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ROLE OF COENOTIC RELATIONS IN THE FORMATION OF PLANT COMMUNITIES (ON THE EXAMPLE OF THE LOWER LAYERS OF FORESTS OF THE NORTH-EAST OF UKRAINE)

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Abstract

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The article focuses on the study of associativity and conjugation of 20 plant species of live ground cover of broad-leaved forests in the North-East of Ukraine. Two groups such as cenosis forming species and species-intruders were determined based on the research findings. The first group (cenosis forming species) includes species with high occurrence and abundance. They are characterized by mutual positive associativity that reveals a significant trend towards common growth. The second group consists of species with negative associativity both among themselves and the species of the first group.

Key words: broad-leaved forest; live ground cover; cenogenesis; associativity; conjugation of species

Introduction

The beginning of the twentieth century was marked by the formation of two opposite points of view regarding the formation of plant communities. According to F. Clements and V. M. Sukachov, they are the integrities, formed on the basis of active coenotic relations among the species which comprise them, and according to H. Gleazon and L. G. Ramenskiy, they are the segments of the vegetation continuum within which plant species are organized by the differentiation of ecological niches (Trass, 1976).

Over the past few decades, a great number of works, showing that the interaction of plants is one of the most important components of cenogenesis, have been appeared in the Ukrainian and foreign geobotanical literature. The confirmation of this view comes from the arrangement of a special discussion about the mechanisms of cenogenesis or, as they are sometimes called, "assembly rule", by one of the leading journals in the field of vegetation science "Journal of Vegetation Science" in 1994-1995 on the initiative of B. Wilson and E. van der Maarel (Solodukhina, 2010; Devis et al., 2015; Maarel et al., 1995; Wilson et al., 1994; Wilson et al., 1995). Thus, the definition of role of coenotic relations in the formation of plant communities is an important scientific problem.

The live ground cover of broad-leaved forests with high species diversity, vegetation mosaic, sufficient length of forest gradients (Whitmore, 1982) acts as a convenient object to decide the issues of the role of coenotic relations in the formation of plant communities. Our research goal was to study the associativity of plants and their role in cenogenesis of the lower layers of forests of the North-East of Ukraine, which comprise the live ground cover in the forests, experiencing minimal anthropogenic load due to long stay (since 1974) in protected areas.

Materials and Methods

Our research was conducted in the forests of the North-East of Ukraine. The general characteristics of this region

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are presented in the works of Ya. P. Didukh and I. B. Sukhuy (Didukh and Sukhuy, 1984). The geobotanical descriptions are limited to the mixed broad-leaved forests, the forest-forming species of which are presented by *Acer platanoides L.*, *Tilia cordata* Mill., *Ulmus glabra Huds*., *Quercus robur* L., *Fraxinus excelsior L.* and *Betula pendula Roth* occur in the forests in addition to the dominant species. The herb layer of the forests is represented by the species which are typical for broad-leaved forests. In the forest reserve there are relic species for the region *Festuca altissima All.* and *Matteuccia struthiopteris (L.)* Tod., and the Red Book species such as *Lunaria rediviva L., Allium ursinum L.*

900 sampling plots of 1m x 1m were laid in order to establish relationships between the plant species of the live ground cover. The plots were laid in a random way. All plant species growing on each plot of 1 m^2 were recorded. The projective cover of all plant species was determined within these plots. In most cases, the perennials such as *Aegopodium podagraria* L., *Asarum europaeum* L., *Stellaria holostea* L., *Galium odoratum* Scop., *Polygonatum multiflorum* (L.) All., *Glechoma hederacea* L., *Urtica dioica* L. were the main cenosis forming plant species of 41 vascular plant species identified in the live ground cover. They seem to "conserve" cenosis forming relationships that develop over several years of joint growth in the same block group. This makes them the most informative ones in the study of coenotic relations in the layer of the live ground cover.

Cenotic relations among species were estimated in two independent ways: by finding associativity and defining conjugation (in understanding of O.O. Uranov (Uranov, 1935; 1955). Associativity was calculated based on the ratio of *Ass* with the usual notations of four-column table:

$$Ass = \frac{a - b - c}{a + b + c},$$

where: a is the number of cases of common occurrence of A and B species; b – is the number of cases of common occurrence of A species; c – is the number of cases of common occurrence of B species.

The ratio of *Ass* has some advantages over other ratios of associativity: it is symmetric, and adequately reflects the ability of species to grow together or to avoid each other. The conjugation of plants was calculated by the method of O. O. Uranov (Uranov, 1955) in the form of regression of projective cover of the subordinate species with increase in cover of the existing species. In this form associativity reveals the nature and extent of interaction of the species growing together. In the modern sense, (Zlobin, 2009) associativity is the regression of one species to another. Species with the highest occurrence and abundance are always chosen as the existing species.

Coenotic prosperous species are mainly involved in the analysis (Didukh, 1982). Associativity and conjugation of species with low occurrence (less than 2%) and projective cover are largely statistically inaccurate, so we do not consider them. The computer program ASS (developed by Yu. A. Zlobin) to determine associativity and the program TableCurve of the company Jandel Scientific, version 2.03 to determine conjugation were used as well.

Results and Discussion

The research covers 20 plant species of the live ground cover. Table 1 shows the results of the calculation of associativity. Two groups such as cenosis forming species and species-intruders can be picked out of the main species of the live ground cover. The first group (cenosis forming species) includes species with high occurrence and abundance (*Aegopodium podagraria, Asarum europaeum, Stellaria holostea, Polygonatum multiflorum, Glechoma hederacea, Pulmonaria obscura* Dumort., *Lamium maculatum* (L.) L., *Viola mirabilis* L.). They are characterized by mutual positive associativity that reveals a significant trend towards common growth. The second group consists of species with negative associativity both among themselves and the species of the first group (*Actaea spicata* L., *Brachypodium sylvaticum* (Huds.) Beauv., *Adoxa moschatellina* L., *Mercurialis perennis* L., *Orobus vermis* (L.) Bernh., *Galium odoratum, etc.).*

The first group acts as cenosis forming one, and the second group includes the species-intruders that occupy free ecological niches and compete for them both with cenosis forming species and with each other. Intermediate coenotic tactics is typical for *Caгex pilosa* Scop. The actual material obtained generally confirms the D. Tilman's idea (Tilman, 1988) of the individual nature of interspecific plant relations as opposed to the opinion, which limits the diversity of plant relations to any diffuse competition in general. The discrepancy in the relationship of cenosis forming species and intruders is illustrated in Figure 1, which shows that the first group of species is characterized by the presence of a full range of associations with other components of aggregation – from strong repulsion to strong interdependence. Species-intruders, on the contrary, are marked by associations that lie entirely in the zone of negative values of the ratio of associativity.

Definition of species conjugation has allowed us to detail the nature of the relationship between the plants of the live ground cover (Table 2).

Table 1
Associativity of the main species of live ground cover

Species	Occurence in %	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Aegopodium podagraria L.	98.8	X																			
Asarum europaeum L.	97.8	0.978	X																		
Stellaria holostea L.	87.8	0.775	0.753	X																	
Polygonatum multiflorum (L.) All.	87.8	0.733	0.711	0.551	X																
Glechoma hederacea L.	86.7	0.753	0.773	0.609	0.489	X															
Pulmonaria obscura Dumort.	82.2	0.622	0.682	0.517	0.477	0.663	X														
Lamium maculatum (L.) L.	78.9	0.596	0.614	0.371	0.371	0.548	0.625	X													
Urtica dioica L.	76.7	0.551	0.528	0.364	0.326	0.419	0.287	0.415	X												
Viola mirabilis L.	71.1	0.438	0.455	0.365	0.326	0.302	0.366	0.293	0.023	X											
Geum urbanum L.	61.1	0.236	0.25	0.08	0.116	0.167	0.146	0.36	0.351	0.013	X										
Carex pilosa Scop.	51.1	0.034	0.045	0.125	-0.093	0.139	0.038	-0.214	-0.326	0.056	-0.475	X									
Geranium robertianum L.	48.9	-0.044	-0.067	-0.205	-0.036	-0.163	-0.19	-0.125	0.096	-0.3	-0.088	-0.568	X								
Dentaria bulbifera L.	47.8	-0.034	-0.023	-0.06	-0.163	0.025	0.039	-0.144	-0.165	-0.291	-0.278	-0.403	-0.303	X							
Galium odoratum (L.) Scop.	47.8	-0.067	-0.089	-0.095	-0.095	-0.218	-0.341	-0.286	-0.235	-0.221	-0.907	-0.549	-0.303	-0.676	X						
Orobus vernus L.	40	-0.191	-0.213	-0.125	-0.229	-0.185	-0.317	-0.482	-0.5	-0.26	-0.605	-0.647	0.216	-0.41	-0.127	X					
Mercurialis perennis L.	40	-0.191	-0.182	-0.229	-0.326	-0.185	-0.25	-0.358	-0.407	-0.222	-0.507	-0.612	-0.071	-0.322	-0.322	-0.222	X				
Adoxa moschatellina L.	13.3	-0.73	-0.753	-0.725	-0.725	-0.831	-0.877	-0.872	-0.718	-0.797	-0.906	-0.76	-0.811	-0.843	-0.5	-0.797	-0.659	X			
Brachypodium sylvatica (Huds.) Beauv.	6.7	-0.865	-0.864	-0.848	-0.848	-0.873	-0.838	-0.861	-0.826	-0.91	-0.86	-0.826	-0.878	-0.822	-0.87	-0.91	-0.846	-0.882	X		
Stellaria media (L.) Vill.	5.6	-0.888	-0.886	-0.9	-0.873	-0.872	-0.865	-0.889	-0.886	-0.877	-0.966	-0.958	-0.875	-0.867	-0.957	-0.877	-0.897	-0.875	-1	X	
Actaea spicata L.	2.2	-0.955	-0.955	-0.975	-0.975	-0.949	-0.973	-0.944	-0.942	-0.969	-0.927	-0.956	-0.957	-0.955	-0.907	-0.969	-0.889	-0.846	-1	-1	X

Table 2
Conjugation of the main species of live ground cover

Species	b	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Aegopodium podagraria L.	0.25	X																			
Asarum europapeum L.	0.191	∩	X																		
Stellaria holostea L.	0.03	∩	∩	X																	
Polygonatum multiflorum (L.) All.	0.099	↗	∩	↘	X																
Glechoma hederacea L.	0.089	↗	↗	↗	∩	X															
Pulmonaria obscura Dumort	0.049	∩	∩	↗	↗	∩	X														
Lamium maculatum (L.) L.	0.069	↗	↗	↘	↗	↗	∩	X													
Urtica dioica L.	0.112	↘	↗	1	∩	↘	∩	1	X												
Viola mirabilis L.	0.164	↗	↗	1	↗	1	1	↗	1	X											
Geum urbanum L.	0.023	↘	↗	↗	↘	↗	↘	↗	↗	1	X										
Carex pilosa Scop.	0.066	↗	∩	↗	↘	∩	∩	↘	↘	1	1	X									
Geranium robertianum L.	0.06	↘	1	↘	↗	1	1	1	1	↘	1	↘	X								
Dentaria bulbifera L.	-0.008	↘	↗	↗	↗	↗	↗	↗	↗	↘	↗	1	1	X							
Galium odoratum (L.) Scop	-0.049	↘	∩	↘	↗	↘	↘	↘	↘	1	↘	↘	↗	1	X						
Orobus vernus L.	0.051	↗	↘	1	↗	↗	1	1	↘	↗	1	1	1	↗	↗	X					
Mercurialis perennis L.	0.037	∩	∩	∩	1	↘	↗	↘	↘	↗	↘	1	↘	↗	↗	↗	X				
Adoxa moschatellina L.	0.057	↘	↗	↘	↗	1	↗	↘	↘	↗	1	↘	1	1	↗	1	1	X			
Brachypodium sylvatica (Huds.) Beauv.	-0.001	↗	↗	1	↗	↗	↗	↗	↘	↘	↗	↘	1	↗	↗	1	↗	↘	X		
Stellaria media (L.) Vill.	0	↗	↘	↗	1	1	1	↗	↘	1	1	1	1	1	1	1	1	1	1	X	
Actaea spicata L.	0	↗	↘	1	1	↘	1	1	1	1	1	↘	↘	↘	↗	↘	↗	1	1	1	X

Note: ∩ – double-valued conjugation; ↘ – negative; ↗ – positive; 1 – neutral), b –coefficient - extent of response to the general background of "Diffuse Competition"

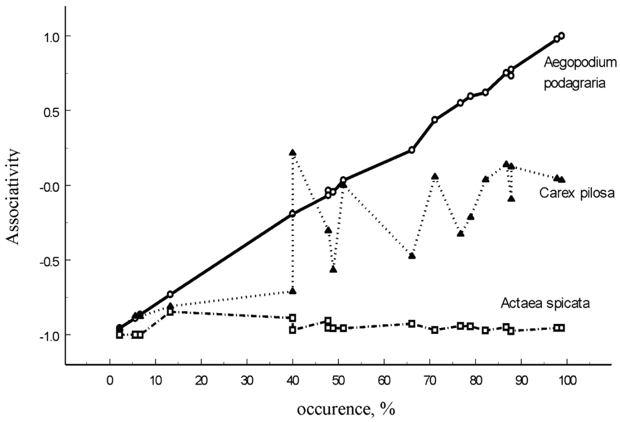

Fig. 1. Associativity of cenosis forming species (*Aegopodium podagraria* L.), intermediate species (*Carex pilosa* Scop.) and species-intruder (*Actaea spicata* L.) in the live ground cover

It has been found that cases with positive, negative and neutral species conjugation comprise about the same percentage (34.2 percent, or 25.3%, 31.0%, respectively). Double-valued conjugation has been found in 9.5% of cases. The nature of the relationship of species is always individual.

So, 4 cases of double-valued conjugation were defined for *Aegopodium podagraria*: 9 – positive, 6 – negative; for *Carex pilosa* – 3 – double-valued, 2 – positive, 8 – negative and 6 – neutral. Neutral conjugation is often observed among the species-intruders with low occurrence.

A sufficiently large actual material on changes in projective cover of 20 species of herbaceous plants was used to test the hypothesis about diffuse competition (Giller, 1988) as the main controller of abundance of species in plant communities. Variability of projective cover of each studied species was separately determined by the gradient of change in the total projective cover of the live ground cover. In this case, the curves of conjugation were approximated by a straight line, and the ratio "b" in the equation $y = a + bx$ was the degree of reaction of species to the general background of "diffuse competition". It has been revealed (Table. 2) that only 3 of 20 species (*Dentaria bulbifera* L., *Galium odoratum, Brachypodium sylvaticum*) perceive a diffuse background of the live ground cover, which has a competitive impact on them. This background was neutral for two species (*Stellaria media* (L.) Vill., *Actaea spicata*) and positive for the other 15 species (75%): with increase in the total projective cover of each of these species.

This can be seen as a high adaptability of the studied species to the ecological and coenotic conditions of the lower layer of broad-leaved forests. Thus, the concept of diffuse competition is not confirmed with respect to the live ground cover of broad-leaved forests. In the first stages plant communities are formed by means of differentiation of plant species by ecological niches, but due to the high similarity of requirements of all plants for the light, water and mineral nutrients, and all in all, it is the active interactions of species with each other that determine the floristic composition of phytocenoses and their composition. P. Grubb's opinion is obviously just (Devis et al., 2015) that during the study of phytocenotic effects simple theories are gradually being replaced by integrated, more realistic ones and the theories which are more appropriate for the complex nature of plant communities.

A high proportion of positive interactions among plant species and their response to the general coenotic background (as in the case of pair interactions of species of live ground cover of the forest) is not unexpected. In recent years, a number of researchers have drawn attention to the importance of relationships for facilitation of cenotic processes (Zlobin, 1994; Bertness and Callaway, 1995; Hunter and Aarssen, 1988). G. Brooker and T. Callighan consider the study of this type of plant relationship to be "unfairly ignored branch of ecology" (Brooker and Callighan, 1998).

Conclusions

The curves of conjugation indicate that a specific type of relationship is characteristic of each pair of species. The response of herbaceous plants to the general coenotic background of herbaceous-subshrub layer is mainly positive. This type of response occur in 75% of the studied plant species in the forest communities, which indicates the identified adaptation of the herbaceous plants to joint growth.

The main peculiarity of coenotic relationships between the species of herbaceous-subshrub layer lies in the fact that they occur against the background of the pronounced edificator action of the upper layers of the forest communities – trees and shrubs. Such relationships are fundamentally distinguished from the relationships established between the herbaceous-subshrub plants of meadows and steppes.

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