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THE FORMATION AND STRUCTURE OF CLONES OF FOREST HERBS IN ECOSYSTEMS OF NORTH-EASTERN UKRAINE

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Summary

The clonal structure of forest herbs of north-eastern Ukraine, such as *Aegopodium podagraria* L., *Asarum europaeum* L., *Carex pilosa* Scop., *Stellaria holostea* L., has been examined using the total mapping method. The regularities of changes within the radii of clones, density of partial bushes and their age have been found out. The author has suggested an original statistical and graphical method which allows to estimate age state of each clone and make its land zoning.

Keywords

forest herbs • populations • clones • partial bush • age state

1. Introduction

There are three main types of reproduction in forest plants: sexual, asexual and vegetative. Sexual and vegetative reproduction can occur in seed plants. There are often specific situations where certain types of plants are dominated by one of these two types of reproduction. Vegetative reproduction often predominates in forest herbs.

Vegetative reproduction is common among forest herbs. It compensates for possible low efficiency of sexual reproduction in forest ecosystems with high species saturation and intense competition. Vegetative reproduction evolutionary proved to be useful in connection with immobility of vegetative organisms and frequent cases of alienation of their aerial parts by any phytophagous. Under these conditions, the ability to re-growth turned to be an important adaptation for survival. In this regard, G.Y. Levina [1981] noted that vegetative reproduction in plants essentially performs two functions: firstly, it ensures the longevity of the species existence due to re-growth and, secondly, increases the number of species in ecosystem (actually reproduction). Vegetative reproduction has other progressive feature as well. Young new species in vegetative reproduction are better provided with all kinds of resources through relations with the parent plants, and therefore their survival is much higher than in young plants, originating from diaspores of sexual reproduction.

Length of the respective structures (rhizomes, roots with tillers, tendrils and the like), their ability to branching and depth [Bell 1980] are of importance, when evaluating vegetative reproduction.

All kinds of vegetative mobile plants are characterized by the formation of clones, which are a population of ramets – descendants of one genet. Due to the clonal formation, these plants are more competitively sustainable, capable of capturing the space and holding it for long, preventing other plant species from populating the clone area. Cloning benefits from succession changes in forest phytocenoses. The stability of clones is largely determined by the fact that in the early stages of the ramet formation they receive the necessary organic matters from genet, and therefore are much more stable than regular shoots and sprouts. Thus, the structure of clones, the rate of their formation and stability are not the same [Korovkin 2002] in clone plants with different ways of vegetative reproduction (rhizomes, mustache, stolons, root sprouts, etc.).

2. Objects and methods of the study

The studies were conducted in forest ecosystems of the north-east of Ukraine. A detailed analysis of the clone formation and structure was made for the following model group of grasses: *Aegopodium podagraria L., Asarum europaeum L., Carex pilosa Scop., Stellaria holostea L.* The list and main features of the phytocoenoses in which the clones of the model plants of grass and subshrub layer have been studied, are shown in Table 1.

Table 1. Brief geobotanical characteristics of forest associations with participation of herb and shrub layer dominants

Number and name of association	Stand composition	Stand density	Average stand age [year]	Average stand height [m]	Average projective cover of dominant [%]
Aegopodium podagraria					
I. Quercetum coryloso-aegopodiosum	6Q4P	0.7	79	27	55
II. Querceto-Pinetum coryloso-aegopodiosum	7P3Q	0.6	61	27	60
III. Betuleto-Pinetum coryloso-aegopodiosum	6P4B+Q	0.8	53	24	55
Asarum europaeum					
I. Quercetum coryloso-asarosum	8Q2P+B	0.7	65	23	60
II. Pinetum coryloso-asarosum	9P1Q+B	0.8	68	24	50
III. Querceto-Pinetum asarosum	6P4Q	0.5	59	22	65
Carex pilosa					
I. Querceto-Pinetum caricosum (pilosae)	6P4Q	0.6	48	20	65
II. Quercetum coryloso-caricosum (pilosae)	8Q2P	0.7	53	21	60
III. Betuleto-Quercetum coryloso-caricosum (pilosae)	6Q4B	0.8	55	23	50

Stellaria holostea						
I.	Querceto-Pinetum coryloso-stellariosum	7P3Q+B	0.6	52	22	55
II.	Quercetum coryloso-caricoso (pilosae)-stellariosum	8Q2P	0.7	55	24	50
III.	Querceto-Pinetum stellariosum	6P4Q	0.5	51	21	60

Explication: Q – *Quercus robur* L., P – *Pinus sylvestris* L., B – *Betula pendula* Roth.

Source: author's study

Source: https://yandex.ua/images

Fig. 1. The territory of the investigations

Overall, from 20 to 30 clones were investigated for each species (Figure 1). From four to six clones of each species (Figure 2) were selected as the most typical ones of the region of the studies.

Aegopodium podagraria L.

Asarum europaeum L.

Stellaria holostea L.

Carex pilosa Scop.

Photos by Kovalenko

Fig. 2. The species

The study of the clones of plant populations of forest herbs in north-eastern Ukraine was conducted by total mapping of the area occupied by clone. The area was divided into squares (50 × 50 cm). For each square horizontal projection was made, on which the location of partial bushes of the investigated species, their number and age state of each were indicated. After that, the litter and surface soil were removed, and the position of rhizomes was marked in the scheme being made.

Clones are significantly different from each other by the ratio of partial bushes of different age, and location of bushes of different age is not accidental within each clone. To estimate the total age state of clones the author has developed three new indexes: the index of recovery ($I_{rec.}$), the index of aging ($I_{ag.}$) and the index of generativity ($I_{generat.}$), based on the theory of M.V. Glotova [1998]. They were calculated according to the following formulas:

The index of recovery as the ratio of pre-generative partial bushes to their total number:

$$I_{\text{rec.}} = \frac{\sum_{i=1}^{p-v} n_i}{\sum_{i=1}^{p-s} n_i} \cdot 100$$

where:

p... s – age state of partial bushes in standard designations.

The index of aging as the ratio of partial bushes of age state *g3, ss* and *s* to their total number:

$$I_{\text{ag.}} = \frac{\sum_{i=1}^{g_3-s} n_i}{\sum_{i=1}^{p-s} n_i} \cdot 100$$

The index of generativity as the ratio of number of generative partial bushes to their total number:

$$I_{\text{generat.}} = \frac{\sum_{i=1}^{g_1-g_3} n_i}{\sum_{i=1}^{p-s} n_i} \cdot 100$$

3. Results of the study and their discussion

3.1. *Aegopodium podagraria*

The study of *A. podagraria* clones was made in three associations (Table 1).

Vegetative reproduction plays the main role in self-recovery of *A. podagraria* populations in the forests of north-eastern Ukraine. The result is a spatial arrangement of partial shoots around female parent. A special structural element (clone) is consequently created. *A. podagraria* clone consists of ramets that represent rosette-like partial shoots, parts of which are connected by living rhizomes, and the rest are independent after rhizome digestion.

In all investigated forest types, glague cover is solid due to the closure and convergence of clones. But in some places it was possible to find *A. Podagraria* clones, fairly isolated from each other. They had a round or ameboid form. The five clones were described in various associations of about the same size within a radius of 8 to 14 m each.

The analysis of counting the number of *A. podagraria* partial bushes on the investigated patches within a radius of clone from its centre to the periphery has shown (Figure 1a, b) that the density of partial bushes throughout the clone area is about the same with a slight tendency of its decline from 58 to 53 bushes per square meter to the periphery of clone, which corresponds to the regression equation, given by: $y = 57.7 - 0.2x$. Thus, *A. podagraria* clones by structure are, in the understanding of A. Zlobin [1997], clones-fields. These clones are evenly filled with partial bushes. The average density of partial bushes, characteristic of the investigated forest associations, is at a level of 45–70 pieces · m^{-2}.

The results of these calculations are shown in Table 2.

Clones No. 4 and No. 1 can be estimated as young: they are absolutely dominated by partial bushes of pre-generative age state that constitute more than 50%. Clones No. 2 and No. 3 are middle-aged. These two clones have the highest generativity (over 60%), and pre-generative and post-generative bushes in equal parts. Of all studied clones, Clone No. 5 is the oldest one: it has the highest index of aging, and reduced generativity in comparison with the middle-aged clones.

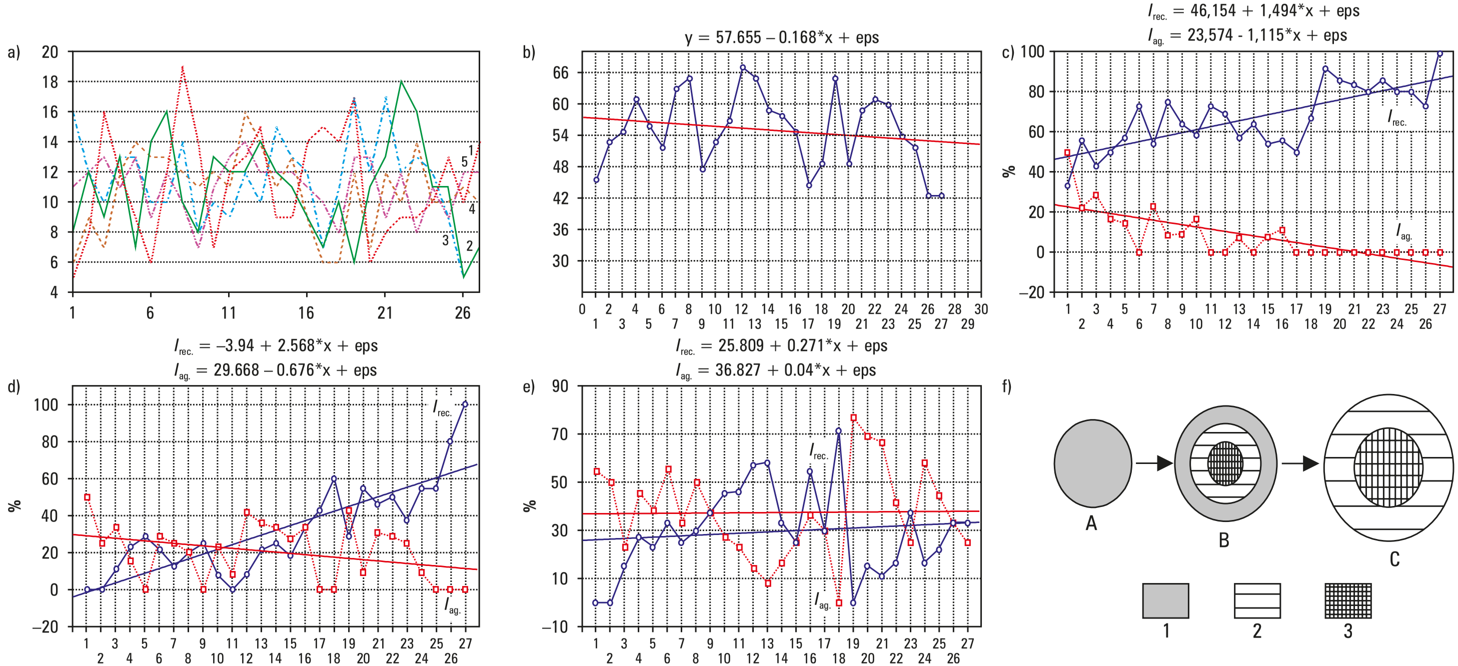
Table 2. Age state of *A. podagraria* clones in forest associations of north-eastern Ukraine

Clones	$I_{rec.}$	$I_{ag.}$	$I_{generat.}$
1	61.3	12.5	31.8
2	29.9	20.8	65.3
3	26.2	16.5	65.4
4	67.8	7.3	29.8
5	28.9	37.5	54.2

Source: author's study

A certain regularity was observed in distribution of partial bushes of *A. podagraria* in clones area. Young clones (clone No. 4 is taken as an example, Figure 3) are dominated by pre-generative partial bushes, the regression line for the index of recovery is higher than the regression line for the index of aging. Pre-generative partial bushes, in comparison with partial bushes of other age-related conditions, mostly occur throughout the area of clone, and they obviously predominate in the peripheral area of a clone. Bushes of age status *g3* (subsenile and senile) are not available at the periphery of a clone. They occur in small numbers only in the central zone of clone.

The older clones that can be evaluated as middle-aged (clone No. 2, Figure 3d) are characterized by intersection of the regression lines for the index of recovery and the index of aging in the intermediate part of a clone, so that in the very centre of a clone, subpopulation of partial bushes of *A. podagraria* is composed mainly of generative and post-generative partial bushes of glague, whereas post-generative partial bushes hardly



Source: author's study

Fig. 3. *A. podagraria*: a) change in the number of partial bushes on the investigated patches from the centre (on the left) to the periphery of clones (1–5 numbers of clones); b) change in the average number of partial bushes on patches from the centre (on the left) to the periphery of a clone; c) value change in the index of recovery and the index of aging of partial bushes in clone No. 4; d) value change in the index of recovery and the index of aging of partial bushes in clone No. 2; e) value change in the index of recovery and the index of aging of partial bushes in clone No. 5; (f) diagram of the structural models of *A. podagraria* clones at different stages of development: A – clone, in the creation of which pre-generative partial bushes are involved; B – clone, in the creation of which pre-generative, virginal, generative and post-generative partial bushes are involved; C – clone, in the creation of which virginal, generative and post-generative partial bushes are involved. 1 – a population of partial bushes of invasive type; 2 – a population of partial bushes of normal type; 3 – a population of partial bushes of regressive type

ever occur at the periphery. Pre-generative partial bushes dominate here. In much older clones (clone No. 5, Figure 3e) the value of the index of aging is, on average, higher than the value of the index of recovery at all patches within a radius of clone. The first of these regression lines is higher than the second one. Pre-generative partial bushes are absent in the very centre of this clone, but they both occur in the intermediate and peripheral zones of a clone. It can assumed that older clones of *A. podagraria*, which in the forests of the northern-eastern Ukraine have not been found, are dominated by aging partial bushes, and clone is gradually dying off completely.

The author developed the method of evaluating clone aging with the calculation of the indexes of recovery and aging, which allows for internal clone zoning with the separation of the clone area into three concentric zones: central, intermediate and peripheral. The boundaries among them, of course, have a fuzzy nature, but the areas are significantly different from each other.

As a result of generalization of the conducted population studies of *A. podagraria* in forest ecosystems, the three structural models of clones were created which differed in the ratio of partial bushes of different age state and their position (Figure 3f). On average, the rate of expansion of *A. podagraria* clones under the conditions of the National Nature Park "Desniansko-Starogutsky" is about 20 cm per year. The length of the perennial underground shoots of one plant greatly varies depending on the growth conditions and is up to 2–2,5 m.

A number of structural features of *A. podagraria* clones are determined by the density of ramets: it has been found that separate ramets are smaller in size and have poor flowering in dense clones. This effect has previously been described by Y.V. Lavrychenko [1985]. In general, the clones of this species grow well only under the conditions of highlight [Mikhaylova 2006].

3.2. Asarum europaeum

The study of *A. europaeum* clones, was conducted in the three associations (Table 1).

Vegetative reproduction plays the main role in self-recovery of *A. europaeum* populations in the forest ecosystems. It results in spatial distribution of monocarpic shoots (partial bushes) around the primary partial bush. The thickets of wild ginger (clones) are consequently created. *A. europaeum* clone consists of partial bushes that are monocyclic shoots, growing acrosympodially.

The six isolated clones of *A. europaeum* were described in various associations. They have a round or oval-elongated shape.

The analysis of counting the number of *A.europaeum* partial bushes on the investigated patches within a radius of clone from its centre to the periphery has shown (Figure 4a) that it is individual and depends on the size and age of a clone. In contrast to the clonal structure of glague, wild ginger is characterized by tends to decrease the density of partial bushes within a radius of a clone from the centre to its periphery. This pattern corresponds on average to the linear regression, given by: $y = 28.5 - 1.2\,x$ (Figure 4b). In the clones with a diameter of 6–9 meters from the centre of a clone to the periphery the density of partial bushes is reduced from about 90–100 to 28–30 pieces · m^{-2}. This difference in regularities of clone assemblage, as in *A. podagraria*, may be due to significant differences in the morphology and anatomy of leaves. In *A. europaeum*, unlike *A. podagraria*, they are thick, leathery and almost light-proof.

In the ratio of partial bushes of different age, clones are significantly different from each other, and location of bushes of different age is not accidental within each clone. In order to estimate the total age state of *A. europaeum* clones, the author used the index of recovery ($I_{rec.}$), the index of aging ($I_{ag.}$) and the index of generativity ($I_{generat.}$), the formula for computation of which had been mentioned above.

Clones No. 1 and No. 3 can be estimated as young: they are absolutely dominated by more than 70–80% of partial bushes of pre-generative age state. Clones No. 2, 4 and 6 are middle-aged. These three clones have the highest generativity (over 50%) and pre-generative and post-generative bushes in equal parts. Of all studied clones, Clone No. 6 is the oldest one: it has the highest index of aging (37.5%), and reduced generativity in comparison with the middle-aged clones. (Table 3).

The assignment of clone *A. europaeum* into the category of young, middle-aged or old clones is conditional. Aging of each clone is determined by the ratio of two indexes – the index of recovery and the index of aging, and by this ratio clones constitute the entire continuum of aging.

Table 3. Age state of *A. europaeum* clones in forest associations of north-eastern Ukraine

Clones	$I_{rec.}$	$I_{ag.}$	$I_{generat.}$
1	86.7	3.9	11.7
2	34.1	1.6	65.4
3	69.3	6.7	27.4
4	38.6	3.9	60.1
5	28.9	37.5	54.2
6	26.4	17.1	71.1

Depending on the age of wild ginger clone, there are regular changes as to the spatial distribution of partial bushes in it. In young clones (clone No. 1, Figure 4) the entire area is dominated by pre-generative partial bushes, the regression line of the index of recovery is much higher than the regression line of index of aging. Pre-generative partial bushes, in comparison with the partial bushes of other age-related conditions, are more common throughout the clone area. Bushes of age status *g3*, *ss* and *s* are not marked.

The middle-aged (clone No. 6, Figure 4d) clone is characterized by a decrease in the intensity of the process of new partial bushes formation and an increase in the aging process of partial bushes.

The regression line of the index of recovery is on the level of 15–10% that is considerably below the regression line of the index of aging, on average, it has the value of 50%.

In older clones (clone No. 5, Figure 4e), the value of the index of aging is, on average, higher than the value of the index of recovery at all patches within a radius of a clone. It can be assumed that in much older clones of wild ginger, which have not been found in the forests of north-eastern Ukraine, aging partial bushes predominate, and clone is gradually dying out completely.

The author have developed the method of evaluation of clone aging which allows, as in the case of clones of *A. podagraria*, for internal zoning of wild ginger clones with the separation of the clone area into three concentric zones: central, intermediate and peripheral.

As a result of generalization of the conducted population studies of *A. europaeum* clone formation in forest ecosystems, the three structural models of clones were created which differed in the ratio of partial bushes of different age state and their position (Figure 4f). The capture of a new area by means of *A. europaeum* clone formation is slow. The main thing in this case is seed propagation.

3.3. Carex pilosa

The study of *C. pilosa* clones was conducted in the three associations (Table 1).

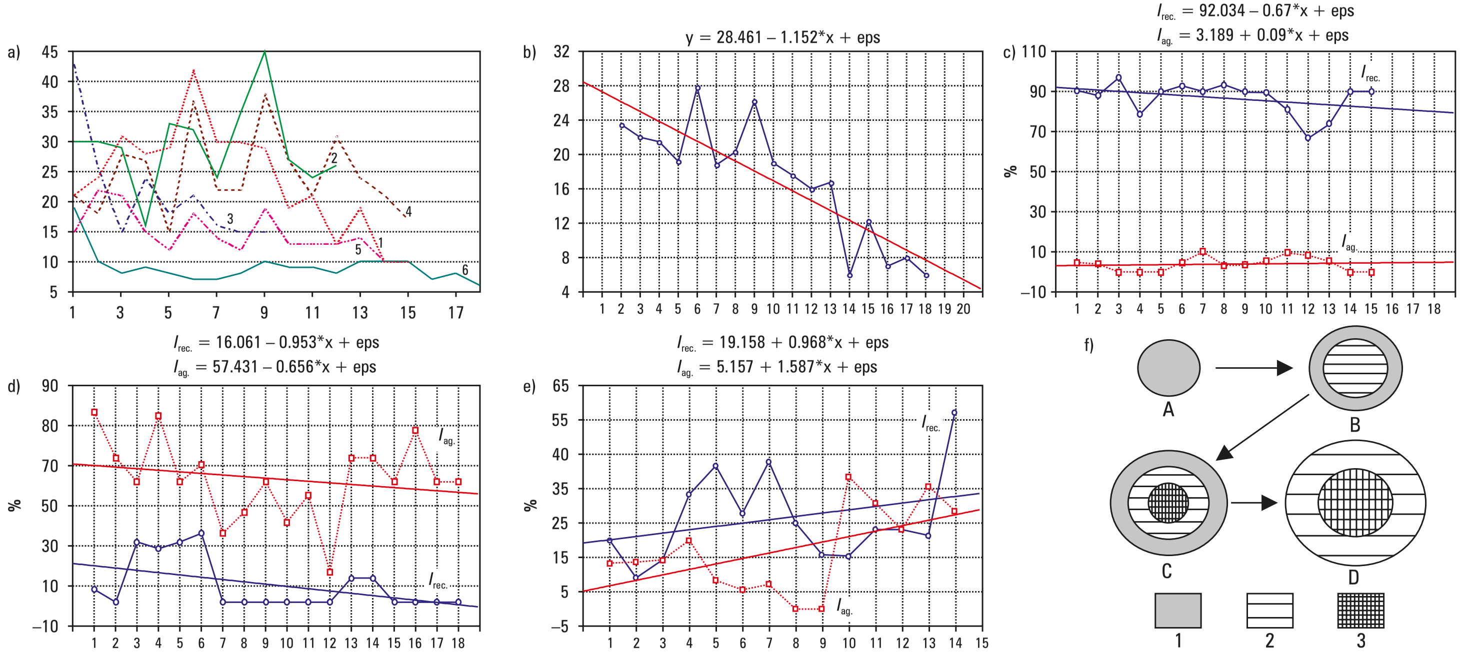
In self-recovery of *C. pilosa* in the forests of Ukrainian Polissya vegetative reproduction plays the main role, which is a division of multi-bushy female parent into several filials. No isolated partial bushes, but systems of partial bushes, interconnected by underground shoots, are separated. Collectively such individuals are clones.

The five isolated clones of *C. pilosa* are identified in various associations. From the centre to the periphery, whether in case of individual clones of sedge (Figure 5a) or, on average, for all investigated clones (Figure 5b), the density of partial bushes is sharply (3–4 times) reduced. These clones would take an intermediate position between the clones-fields and clones-individuals.

The regularity of reduction in the density of partial bushes of sedge within a radius of a clone can approximate equation of the form: $y = 12.2 - 0.4\,x$. The average density of partial bushes are 12–65 pieces · m^{-2}.

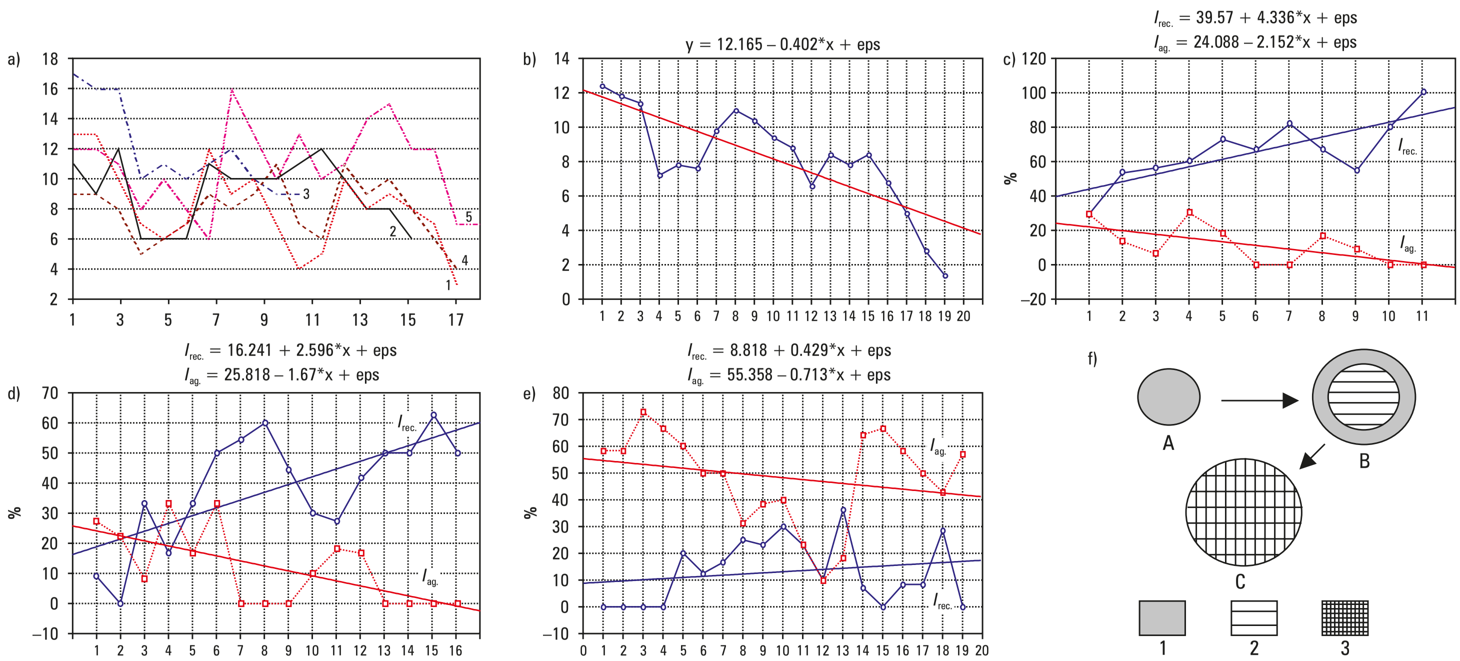
In accordance with the values of the indexes of aging, recovery and generativity of partial bushes, clone No. 3 can be regarded as young (Table 4). It has the highest index of recovery (65.6%) and the lowest index of aging (11.2 %). Clone No. 1, by contrast, is the oldest one. It has the highest index of aging and the lowest index of recovery (63.3% and 10.2%, respectively). Other clones are middle-aged. They are characterized by high generativity.

Pre-generative partial bushes prevail in young clones. The regression line for the index of recovery within a radius of a clone is significantly higher than the regression line for the index of aging (Figure 5c). In the middle-aged clones, these two regression lines overlap, because the aging process of partial bushes clearly dominates in the central part of a clone (Figure 5d). In the older clones, the regression line for the index of aging is higher than the regression line for the index of recovery (Figure 5e). In such clones the aging of partial bushes covers the periphery of a clone.



Source: author's study

Fig. 4. *A. europaeum*: a) change in the number of partial bushes on the investigated patches from the centre (on the left) to the periphery of clones (1–6 – numbers of clones); b) change in the average number of partial bushes on patches from the centre (on the left) to the periphery of clone; c) value change in the index of recovery and the index of aging of partial bushes in clone No. 1; d) value change in the index of recovery and the index of aging of partial bushes in clone No. 6; e) value change in the index of recovery and the index of aging of partial bushes in clone No. 5; f) diagram of the structural models of *A. europaeum* clones at different stages of development: A – clone, in the creation of which pre-generative partial bushes are involved; B – clone, in the creation of which pre-generative, virginal, generative partial bushes are involved; C – clone, in the creation of which pre-generative, virginal, generative and post-generative partial bushes are involved; D – clone, in the creation of which virginal, generative and post-generative partial bushes are involved. 1 – a population of partial bushes of invasive type; 2 – a population of partial bushes of normal type; 3 – a population of partial bushes of regressive type



Source: author's study

Fig. 5. *C. pilosa*: a) change in the number of partial bushes on the studied patches from the centre (on the left) to the periphery of clones (1–5 – numbers of clones); b) change in the average number of partial bushes on patches from the centre (on the left) to the periphery of clone; c) value change in the index of recovery and the index of aging of partial bushes in clone No. 3; d) value change in the index of recovery and the index of aging of partial bushes in clone No. 2; e) value change in the index of recovery and the index of aging of partial bushes in clone No. 5; f) diagram of the structural models of *C. pilosa* clones at different stages of development: A – clone, in the creation of which pre-generative partial bushes are involved; B – clone, in the creation of which pre-generative, virginal and generative partial bushes are involved; C – clone, in the creation of which post-generative partial bushes are involved. 1 – a population of partial bushes of invasive type; 2 – a population of partial bushes of normal type; 3 – a population of partial bushes of regressive type

Table 4. Age state of *C. pilosa* clones in forest associations of north-eastern Ukraine

Clones	$I_{rec.}$	$I_{ag.}$	$I_{generat.}$
1	10.2	63.3	57.9
2	38.3	11.6	59.9
3	65.6	11.2	28.0
4	16.4	45.9	69.4
5	13.1	48.2	66.6

Source: author's study

Based on changes in the density of partial bushes and their age state, the specific zones have been destinguished in *C. pilosa* clones: the central zone is mainly occupied by senile ramets; the intermediate zone is inhabited by ramets that form the subpopulation of partial bushes of normal age type, and the peripheral (invasive) zone, presented by ramets of young vegetative and sometimes generative state. Details of the distribution of *C. pilosa* partial bushes of different age state depend on its age after the clone zoning.

As a result of generalization of conducted population studies of *C. pilosa* clone structure in forest phytocenoses, three models of clonal structure were created that differed in the ratio of partial bushes of different age state and their location (Figure 5f).

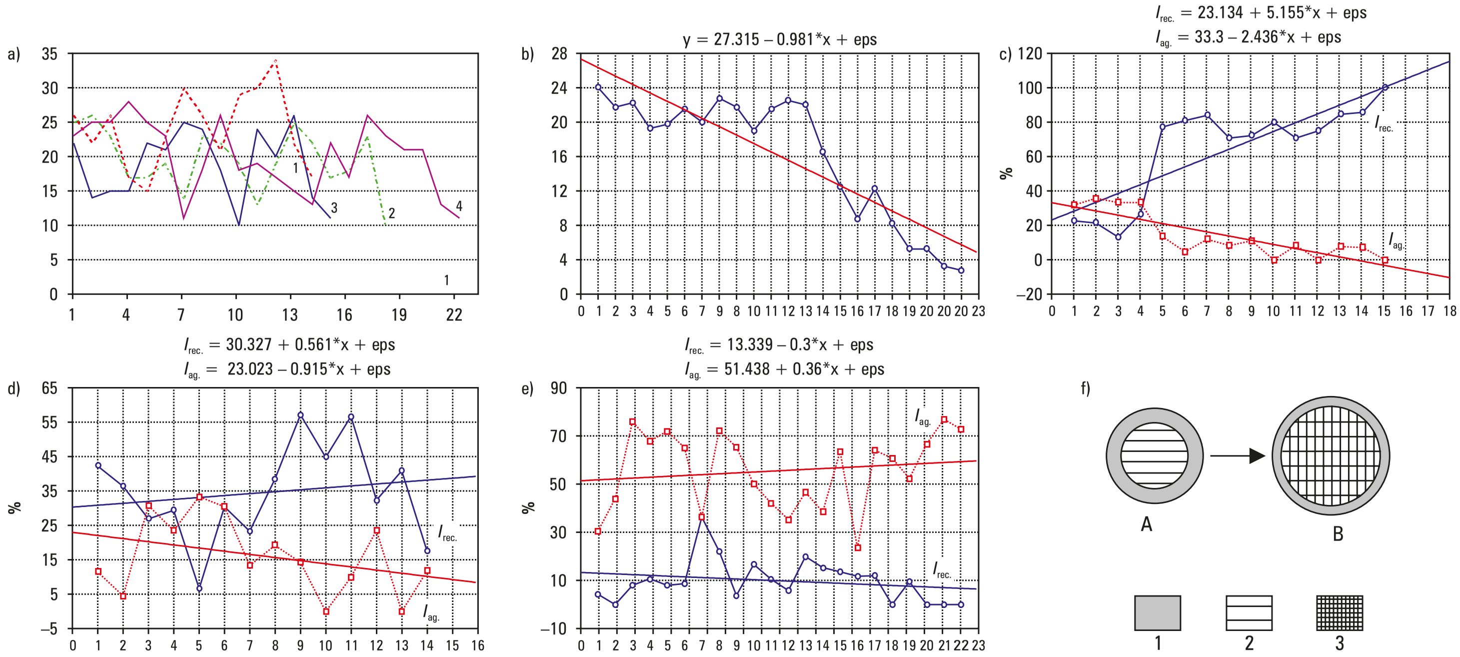
3.4. *Stellaria holostea*

The study of *S. holostea* clones was conducted in the three forest associations (Table 1).

Vegetative reproduction plays the leading role in dispersal of *S. holostea* in forests. This is also confirmed by the clonal expansion model of this plant species, developed by N.V. Mikhailova et al. [2006]. Its consequence is the placement of partial bushes around the primary partial bush. The result is the formation of *S. holostea* clones.

The four isolated clones of *S. Holostea* have been distinguished. They have a diameter of 15 to 20 m, and often interpenetrate one another. In isolated clones, 40–135 partial bushes of *S. holostea* occur per square meter. They are unevenly distributed (Figure 6a, b): their number in the centre of clones is 5–6 times greater. The regression equation for changes in the number of partial bushes within a radius of a clone is given by: $y = 27.3–0.98\ x$.

Clones of *S. holostea* differ from each other by the ratio of partial bushes of different age state and, accordingly, by values of the indexes of recovery, aging, generativity (Table 5). In young clone No. 3 the index of recovery is equal to 64.4% with low indexes of aging and generativity (respectively 13.8 and 28.6 %). On the general graphs the changes in values of the indexes of recovery and aging within a radius of a clone the regression line of the index of recovery is always above the regression line of the index of aging (Figure 6c). During aging of clones the value of the index of recovery is reduced, and the index of aging is growing. In the middle-aged clones No. 1



Source: author's study

Fig. 6. *S. holostea*: a) change in the number of partial bushes on the studied patches from the centre (on the left) to the periphery of clones (1–4 numbers of clones); b) change in the average number of partial bushes on patches from the centre (on the left) to the periphery of clone; c) value change in the index of recovery and the index of aging of partial bushes in clone No.3; d) value change in the index of recovery and the index of aging of partial bushes in clone No. 1; e) value change in the index of recovery and the index of aging of partial bushes in clone No. 4; f) diagram of the structural models of *S. holostea* clones at different stages of development: A – clone, in the creation of which pre-generative, virginal and generative partial bushes are involved; B – clone, in the creation of which pre-generative and post-generative partial bushes are involved. 1 – a population of partial bushes of invasive type; 2 – a population of partial bushes of normal type; 3 – a population of partial bushes of regressive type.

and 2 (Figure 6d) the index of recovery goes down to 30–35%, and the index of aging increases by 15–16%. Index of generativity reaches its maximum (60–65%) in such clones. In older clones (clone No. 4, Figure 6e) the index of recovery is about 10%, and the index of aging exceeds 50%.

Table 5. Age state of *S. holostea* clones in forest associations of north-eastern Ukraine

Clones	$I_{rec.}$	$I_{ag.}$	$I_{generat.}$
1	34.5	16.2	60.5
2	31.9	15.4	65.4
3	64.4	13.8	28.6
4	9.9	55.6	66.6

Source: author's study

The three types of allocation of partial bushes subpopulations have been distinguished in the structure of *S. holostea* clone: invasive, normal and regressive. Subpopulations of partial bushes of invasive type are mainly formed by pre-generative and adult vegetative bushes: the normal type is formed by bushes of normal age-related condition, the regressive type is mainly formed by bushes of post-generative age state.

As a result of generalization of the conducted population studies of *S. holostea* in forest ecosystems of Ukrainian Polissya, the two structural models of clones were created which differed in the ratio of partial bushes of different age status and their location (Figure 6f).

Clones dominated by pre-generative partial bushes and existence of post-generative partial bushes in the centre of clone (A) are typical for association of *Quercetum coryloso-caricoso-stellariosum*; clones with a higher proportion of pre-generative, adult vegetative and generative partial bushes (B) are typical for associations of *Querceto-Pinetum coryloso-stellariosum* and *Querceto-Pinetum stellariosum*.

4. Conclusions

The use of the methods of plant population ecology combined with the original statistical and graphical modeling approach has allowed us to establish regularities of formation and spatial arrangement of clones of four species of forest herbs: *Aegopodium podagraria* L., *Asarum europaeum* L., *Carex pilosa* Scop., *Stellaria holostea* L., which are the main species in some forest ecosystems of north-eastern Ukraine.

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