47	6.56
120	*Deschampsietum caespitosae*	6.79	5.52	3.67	6.45	6.03	3.83
121	*Alopecuretum pratensis*	7.05	5.33	3.87	5.58	6.28	5.86
122	*Arrhenatheretum elatioris*	7.07	5.61	3.96	5.26	5.95	5.05
123	*Poo-Festucetum rubrae*	7.04	5.72	3.74	5.45	6.15	5.24
125	*Trisetetum flavescentis*	7.15	5.50	3.77	4.55	5.71	4.49
126	*Lolio-Cynosuretum*	6.98	5.35	3.44	5.32	5.76	5.29
127	*Festuco-Cynosuretum*	7.00	5.29	3.86	5.19	5.99	4.79
	class *Artemisietea vulgaris*						
132	*Carduetum acanthoidis*	8.02	5.51	5.24	4.63	7.49	6.76
133	*Echio-Meliloletum*	7.83	5.95	4.84	4.33	7.29	5.32
135	*Leonuro-Arctietum tomentosi*	7.55	5.57	5.26	5.12	7.47	7.63
136	*Balloto-Chenopodietum*	7.57	5.87	4.82	4.87	7.17	6.94
137	*Artemisio-Tanacetum vulgaris*	7.63	5.91	4.84	4.97	7.30	6.72
138	*Sambucetum ebuli*	7.65	5.95	3.78	4.95	7.58	6.85
145	*Polygonetum cuspidati*	7.29	5.97	4.62	5.19	7.11	7.56
	class *Agropyretea intermedio-repentis*						
154	*Agropyretum repentis*	7.31	5.98	5.66	4.67	7.14	6.03
155	*Convolvulo arvensis-Agropyretum repentis*	7.24	5.98	5.34	4.32	7.06	5.80
	Pyrogenic succession						
500	Plant community of the first stage of succession	7.00	5.75	4.22	4.67	7.33	5.93

Note: L - illumination, T - thermal regime, K - continentality, F - moisture regime, R - acidity, N - nitrogen content, pts; * - numbering of syntaxons corresponds to their serial number in the vegetation database of the Ukrainian Roztochya.

$$\mathbf{Root}_3 = 0.004\times L - 0.692\times T + 1.072\times K - 0.756\times F - 0.457\times R + 0.206\times N + 5.102,\ l_3=0.60;$$

where: $Root_i$ – complex gradients of the environment, axes of the typological scheme; L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content; l_i – eigenvalues of vectors.

The first axis of the typological scheme (Fig. 1) explains 76.4% of the total variance. Its values depend mainly on the illumination regime (correlation coefficient r = 0.94), soil pH (r = 0.57), nitrogen content (r = 0.54) and temperature (r = 0.53). The discriminant function $Root_1$ somewhat reflects the ecological features of the formation of dry meadows and synanthropic communities on the site of deforestation, namely, an increase in illumination, temperature, soil pH and nitrogen content. Forest vegetation is characterised by the lowest values of the $Root_1$ function (Fig. 1).

The second axis additionally explains 17.1% of the total variance in the data. Its values depend mainly on nitrogen content (r = 0.74) and soil pH (r = 0.76). Higher values of the discriminant function $Root_2$ are observed in the associations of deciduous forests of the *Querco-Fagetea* class compared to coniferous and mixed forests of the *Vaccinio-Piceetea* class, as well as synanthropic associations of the *Artemisietea vulgaris* and *Agropyretea intermedio-repentis* classes compared to meadow vegetation of the *Molinio-Arrhenatheretea* class. The third discriminant function $Root_3$ explains only 5.8% of the total variance of the data, it depends on soil moisture (r = -0.76).

The similarity of the studied plant community of post-pyrogenic succession to the associations of meadow and synanthropic vegetation can be explained on the basis of graphical visualisation of their location on the typological scheme (Fig. 1) and the distance between points. With a probability of 0.403, the plant community belongs to the *Artemisietea vulgaris class*, with a probability of 0.333 to the *Agropyretea intermedio-repentis* class, and with a probability of 0.265 to the *Molinio-Arrhenatheretea* class.

The heterogeneous grass associations of the *Molinio-Arrhenatheretea* class are often derived from places where natural phytocoenoses have been destroyed (Soroka, 2008). They undergo rapid succession changes as a result of haying, grazing, fertilisation and grass seeding. Mathematical model 2 describes the ecological features of the habitats of the post-pyrogenic succession plant community and 26 associations of meadow vegetation. The results of mathematical modelling (Table 3) can be represented by the following equations:

$$\mathbf{Root}_1 = -0.175\times L - 0.406\times T - 0.812\times K + 1.829\times F + 0.187\times R - 1.459\times N + 2.105, \quad l_1 = 11.268;$$

$$\mathbf{Root}_2 = 0.120\times L - 0.750\times T - 0.825\times K - 1.436\times F + 0.875\times R - 1.559\times N + 18.367, \quad l_2 = 3.88;$$

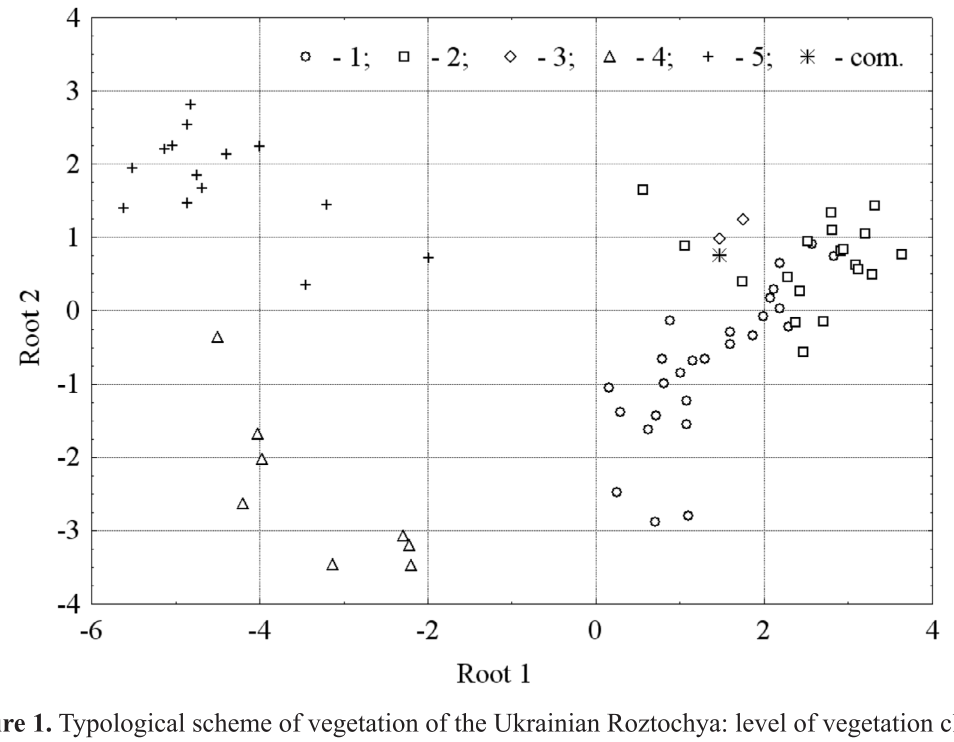

Figure 1. Typological scheme of vegetation of the Ukrainian Roztochya: level of vegetation classes
Vegetation classes: 1 – Molinio-Arrhenatheretea, 2 – Artemisietea vulgaris, 3 – Agropyretea intermedio-repentis, 4 – Vaccinio-Piceetea, 5 – Querco-Fagetea; com. – plant community of the first stage of post-pyrogenic succession.

$$\textbf{Root}_3 = 4.450 \times L + 0.598 \times T + 1.741 \times K + 0.552 \times F + 0.148 \times R - 0.502 \times N - 43.057,$$
$$l_3 = 2.06,$$

where: $Root_i$ – complex environmental gradients, axes of the typological scheme; L - illumination, T - thermal regime, K - continentality, F - moisture regime, R - acidity, N - nitrogen content; l_i - eigenvalues of vectors.

The first axis of the typological scheme explains 55.8% of the total variance. Its values depend mainly on the temperature regime (correlation coefficient r = -0.84), soil moisture availability (r = 0.81), nitrogen content (r = -0.74) and soil pH (r = -0.53). The discriminant function $Root_1$ reflects the differences in the formation of dry and floodplain meadows, namely: with an increase in soil moisture, the nitrogen content and temperature parameter decrease, and soil acidity increases. The maximum values of the $Root_1$ function are observed in the cenoses of wet floodplain meadows: *Molinietum coeruleae, Junco-Molinietum, Epilobio-Juncetum effusi, Junco-Cynosuretum, Scirpetum sylvatici associations*. The studied plant community of the post-pyrogenic succession is characterised by the minimum values of the $Root_1$ function (Table 3) together with the associations *Polygonetum avicularis, Poetum annuae*.

The second axis additionally explains 19.2% of the total variance of the data. Its values depend mainly on the nitrogen content (r = -0.60), soil moisture (r = -0.59) and continentality (r = -0.50). The plant community of post-pyrogenic succession is characterised by drier and richer conditions compared to most meadow communities, and therefore has rather high values of the second discriminant function $Root_2$. The third discriminant function, $Root_3$, explains 10.2% of the total variance of the data and depends on the illumination (r = -0.71).

In general, the studied plant community is located on the periphery of the eco-phytocoenotic space of meadow vegetation of the *Molinio-Arrhenatheretea* class, which is characterised by low values of the $Root_1$ function and high values of the $Root_2$ function (Table 3).

According to the set of environmental parameters (Table 2) and the position on complex environmental gradients (Table 3), it belongs to the Arrhenatheretum elatioris association with a probability of 0.357, and to the Bryo-Saginetum procumbentis association with a probability of 0.206. The Bryo-Saginetum procumbentis association is a ruderal community of mosses and terrophytic herbs, which looks like a pioneer and is formed in places devoid of perennial plants (Soroka, 2008). It forms on trampled places, destroyed lawns, and as a pioneer community in cracks in destroyed asphalt and concrete pavement or on very poor soils. The Arrhenatheretum elatioris association is more likely to form on the site of a fire-damaged community. It is common on rich, fresh turfy soils with good drainage and aeration (Soroka, 2008).

It was also observed that successional processes affected not only plant communities but also microbial biota, particularly fungal assemblages, which are highly sensitive to fire disturbance – a trend confirmed in subtropical peatlands (Tian et al., 2021).

The class *Artemisietea vulgaris* includes communities of nitrophilic mesophyte perennials on rich, well aerated soils (Soroka, 2008). The ecological features of the habitats of 19 associations of this vegetation class are described by mathematical model 3. The results of mathematical modelling (Table 3) can be represented by the following equations:

$$\textbf{Root}_1 = -4.004 \times L - 0.227 \times T - 0.168 \times K - 0.546 \times F - 0.172 \times R - 1.085 \times N + 28.787,$$
$$l_1 = 10.18;$$

$$\textbf{Root}_2 = -1.723 \times L + 7.877 \times T - 0.089 \times K - 0.637 \times F + 0.437 \times R + 0.357 \times N - 35.456,$$
$$l_2 = 5.61;$$

$$\textbf{Root}_3 = -0.014 \times L + 3.107 \times T + 0.953 \times K + 3.191 \times F - 1.768 \times R - 0.824 \times N - 20.900,$$
$$l_3 = 3.58;$$

where: $Root_i$ – complex environmental gradients, axes of the typological scheme; L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content; l_i – eigenvalues of vectors.

The first axis of the typological scheme explains 43.7% of the total variance. Its values depend mainly on illumination (correlation coefficient r = -0.97), soil moisture (r = 0.63), nitrogen content (r = 0.69) and continentality (r = -0.65). The minimum values of the discriminant function $Root_1$ are typical for the associations Berteroetum incanae and Salvio verticillatae-Artemisietum, and the maximum values – for the associations *Alliario-Chaerophylletum* temuli and *Chaerophylletum aromatici*. Berteroetum incanae occupies

Table 3. Habitat typing results

No.	Syntaxon	Root 1	Root 2	Root 3	p**
	Model 1: *level of vegetation classes*				
I	*Molinio-Arrhenatheretea*	1.38	-0.69	-0.85	0.265
II	*Artemisietea vulgaris*	2.62	0.75	0.67	0.403
III	*Agropyretea intermedio-repentis*	1.62	1.12	1.46	0.333
IV	*Vaccinio-Piceetea*	-3.36	-2.43	0.91	0.000
V	*Querco-Fagetea*	-4.30	1.71	-0.32	0.000
500	Com.***	1.47	0.75	0.01	-
	Model 2: *Molinio-Arrhenatheretea*				
102	*Lolio-Polygonetum arenastri*	-3.16	0.34	-0.19	0.082
104	*Bryo-Saginetum procumbentis*	-3.00	0.96	-1.02	0.206
105	*Prunello-Plantaginetum*	-2.94	-0.61	-0.16	0.031
107	*Polygonetum avicularis*	-5.22	-0.64	0.50	0.044
108	*Lolio-Potentilletum anserinae*	-2.64	-0.77	-1.06	0.010
121	*Alopecuretum pratensis*	-1.60	0.38	-0.70	0.075
122	*Arrhenatheretum elatioris*	-1.25	1.52	-0.07	0.357
123	*Poo-Festucetum rubrae*	-1.01	1.21	-0.52	0.080
125	*Trisetetum flavescentis*	-1.60	3.45	-0.27	0.020
126	*Lolio-Cynosuretum*	-1.00	1.51	-1.66	0.025
127	*Festuco-Cynosuretum*	-0.78	2.38	-0.66	0.071
500	Com.	-3.62	1.89	-0.43	-
	Model 3: *Artemisietea vulgaris*				
133	*Echio-Meliloletum*	-2.58	-0.15	-1.35	0.025
136	*Balloto-Chenopodietum*	-0.02	-0.15	-1.02	0.567
137	*Artemisio-Tanacetum vulgaris*	-0.58	-0.03	-0.62	0.346
138	*Sambucetum ebuli*	-0.40	0.50	-2.17	0.025
145	*Polygonetum cuspidati*	1.60	1.06	-0.31	0.034
500	Com.	1.36	-0.25	-2.07	-
	Model 4: *Artemisietea vulgaris + Agropyretea intermedio-repentis*				
136	*Balloto-Chenopodietum*	0.01	-0.22	0.75	0.054
137	*Artemisio-Tanacetum vulgaris*	0.56	-0.23	0.30	0.025
154	*Agropyretum repentis*	0.04	0.76	0.22	0.123
155	*Convolvulo arvensis-Agropyretum repentis*	-0.31	1.24	1.29	0.790
500	Com.	-1.57	-0.14	2.22	-
	Model 5: *Vaccinio-Piceetea + Querco-Fagetea*				
14	*Potentillo albae-Quercetum*	0.04	-1.64	-0.12	0.999
27	*Tilio cordatae-Carpinetum betuli*	4.39	0.00	0.83	0.001
500	Com.	1.85	-2.13	2.08	-
	Model 6: *level of vegetation associations*				
102	*Lolio-Polygonetum arenastri*	-0.25	-1.59	-0.55	0.003
104	*Bryo-Saginetum procumbentis*	0.21	-1.20	-0.74	0.108
105	*Prunello-Plantaginetum*	-1.17	-2.45	0.79	0.000
107	*Polygonetum avicularis*	1.57	-1.24	1.40	0.007
121	*Alopecuretum pratensis*	-3.60	0.45	-0.56	0.000
122	*Arrhenatheretum elatioris*	-4.11	0.26	0.18	0.000
123	*Poo-Festucetum rubrae*	-3.46	-0.59	0.04	0.000
127	*Festuco-Cynosuretum*	-5.33	1.85	-0.43	0.000
133	*Echio-Meliloletum*	0.46	3.31	-1.72	0.000
136	*Balloto-Chenopodietum*	1.89	0.46	-0.26	0.015
137	*Artemisio-Tanacetum vulgaris*	1.78	0.79	-0.73	0.004
138	*Sambucetum ebuli*	2.16	-0.06	-2.24	0.002
145	*Polygonetum cuspidati*	2.60	-1.66	0.94	0.000
154	*Agropyretum repentis*	1.24	1.88	1.67	0.050
155	*Convolvulo arvensis-Agropyretum repentis*	1.04	1.97	1.77	0.811
500	Plant community of the 1st stage of succession	0.25	1.48	0.43	-
	Extrapolation results: forest vegetation				
14	*Potentillo albae-Quercetum*	-5.91	-0.87	8.95	-
27	*Tilio cordatae-Carpinetum betuli*	-7.66	-2.12	5.92	-
17	*Dentario glandulosae-Fagetum*	-4.08	-4.15	13.64	-
20	*Carici pilosae-Fagetum*	-3.89	-6.05	14.62	-
35	*Cladonio-Pinetum*	-11.7	1.28	3.34	-
38	*Molinio-Pinetum*	-15.0	-1.33	3.04	-
39	*Festuco ovinae-Pinetum*	-11.2	1.01	3.81	-
40	*Querco roboris-Pinetum*	-8.79	-2.11	10.64	-
41	*Vaccinio uliginosi-Pinetum*	-16.5	-3.33	6.63	-

Note: $Root_{1-3}$ – axes of the typological scheme, complex environmental gradients; * – numbering of syntaxons corresponds to their serial number in the vegetation database of the Ukrainian Roztochya; ** – probability of the plant community of post-pyrogenic succession belonging to the association; *** Com. – plant community of the first stage of post-pyrogenic succession.

dry roadsides, railway embankments, and Salvio verticillatae-Artemisietum, in addition to roadsides, borders of grain crops, and abandoned fallow land (Soroka, 2008). The *Alliario-Chaerophylletum temuli* and *Chaerophylletum aromatici associations* represent ecotone communities of wet forests and are often common in places of destroyed deciduous forests (Soroka, 2008).

The second axis additionally explains 23.1% of the total variance in the data. Its values depend mainly on the temperature regime (r = 0.90). The third discriminant function, $Root_3$, explains 7.0% of the total variance in the data and depends on soil pH (r = 0.54) and moisture content (r = 0.49). The centre of the ecological space of the *Artemisietea vulgaris* class is occupied by the *Balloto-Chenopodietum* and *Artemisio-Tanacetum vulgaris* associations. With a probability of 0.567 and 0.346, respectively, they belong to the plant community of post-pyrogenic succession (Table 3).

The class Agropyretea intermedio-repentis unites plant communities on dry, compacted soils. Since only 2 associations of this class were identified in the region, its ecological space was studied together with the *Artemisietea vulgaris* class. The results of mathematical modelling (Table 3) can be represented by the following equations:

$$\mathbf{Root}_1 = 4.122\times L + 0.306\times T + 0.240\times K + 0.619\times F - 0.009\times R - 1.053\times N - 29.770,$$
$$l_1 = 9.43;$$

$$\mathbf{Root}_2 = -1.914\times L + 7.351\times T - 0.111\times K - 1.140\times F + 0.259\times R + 0.427\times N - 27.646,$$
$$l_2 = 5.13;$$

$$\mathbf{Root}_3 = -0.540\times L - 4.000\times T - 0.487\times K - 3.240\times F + 1.379\times R + 0.510\times N + 33.033,$$
$$l_3 = 2.85,$$

where: $Root_i$ – complex environmental gradients, axes of the typological scheme; L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content; l_i – eigenvalues of vectors.

The environmental space of the set of associations of the Agropyretea intermedio-repentis and Artemisietea vulgaris classes (model 4) generally repeats the patterns of formation of the Artemisietea vulgaris class (model 3), but in the mirror image. Thus, the first axis of the typological scheme explains 44.5% of the total variance. Its values depend mainly on illumination (correlation coefficient r = 0.96), soil moisture (r = -0.60), nitrogen content (r = -0.65) and continentality (r = 0.62). The maximum values of the discriminant function $Root_1$ are typical for the associations *Berteroetum incanae* and *Salvio verticillatae-Artemisietum*, and the minimum values – for the associations *Alliario-Chaerophylletum temuli* and *Chaerophylletum aromatici*. In fact, similar conclusions were obtained as in the previous model, but the correlation coefficients have the opposite sign.

The second discriminant function, $Root_2$, additionally explains 24.1% of the total variance in the data. Its values depend mainly on the temperature regime (r = 0.88). The third discriminant function, $Root_3$, explains 13.5 per cent of the total variance in the data, and depends on soil pH (r = 0.38) and moisture content (r = -0.57). The center of the environmental space of the set of associations of the *Agropyretea intermedio-repentis* and *Artemisietea vulgaris* classes is also occupied by the *Balloto-Chenopodietum* and *Artemisio-Tanacetum vulgaris* associations (Table 3). The associations of the *Agropyretea intermedio-repentis* class – *Agropyretum repentis* and *Convolvulo arvensis-Agropyretum* repentis – occupy a close position to them, but differ in slightly higher values of the second discriminant function $Root_2$. The plant community of the post-pyrogenic succession belongs to the Convolvulo arvensis-Agropyretum repentis association with a probability of 0.790, and to the Agropyretum repentis association with a probability of 0.123 (Table 3).

The plant community of the post-pyrogenic succession differs significantly in its environmental parameters from the associations of forest vegetation of the Vaccinio-Piceetea and Querco-Fagetea classes (Fig. 1, Table 1). However, theoretically, in the absence of anthropogenic impact, forest vegetation should be restored in the place of dry meadows. In this case, mathematical model 5 provides an opportunity to predict the direction of dynamics of the post-pyrogenic plant community. The results of mathematical modelling (Table 3) can be represented by the following equations:

$$\mathbf{Root}_1 = -0.957\times L - 0.161\times T + 0.521\times K + 0.020\times F + 0.512\times R + 1.744\times N - 6.915,$$
$$l_1 = 17.53;$$

$$\mathbf{Root}_2 = -0.094\times L - 0.556\times T + 1.246\times K + 2.467\times F - 0.106\times R + 0.013\times N - 14.350,$$
$$l_2 = 6.47;$$

$$\mathbf{Root}_3 = 1.004\times L - 1.291\times T - 2.812\times K + 0.292\times F + 0.965\times R - 0.500\times N + 8.876,$$
$$l_3 = 1.96;$$

where: $Root_i$ – complex environmental gradients, axes of the typological scheme; L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content; l_i – eigenvalues of vectors.

The first axis of the $Root_1$ typological scheme explains 62.7% of the total variance. Its values depend mainly on nitrogen content (correlation coefficient r = 0.99), soil pH (r = 0.90) and illumination (r = -0.89). The discriminant function $Root_1$ reflects the differences in the formation of coniferous and broadleaf forests. The minimum values of the $Root_1$ function are characterised by pine forests on poor soils of the *Cladonio-Pinetum* ($Root_1$ = -6.42) and *Festuco ovinae-Pinetum* ($Root_1$ = -5. 95), and the highest – beech and oak forests of the associations *Dentario glandulosae-Fagetum* ($Root_1$ = 5.29), *Tilio cordatae-Carpinetum betuli* ($Root_1$ = 4.39), *Mercuriali-Fagetum* ($Root_1$ = 4.16).

The second axis additionally explains 23.1% of the total variance of the data. Its values depend mainly on soil moisture (r = 0.97). The minimum values of the $Root_1$ function are characterised by pine forests on dry soils of the *Cladonio-Pinetum* ($Root_2$ = -3.52) and *Festuco ovinae-Pinetum* ($Root_2$ = -2.87) associations, and the maximum values are characterised by pine forests on wet soils of the *Vaccinio uliginosi-Pinetum* ($Root_2$ = 5.05) and *Molinio-Pinetum* ($Root_2$ = 3.73) associations. The third discriminant function, $Root_3$, explains 7.0% of the total variance in the data and depends on continentality (r = -0.74).

In general, the studied plant community of post-pyrogenic succession is located on the periphery of the environmental and phytocoenotic space of forest vegetation, in the fourth quarter of the typological scheme, which is characterised by relatively high values of the $Root_1$ function and low values of the $Root_2$ function (Table 3). According to the set of environmental parameters (Table 2) and the position on the complex environmental gradients (Table 3), it belongs to the *Potentillo albae-Quercetum* association with a probability of 0.999, and to the Tilio cordatae-Carpinetum betuli association with a probability of 0.001. The *Potentillo albae-Quercetum* association is a thermophilic oak forest that occupies the southern and southwestern macro-slopes of the region on rich, loose soils (Soroka, 2008). The Tilio cordatae-Carpinetum betuli association is the most widespread type of broadleaf phytocoenosis in the region, being the final, homeostatic type in the succession of forest vegetation (Soroka, 2008).

Since this study was conducted in the Roztochya region, it is important to consider the botanical specificity of the area, thoroughly described by Soroka (2008), who characterized the vegetation of the Ukrainian Roztochya.

The mathematical modelling of the environmental and phytocoenotic space of different vegetation classes identified plant associations that could be used for post-pyrogenic succession of dry meadow. These associations formed the basis for the final stage of complex environmental gradients modelling. After considering several variants of mathematical modelling, forest vegetation was excluded from the calculation procedure. The position of the forest vegetation associations compared to the post-pyrogenic succession vegetation was determined by extrapolation. The results of mathematical modelling (Fig. 2, Table 3) can be represented by the following equations:

$$\mathbf{Root}_1 = 0.067\times L + 2.914\times T + 0.315\times K - 0.986\times F + 1.433\times R + 1.478\times N - 32.978, \quad l_1=6.17;$$

$$\mathbf{Root}_2 = 1.221\times L - 4.093\times T + 0.962\times K - 0.991\times F + 1.584\times R - 1.300\times N + 13.118, \quad l_2=2.66;$$

$$\mathbf{Root}_3 = -3.950\times L + 2.012\times T + 1.217\times K - 0.705\times F - 1.103\times R + 0.532\times N + 19.593, \quad l_3=1.49;$$

where: $Root_i$ – complex environmental gradients, axes of the typological scheme; L – illumination, T – thermal regime, K – continentality, F – moisture regime, R – acidity, N – nitrogen content; l_i – eigenvalues of vectors.

The first axis of the $Root_1$ typological scheme explains 53.9 % of the total variance and reflects the main features of the post-pyrogenic succession of the dry meadow plant community. Its values depend mainly on soil pH (correlation coefficient r = 0.82), nitrogen content (r = 0.77), and temperature (r = 0.71). It reflects the complex gradient of the environment of the Molinio-Arrhenatheretea, Artemisietea vulgaris and Agropyretea intermedio-repentis vegetation classes: with increasing illumination, the parameters of the thermal regime, nitrogen content and soil pH increase, while there is a tendency to decrease the soil moisture availability. The minimum values

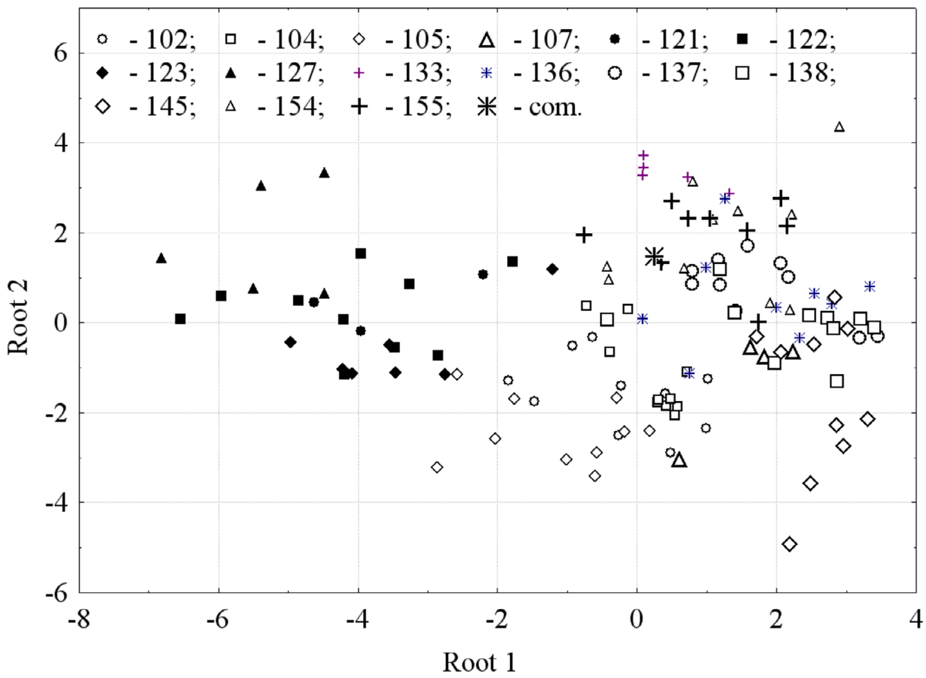

Figure 2. Typological scheme of the vegetation of the Ukrainian Roztochya: level of associations
The numbering of associations corresponds to Table 3; com. is the plant community of the first stage of post-pyrogenic succession.

of the discriminant function $Root_1$ are typical for the most common meadow vegetation association Arrhenatheretum elatioris in the region, as well as the most common broadleaf forest association *Tilio cordatae-Carpinetum betuli*. The decrease in the values of the first discriminant function $Root_1$ reflects the direction of restoration of natural vegetation in place of dry meadows (Table 3).

The second axis, $Root_2$, additionally explains 23.2% of the total variance of the data. Its values depend mainly on continentality (r = 0.60), soil moisture (r = -0.54) and nitrogen content (r = -0.45). The third discriminant function, $Root_3$, explains 13.0% of the total variance in the data, and depends on continentality (r = 0.57) and light (r = -0.50). With a probability of 0.811, the plant community of the first stage of post-pyrogenic succession belongs to the *Convolvulo arvensis-Agropyretum* repentis association (Table 3). This association includes communities of dry, heavily trampled ruderal habitats.

Typological schemes of different classes of vegetation of the Ukrainian Roztochya based on mathematical models of multidimensional ordination allow determining the position of any plant associations on the axes of complex environmental gradients, including different stages of post-pyrogenic succession, and predicting the dynamics of vegetation cover due to anthropogenic impact.

CONCLUSIONS

Based on the obtained results, the following conclusions were drawn:

1. The floristic composition of the post-fire meadow at the first stage of post-fire succession includes meadow, segetal, ruderal and forest species. These vegetation types are the most likely to develop in the direction of the plant community. The restoration of vegetation cover will largely depend on the nature and intensity of anthropogenic impact.
2. Based on the one-factor analysis of variance, the significant importance of illumination, soil acidity and nitrogen content for the ecological differentiation of meadow, ruderal and forest vegetation was established.
3. In the case of promoting the restoration of meadow vegetation on the site of the community destroyed by fire, the Arrhenatheretum elatioris association has a better chance of forming.
4. In the ecological and phytocoenotic space of ruderal vegetation, the associations Convolvulo arvensis-Agropyretum repentis, Agropyretum repentis, Balloto-Chenopodietum and Artemisio-Tanacetum vulgaris are most likely to form on the site of the plant community destroyed by fire.

5. The restoration of forest vegetation through the promotion of natural regeneration or the creation of forest crops is likely to occur with the formation of Potentillo albae-Quercetum and Tilio cordatae-Carpinetum betuli associations.
6. The main feature of the transformation of dry meadow habitat after the fire is the following structure of interrelationships of environmental factors: with increasing illumination, the parameters of thermal regime, nitrogen content and soil pH increase, while there is a tendency to decrease soil moisture availability.

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