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Unitary and iterative growth of clonal species individuals: significance for the spatial structure and the dynamics of population abundance

Unitarny a iteratywny wzrost osobników gatunków klonalnych: znaczenie dla struktury przestrzennej i dynamiki liczebności populacji

SUMMARY

The aim of the study was to determine the dynamics of unitary and iterative genets and the ramets which they produce in the populations of two species represent diverse types of clonal growth: *Filipendula ulmaria* (L.) Maxim. and *Lythrum salicaria* L. An attempt was made to answer the following questions: Is there a demographic balance between the number of ramets produced by genets, i.e. vegetative reproduction, and recruitment of new genets? How significant may quantitative relations between unitary and iterative individuals be for the spatial structure and population abundance dynamics?

There was similarity in the dynamics of the abundance of genets and ramets in the *Filipendula ulmaria* and *Lythrum salicaria* populations. A slight increase in the number of genets and ramets was noted in the second study season. In the subsequent vegetation seasons, a decline in their number was observed. There was no statistically significant differences in the share of unitary and iterative individuals and ramets that they produced. The populations are characterized by a spatial clumped structure. During the observation, an increase in the mean number of ramets per one individual and the aggregation coefficient (Leksis' index) were noted.

Population of the species of hydrogenic habitats situated in river valleys are particularly exposed to groundwater fluctuations. In the study area, a rapid rise of the groundwater level related to beaver activity was observed. Water stress resulted in weaker growth of the existing genets and, first of all, in lower recruitment of new ones. Intensive vegetative growth of *Carex acutiformis* individuals and increase in the necromass layer thickness have a big significance for the population dynamics of the study species.

STRESZCZENIE

Celem badań było określenie dynamiki genetów unitarnych i iteratywnych oraz ramet z nich pochodzących w populacjach dwóch gatunków reprezentujących odmienne typy wzrostu klonalnego: *Filipendula ulmaria* (L.) Maxim. i *Lythrum salicaria* L. Podjęto próbę odpowiedzi na pytania: czy w populacjach badanych gatunków kształtuje się równowaga demograficzna między liczbą ramet produkowanych przez genety, czyli pomnażaniem wegetatywnym, a rekrutacją nowych genetów? Jakie znaczenia dla struktury przestrzennej i dynamiki liczebności populacji mogą mieć relacje ilościowe między osobnikami unitarnymi i iteratywnymi?

Dynamika liczebności populacji *Filipendula ulmaria* i *Lythrum salicaria* ma podobny przebieg. W drugim sezonie badań odnotowano niewielki wzrost liczby osobników i ramet, natomiast w kolejnych sezonach wegetacyjnych obserwowano ich systematyczny spadek. W populacjach badanych gatunków w kolejnych latach badań nie stwierdzono istotnych statystycznie różnic w udziale osobników unitarnych i iteratywnych oraz ramet przez nie wytwarzanych. Populacje charakteryzują się skupiskowym typem struktury przestrzennej. W trakcie badań odnotowano systematyczny wzrost średniej liczby ramet przypadających na jednego osobnika oraz wzrost wartości współczynnika skupiskowości (indeks Leksisa).

Populacje gatunków siedlisk hydrogenicznych usytuowane w obszarze dolin rzecznych narażone są szczególnie na wahania poziomu wód gruntowych. Na badanym obszarze odnotowano gwałtowne podniesienie się poziomu wód spowodowane działalnością bobrów. Stres wodny spowodował osłabienie wzrostu obecnych już genetów, ale przede wszystkim zahamował rekrutację nowych. Duży wpływ na dynamikę populacji *Filipendula ulmaria* i *Lythrum salicaria* ma również intensywne pomnażanie wegetatywne osobników *Carex acutiformis* oraz wzrost miąższości zalegającej warstwy nekromasy.

K e y w o r d s: clonal plants, *Filipendula ulmaria*, *Lythrum salicaria,* unitary and iterative growth, wet meadows

INTRODUCTION

The type of growth reflects the genetically determined architecture pattern of an individual. In plants, we can distinguish a group of organisms which display unitary growth, that is, do not form modules, and organisms exhibiting iterative (modular) growth, which are able to produce structural units of the individual such as shoots, rhizomes or roots. A great majority of higher plants represent the latter type of growth. The consequence of iterative growth is formation of individual complex structures of various size and durability named clonal organisms (11, 17). The diversity in the growth forms is a resultant of the influence of habitat conditions and inter- and intraspecies competitive relations, as well as of adaptive abilities of the organisms themselves. Diversity in clonal growth forms together with higher morphological and physiological plasticity makes better adaptation in various environments possible (12). Iterative organisms utilize environmental resources (space, water, nutrients, solar energy) more effectively, especially when they are scarce or unequally distributed. Their modular structure has important implications for the life history of clonal species: their ability to move by spacers to neighbouring sites enables them to show a flexible response to their local environment, and to escape unfavourable patches and exploit favourable ones. Most studies related to clonal growth have focused on birth and death rates of ramets (21, 26, 27). To understand the population dynamics and life history of clonal plants attention must be given also to the genet level (7, 18, 19, 29). The genet is a developmental product of one zygote; genetic variation occurs mainly at this level apart from variation due to somatic mutations (30). With this approach to the problem, we can concurrently observe the effectiveness of reproduction in the generative and vegetative ways in relation to the influence of the remaining environmental elements which may play the role of a selection factor.

The aim of the study was to determine the dynamics of unitary and iterative genets and the ramets which they produce in the populations of two clonal species: *Filipendula ulmaria* and *Lythrum salicaria*. An attempt was made to answer the following questions: Is there a demographic balance between the number of ramets produced by genets, i.e. vegetative reproduction, and recruitment of new genets? How significant may quantitative relations between unitary and iterative individuals be for the spatial structure and population abundance dynamics?

MATERIAL AND METHODS

The study was conducted in the Szum river valley in the Central Roztocze region. The study area comprises hydrogenic habitats in the waterlogged terrace inhabited by a mosaics of meadow communities of variable moisture of the *Molinio-Arrhenatheretea* class and *Magnocaricion* rushes of the *Phragmitetea* class (4). The meadow vegetation is dominated by macroforbes: *Filipendula ulmaria*, *Lythrum salicaria*, *Lysimachia vulgaris*, *Cirsium rivulare*, and *C. oleraceum. Carex acutiformis* is a species which has increased its share in the recent years owing to elevation of groundwaters.

Two perennial iterative plant species *Filipendula ulmaria* and *Lythrum salicaria* representing different forms of integration and genet durability, were chosen for the study. *Filipendula ulmaria* (*Rosaceae*) belongs to rhizomatous caulophytes (23). The species produces thick rhizomes with short internodes, i.e., growing segments. Mature genets are composed of 20–30 ramets and may cover an area of above 1 m^2. *Filipendula ulmaria* genet life cycle lasts approximately 10 years. This species displays both temporal and spatial dynamics. It contributes to forming a coarse-grained, or even patchy, vegetation mosaics. *Filipendula ulmaria* is characterized by great competitive abilities and is regarded as a succession promoter in meadow communities (9, 10, 13). *Lythrum salicaria* (*Lythraceae*) is a clonal plant which, according to the classification of Łukasiewicz (23), belongs to rhizocaulophytes. *Lythrum salicaria* genets are characterized by compact structure and, as a rule, they are formed by a few or maximally over a dozen of shoots (ramets). This species participates in formation of a fine- or coarse-grained spatial mosaics. The calendar age of the genets is estimated at over 10 years. Strong, well-formed underground organs ensure long-term persistence of the individuals in the area that they cover. Thus, *Lythrum salicaria* displays a temporal rather than spatial dynamics and, likewise *Filipendula ulmaria,* is considered to be a succession promoter (9, 13).

The study was conducted in a permanent plot (5 × 5 m) divided into 1 m^2 squares, situated in a *Lythro-Filipenduletum ulmariae* patch. During four vegetation seasons (2005–2008), 1:10-scaled plans of distribution of the marked genets and ramets were prepared. On this basis, interpolated maps presenting the density of the ramets of the study species were made. The aggregation coefficient *I* (Leksis' index) was calculated to estimate the type of the spatial structure in the *Filipendula ulmaria* and *Lythrum salicaria* populations. Subsequently, the dynamics of the genets and ramets in both species was determined. The two-side test for differences of two structure indices (the U-test) was used to analyze the significance of differences between the share of unitary and iterative genets and ramets.

The nomenclature of the vascular flora follows Mirek et al. (25); the classification of plant communities follows Matuszkiewicz (24).

RESULTS

Patterns of genet and ramet dynamics in the *Filipendula ulmaria* population

A slight increase in the *Filipendula ulmaria* abundance – from 76 to 79 − was noted in the second study season (Fig. 1). In the subsequent vegetation seasons, a decline in the number of genets by 13% in 2007 and another 8% in 2008 was observed. A similar tendency was displayed by the structural elements of genets – the ramets. The biggest number of the ramets was found in the second year of the study – 426, whereas the smallest number – 362 − in the last study year. A significant increase by 15% in the number of the ramets in 2006 is worth noting.

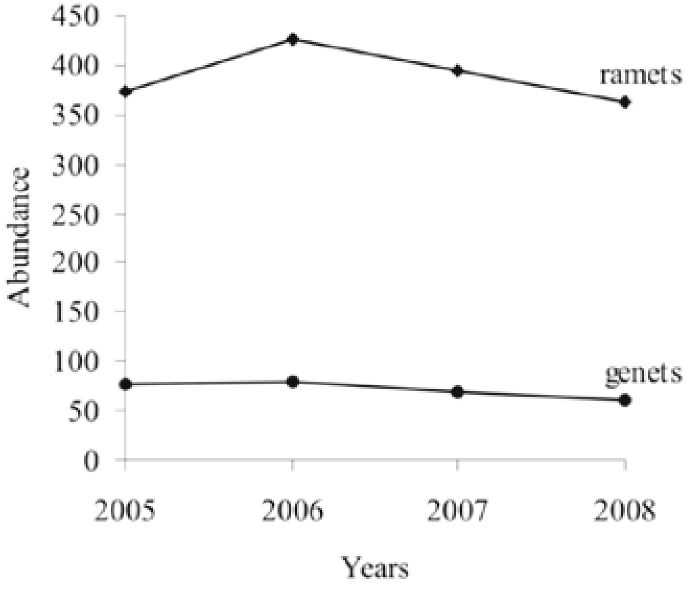

Fig. 1. Genets vs. ramets dynamics in the *Filipendula ulmaria* population

A systematic increase in the mean number of ramets per one individual of *Filipendula ulmaria* (with the maximum of 6 ramets in 2008) was observed during the study (Fig. 2). The individuals were composed of 1 to maximally 21 shoots. Unitary genets constituted the highest percentage in 2006 (Fig. 3a). This was influenced by both recruitment of new individuals into the population and reduction in the number of the existing ramets. In the last year of observations

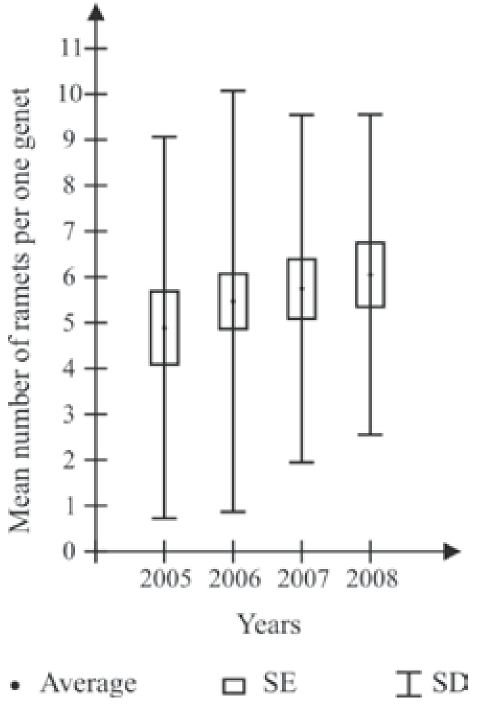

Fig. 2. Changes in numbers of ramets per one genet of the *Filipendula ulmaria* population

the share of one-shoot genets was the lowest and reached only 12.1%. A similar tendency was revealed by means of the analysis of the relations between the number of ramets from unitary and iterative genets (Fig. 3b). In the first two years the share of ramets forming unitary genets was the highest (3.9 and 4.0%, respectively), followed by a two-fold decline in abundance in 2008 (1.9%). There was no significant difference throughout the subsequent study years (U-test: $P< 0.05$), both in the case of the relations between unitary and iterative individuals and the ramets that they produced.

The *Filipendula ulmaria* population is characterized by a spatial clumped structure (Fig. 4, Table 1). During the observation, an increase in the Leksis' index was noted, from 8.8 in 2005 to 11.1 in 2008. In the first and last study years the mean number of ramets in every 1 m^2 was similar (14.0 and 14.3 ramets · m^{-2}, respectively).

Patterns of genet and ramet dynamics in the *Lythrum salicaria* population

In the analyzed vegetation patch, the *Lythrum salicaria* population was characterized by an almost two-fold lower abundance of individuals compared to

Fig. 3. The share of unitary (black fields) and iterative (white fields) genets (a) and ramets originated from unitary and iterative genets (b) of the *Filipendula ulmaria* population

the *Filipendula ulmaria* population (Fig. 5). There was similarity, though, in the dynamics of the genets and ramets. In the *Lythrum salicaria* population, in the second study year, a significant 20% increase in the number of new individuals was observed. An even more remarkable rise was reported in the number of ramets; their number increased by almost 40%. These results indicate great

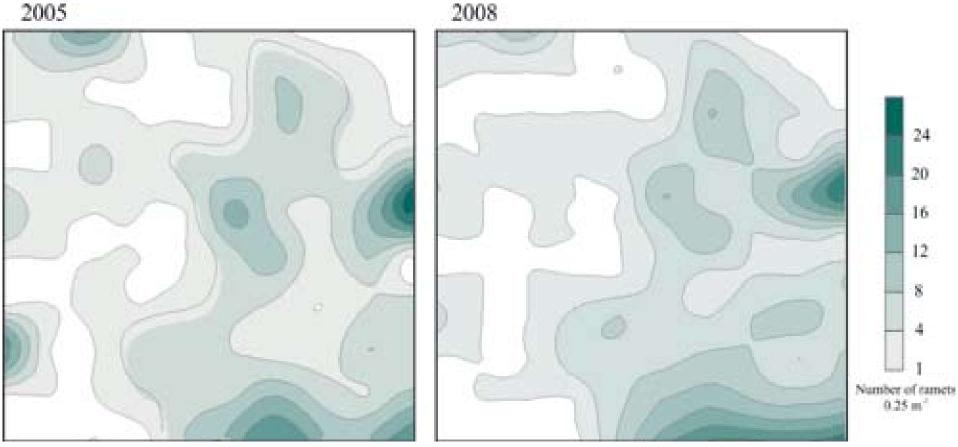

Fig. 4. Changes of ramet density and spatial pattern in the *Filipendula ulmaria* population

Table 1. Changes of abundance, density and dispersion of ramets in the *Filipendula ulmaria* population

Year	Number of ramets	Ramets · m^{-2}			$I = \frac{s^2}{\bar{x}}$
		x̄ ± SD	Min.	Max.	
2005	372	14.0 ± 9.7	0	40	8.8
2008	362	14.3 ± 12.6	0	43	11.1

effectiveness of both generative and vegetative reproduction. In the subsequent seasons the tendency was reverse: the number of individuals of the study species was decreased by 10%, compared to the initial condition.

The relations between the abundances of the genets and ramets in the *Lythrum salicaria* population were on a similar level throughout the study period and ranged, on average, from 2.7 to 3.1 ramets per genet (Fig. 6). The number of unitary individuals decreased from 30% in 2005 to 11% in 2008 (Fig. 7a). The same was concurrently observed on the level of ramets. The number of shoots from unitary individuals was almost three-fold lower than that in the initial condition (Fig. 7b). Likewise in the *Filipendula ulmaria* population, there were no statistically significant differences in the share of unitary and iterative individuals and ramets that they produced (U-test: $P < 0.05$).

The aggregation coefficient values indicate an increased degree of aggregation of *Lythrum salicaria* ramets in the first and last study years (Fig. 8, Table 2). The density of ramets in the research area in the above-mentioned years was comparable (4.5 and 4.3 ramets · m^{-2}).

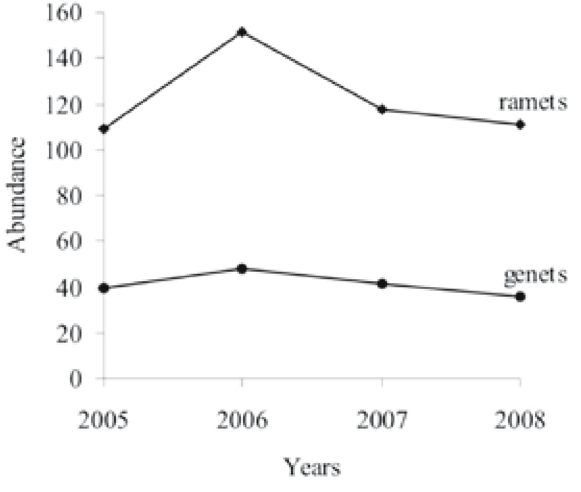

Fig. 5. Genets vs. ramets dynamics in the *Lythrum salicaria* population

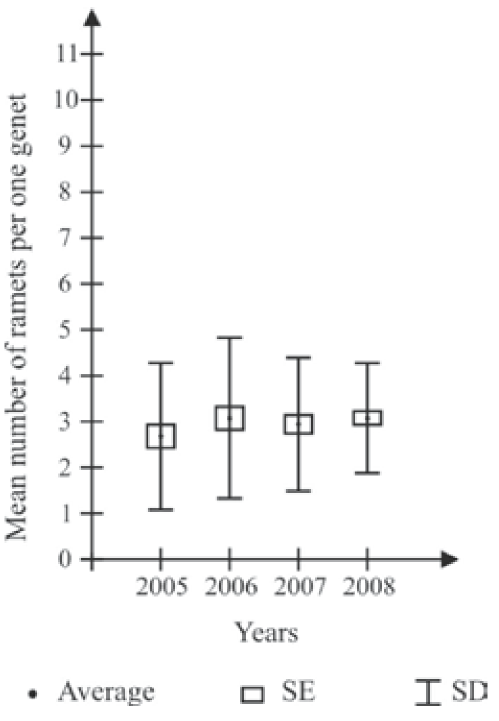

Fig. 6. Changes in numbers of ramets per one genet of the *Lythrum salicaria* population

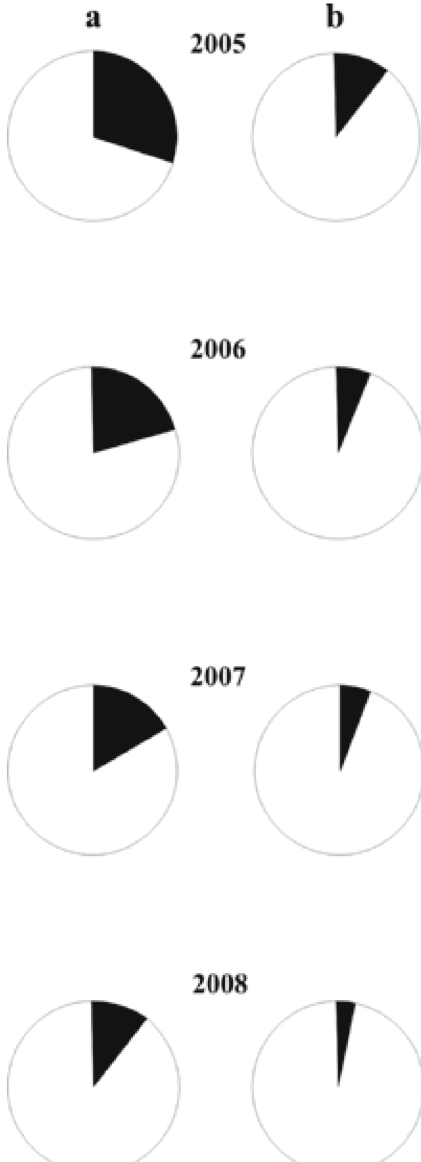

Fig. 7. The share of unitary (black fields) and iterative (white fields) genets (a) and ramets originated from unitary and iterative genets (b) of the *Lythrum salicaria* population

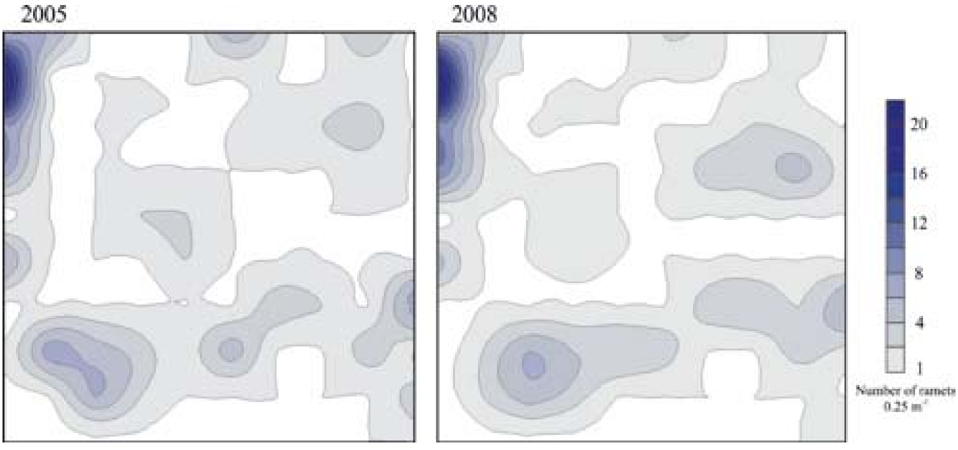

Fig. 8. Changes of ramet density and spatial pattern in the *Lythrum salicaria* population

Table 2. Changes of abundance, density and dispersion of ramets in the *Lythrum salicaria* population

Year	Number of ramets	Ramets · m^{-2}			$I = \frac{s^2}{\bar{x}}$
		$\bar{x} \pm SD$	Min.	Max.	
2005	109	4.5 ± 4.4	0	25	4.3
2008	111	4.3 ± 5.3	0	27	6.5

DISCUSSION

The pattern of changes in genet and ramet abundance in a population depends on the demographic equilibrium between seedling recruitment and the number of new ramets produced by individuals. In clonal species populations, a compromise is established between vegetative reproduction that ensures effective dispersal of best adapted individuals, and generative reproduction leading to increased genetic diversity of the population (6, 17, 20). The colonization success of each species depends on numerous factors, among others, on the habitat conditions, floristic composition of the inhabited area, the way of reproduction, type of growth and life span (9). *Filipendula ulmaria* and *Lythrum salicaria* represent diverse types of clonal growth with particular differences in terms of persistence and the genet size. These species are characterized by the ability of long-term persistence in the area that they occupy and great competitive features (13, 15). The analysis of *Filipendula ulmaria* and *Lythrum salicaria* habitat requirements demonstrates that in the study vegetation patch these species should have optimal growth and development conditions (32). Population of the species of hydrogenic habitats situated in river valleys are particularly exposed to groundwater fluctuations. This may result in stress *sensu* Grime (15) caused by periodical anaerobic conditions (8, 22, 28, 31). At the beginning of the vegetation season in 2006, a rapid rise of the groundwater level (ca. 35 cm) related to beaver activity was observed. This condition persisted till spring 2008. The consequences of the long-term waterlogging were revealed at the levels of individuals and species populations that form the floristic composition. Water stress resulted in weaker growth of the existing genets and, first of all, in lower recruitment of new ones. The lowered rate of recruitment of new genets in the populations of the two species was noted in the second year of the research and it persisted throughout the observation. A similar tendency was reported in the ramets produced by the genets.

The fall in the seed count and the decreased number of small-scale gaps, which play the role of the so-called safe sites for germination (17) or regenerative niches (16), are the most important factors that contribute to reduced effectiveness of generative reproduction. In the study species populations, a systematic decline of the share of ramets producing inflorescence was observed (Franczak, unpubl. data). No generative ramets were observed in the *Filipendula ulmaria* population in the study area during 2007 and 2008 seasons. *Filipendula ulmaria* and *Lythrum salicaria* seedlings occurred in big numbers in the gaps between adult individuals (as many as several tens of seedlings per 0.01 m^2), but they did not usually survive till the end of the vegetation season. Intensive vegetative growth of *Carex acutiformis* individuals seems to have the biggest significance for the population dynamics of the study species. Ramets of this expansive sedge species dispersed at a fast rate into microhabitats which could potentially play the role of safe germination sites for seeds of other species. In the study period, an increase in the necromass layer thickness (ca. 58%) was reported. Necromass may be a physical barrier preventing seeds from access to the soil surface, thus diminishing the soil pool of the seed bank. Additionally, it may worsen the physical and chemical properties, especially light and humidity conditions, of microhabitats in which seedlings grow (1, 2, 14). The sum of these sudden habitat changes and the consequent increased competition between the co-occurent species are reflected in changes in the pattern of spatial organization of *Filipendula ulmaria* and *Lythrum salicaria* populations. An increase in the degree of ramet aggregation in both species was noted. This was caused by both the fall in the generative reproduction share in the population and increased mortality of juvenile genets (usually composed of a small number of ramets), which inhabit local ground depressions and are exposed to waterlogging. The best adapted mature genets oriented first of all to produce new ramets have started to play the most significant role in the population.

The long-term observations of the abundance dynamics and spatial structure of clonal plants indicate that the variable pattern in a given species population is a resultant of environmental conditions and intrapopulation effects (3, 5). It seems that biotope heterogeneity and interspecific competition are the predominant factors that influence the population dynamics. Further observations may be expected to contribute to recognition of the character and significance of interactions at the level of individuals in the population.

REFERENCES

1. Borkowska L. 2004a. Patterns of seedlings recruitment in experimental gaps on mosaic vegetation of abandoned meadow. Acta Soc. Bot. Pol. 73 (4): 343–350.
2. Borkowska L. 2004b. Wzorce rekrutacji siewek gatunków klonalnych w zbiorowisku niekoszonej łąki *Cirsietum rivularis* Ralski 1931. Phytocoenosis 16 (N.S.), Archiv. Geobot. 10: 1–71.
3. Czarnecka B. 1995. Biologia i ekologia izolowanych populacji *Senecio rivularis* (Waldst. et Kit.) DC. i *Senecio umbrosus* Waldst. et Kit. Rozpr. habil. Wydz. BiNoZ 48, Wyd. UMCS, Lublin.
4. Czarnecka B. 2005. Plant cover of the Szum river valley (Roztocze, South-East Poland). Acta Soc. Bot. Pol. 74 (1): 43–51.
5. Czarnecka B. 2008. Spatiotemporal patterns of genets and ramets in a population of clonal perennial *Senecio rivularis*: plant features and habitat effects. Annales Bot. Fen. 45 (1): 19–32.
6. Eriksson O. 1989. Seedling dynamics and life histories in clonal plants. Oikos 55: 231–238.
7. Eriksson O. 1993. Dynamics of genets in clonal plants. Trends Ecol. Evol. 8: 313–316.
8. Ernst W. H. O. 1990. Ecophysiology of plants in waterlogged and flooded environments. Aquatic Bot. 38: 73–90.
9. Falińska K. 1991. Plant Demography in Vegetation Succession. Kluwer Academic Publisher, Dordrecht, Boston, London.
10. Falińska K. 1995. Genet disintegration in *Filipendula ulmaria* for population dynamics and vegetation succession. J. Ecol. 82: 865–877.
11. Falińska K. (red.). 1998. Plant Population Biology and Vegetation Processes. W. Szafer Institute of Botany, Polish Academy of Science, Kraków.
12. Falińska K. 2002. Przewodnik do badań biologii populacji roślin. Wydawnictwo Naukowe PWN, Warszawa.
13. Falińska K. 2003. Alternative pathways of succession: species turnover patterns in meadows abandoned for 30 years. Phytocoenosis 15 (N.S.), Archiv. Geobot. 9: 1–104.
14. Goldberg D. E., Werner P. A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). Oecologia 60: 149–155.
15. Grime J. P. 1979. Plant Strategies and Vegetation Processes. Wiley & Sons, New York.
16. Grubb P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107–145.
17. Harper J. L. 1977. Population Biology of Plants. Academic Press, London.
18. Harper J. L. 1980. Plant demography and ecological theory. Oikos 35: 244–253.
19. Harper J. L., White J. 1974. The demography of plants. Ann. Rev. Ecol. Syst. 5: 419–463.
20. Herben T., Hara T., Marshall C., Soukupová L. 1994. Plant clonality: biology and diversity. Folia Geobot. Phytotax. 29: 113–122.
21. Hutchings M. J. 1997. The structure of plant populations. [In:] Plant Ecology. M. J. Crawley (ed.), 2nd ed. Blackwell Science, Oxford: 325–358.

22. Lenssen J. P. M., Menting F. B. J., van der Putten W. H. 2003. Plant responses to simultaneous stress of waterlogging and shade: amplified or hierarchical effects? New Phytol. 157: 281–290.
23. Łukasiewicz A. 1962. Morfologiczno-rozwojowe typy bylin. Prace Kom. Biol. PTPN, 27 (1): 1–398.
24. Matuszkiewicz W. 2006. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN, Warszawa.
25. Mirek Z., Piękoś-Mirkowa H., Zając A., Zając M. 2002. Flowering Plants and Pteridophytes of Poland. A Checklist. Polish Academy of Sciences, W. Szafer Institute of Botany, Kraków.
26. Navas M. L., Garnier E. 1990. Demography and growth forms of the clonal perennial *Rubia peregrina* in Mediterranean vineyard and unmanaged habitats. J. Ecol. 78: 691–712.
27. Olejniczak P. 2003. Optimal allocation to vegetative and sexual reproduction in plants: the effect of ramet density. Evol. Ecol. 17: 265–275.
28. Šrůtek M. 1997. Growth responses of *Urtica dioica* L. to different water table depth. Plant Ecology 130: 163–169.
29. Watkinson A. R. 1997. Plant population dynamics. [In:] Plant Ecology. M. J. Crawley (ed.), 2nd ed. Blackwell Science, Oxford: 707–717.
30. Widén B., Cronberg N., Widén M. 1994. Genotypic diversity, molecular markers and spatial distribution of genets in clonal plants, a literature survey. Folia Geobot. Phytotax. 29: 245–263.
31. Vartapetian B. B., Jackson M. B. 1997. Plant adaptations to anaerobic stress. Annals Bot. 79 (Suppl. A): 3–20.
32. Zarzycki K., Trzcińska-Tacik H., Różański W., Szeląg Z., Wołek J., Korzeniak U. 2002. Ecological Indicator Values of Vascular Plants of Poland. Polish Academy of Sciences, W. Szafer Institute of Botany, Kraków.