

# Spatiotemporal patterns of genets and ramets in a population of clonal perennial *Senecio rivularis*: plant features and habitat effects

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The study investigates the spatial pattern dynamics of *Senecio rivularis* on different levels of population organization: genets and ramets. The tested null hypothesis was: in the expansion phase of a population, abundance and spatial pattern are affected by the number and diversity of genet clumps, in the stable phase with limited habitat resources population size is controlled mainly within independent clumps of genets. Spatiotemporal patterns of genets were studied within the entire population area and within selected clumps, respectively, while patterns of ramets were observed at a small scale. Additionally, data on genet survival, production of ramets, and rhizome disintegration were collected on the basis of 100 labelled genets in different clumps. The genet spatial pattern concerning ‘structure scale’ and ‘structure intensity’ was very variable on the level of genets but on the level of ramets it was regenerated close to the mean lifespan of genet, i.e. from several to up to 10 years. Variable spatial patterns of genets and ramets were affected by changes in the proportion of unitary and iterative genets, and by the contribution of these categories to the total number of ramets. Different factors seem to be important for the population dynamics in the phases of expansion and fluctuation, respectively: environmental conditions, plant features, and intrapopulation relations, driven by competition for space and habitat resources.

Key words: genet vs. ramet dynamics, long-lived clonal plant, population dynamics, *Senecio rivularis*, spatial pattern

## Introduction

Changes in the numbers, density and dispersal modes of individuals in a population are always considered very fundamental in plant demography (Harper & White 1970, 1974, Harper 1977, 1978, White 1985, Crawley 1990, Silvertown &

Lovett Doust 1993, Watkinson 1997, Falińska 1998). Following the dynamics of spatial patterns is especially difficult and time-consuming with perennial clonal plants, characterised by two-level organization of their population: genets and ramets. The literature provides much information from few to up to 10-year observation periods

of long-lived perennials of different biological and ecological groups (e.g., Barkham 1980a, 1980b, Hutchings 1987, Wells & Cox 1991, Tumidajowicz 1995, Cain & Damman 1997, Czarnecka 2000, Brzosko 2002a). Fewer studies were carried out for 10–20 years (Falińska 1995, Woodward 1997, Adamowski 1998, Primack & Stacy 1998, Meyer & Schmid 1999, Kull 1999, Brzosko 2002b, Czarnecka 2006a). Studies carried out for 30–50 years, with some breaks, are still rather exceptional (Tamm 1972a, 1972b, 1991, Inghe & Tamm 1985, 1988). For the last decade the spatiotemporal patterns of a population seem to have been more often made a subject of mathematical modelling (e.g. Czárán & Bartha 1992, Bascombe & Solé 1995, Haase 1995, Harada & Iwasa 1996, Caswell 2001, Vesk & Westoby 2004), which represents a novel tool to understand the observed demographic patterns as well as to pose challenging hypotheses about the functioning of plant populations.

Long-term observation can provide interesting insights concerning the spatial structure formation on particular organization levels of the study population (genets and their aggregations, or ramets). It can also show the spatial structure of various life stages of individuals, from seedlings to adult genets. The analysis of spatial structure dynamics of plant populations raises numerous questions and problems which, although suggested by various authors, have not always been uniformly and fully addressed.

This study attempts to answer to the following questions: (i) which model of the abundance dynamics (May 1975, Harper 1977, Silvertown & Lovett Doust 1993, Watkinson 1997) is followed by a long-lived clonal plant population: stable, oscillation, stable limit cycle or chaos; (ii) what is the temporal arrangement of ‘structure scale’, understood by Gounot (1962) as the mean values of abundance and size of clumps, and ‘structure intensity’, that is, the degree of contrast between the areas of ‘thickening’ and ‘thinning’ of genets; (iii) how does the changing participation of genets of unitary, i.e. non-clonal compared to iterative, i.e. clonal growth (Harper & White 1974, Harper 1977, 1980) affect the abundance and spatial structure of a population; (iv) what is the relation between the population

spatial structure and the life-stage structure both of genets and ramets; (v) is the spatial pattern regenerated on hierarchical organization levels of a population; and if so, after what time does it happen.

I tested the following null hypothesis: in the expansion phase, the population abundance and large-scale spatial structure is affected first of all by the number of genets and their clumps, but in the stable phase with limited habitat resources population size is controlled mainly within independent clumps of genets, that is, at a small scale. To answer these questions, I choose an island, marginal population of *Senecio rivularis*, because it was possible to observe both its genet and ramet dynamics.

## Material and methods

### The species and study site

*Senecio rivularis* (syn.: *S. crispatus*, *S. crispus*, *Tephrosieris crispa*), Asteraceae, is a central European sub-element of the Alpine–Variscan–Carpathian distribution type. It occurs mainly in the mountains, primarily in damp places (Chater & Walters 1976, Meusel & Jäger 1992). In Poland *S. rivularis* reaches the northeastern border of its geographical range (Czarnecka 1997, Zajac & Zajac 2001). In the Vistula and Bug interfluvium *S. rivularis* is considered to be a threatened plant species (Kucharczyk & Wójciak 1995). It is extremely rare to the east of the Bug river, in Belarus (Parfenov 1980). *Senecio rivularis* prefers full light and seasonal or transitory shade. It usually appears in moist, meso- and eutrophic habitats, moderately or slightly acid, on peaty soils with a considerable proportion of mineral elements (Zarzycki *et al.* 2002).

*Senecio rivularis* is a long-lived, iteroparous rhizomatous clonal plant. It reaches its reproductive stage in the fourth or fifth year of the life cycle. The stem is normally 60–70 cm tall (maximum 120 cm), having 6–10 (rarely up to 14–16) leaves. The inflorescences resemble a loose subumbel and usually consist of about ten heads (sometimes up to 20–30). The brown, naked, ribbed achene, 3–4 mm long, has a 5–6

mm long pappus. One fruiting ramet can produce 200–1370 diaspores that germinate in two seasonal cohorts — in summer, immediately after the seed maturation, and in the next spring (Czarnecka 1995, 1998a, 2006b).

The marginal population of *S. rivularis* was studied in the Roztocze National Park (50°36'N, 22°59'E; 242 m a.s.l.), SE Poland. The species occurs here in a dried-up bog-alder community, with the tree layer dominated by *Alnus glutinosa* and about 90-year-old, introduced *Pinus sylvestris*. More than 80 vascular plant species form the ground flora that covers about 80% of the soil surface. The most abundant species apart from *S. rivularis* are *Deschampsia caespitosa* and *Valeriana simplicifolia*. *Senecio rivularis* occupies slight depressions filled with a peat layer (up to 100 cm deep) with more than 80% of organic matter content and pH 5.7–6.4, while it rarely grows on small mineral hillocks (Czarnecka 1995).

The nomenclature of the vascular flora follows Mirek *et al.* (2002).

## Data collecting and analysis

### Large-scale study: spatiotemporal patterns of genets

In 1987 the whole population area was divided into permanent 5 × 5-m (25-m<sup>2</sup>) plots and mapped at 1:50 scale during the flowering period (May–June) in 1987, 1991 and 1997. I marked the location of each genet, both of unitary (non-clonal) and iterative (clonal) growth on the maps as a point, taking into consideration three life stages: juvenile plants (young vegetative stage), mature vegetative plants (prereproductive and postreproductive, i.e. secondary vegetative, altogether), and reproductive plants (flowering and fruiting). Additionally, I collected data on genet survival, production of ramets, and rhizome disintegration on the basis of 100 genets in different clumps (labelled in spring 1988). The raising of the groundwater level after a series of wet years in the late 1990s, along with habitat disturbance made the continued observation of marked plants impossible and put an end to this project in 2000.

### Small-scale study: spatiotemporal patterns of genets vs. ramets

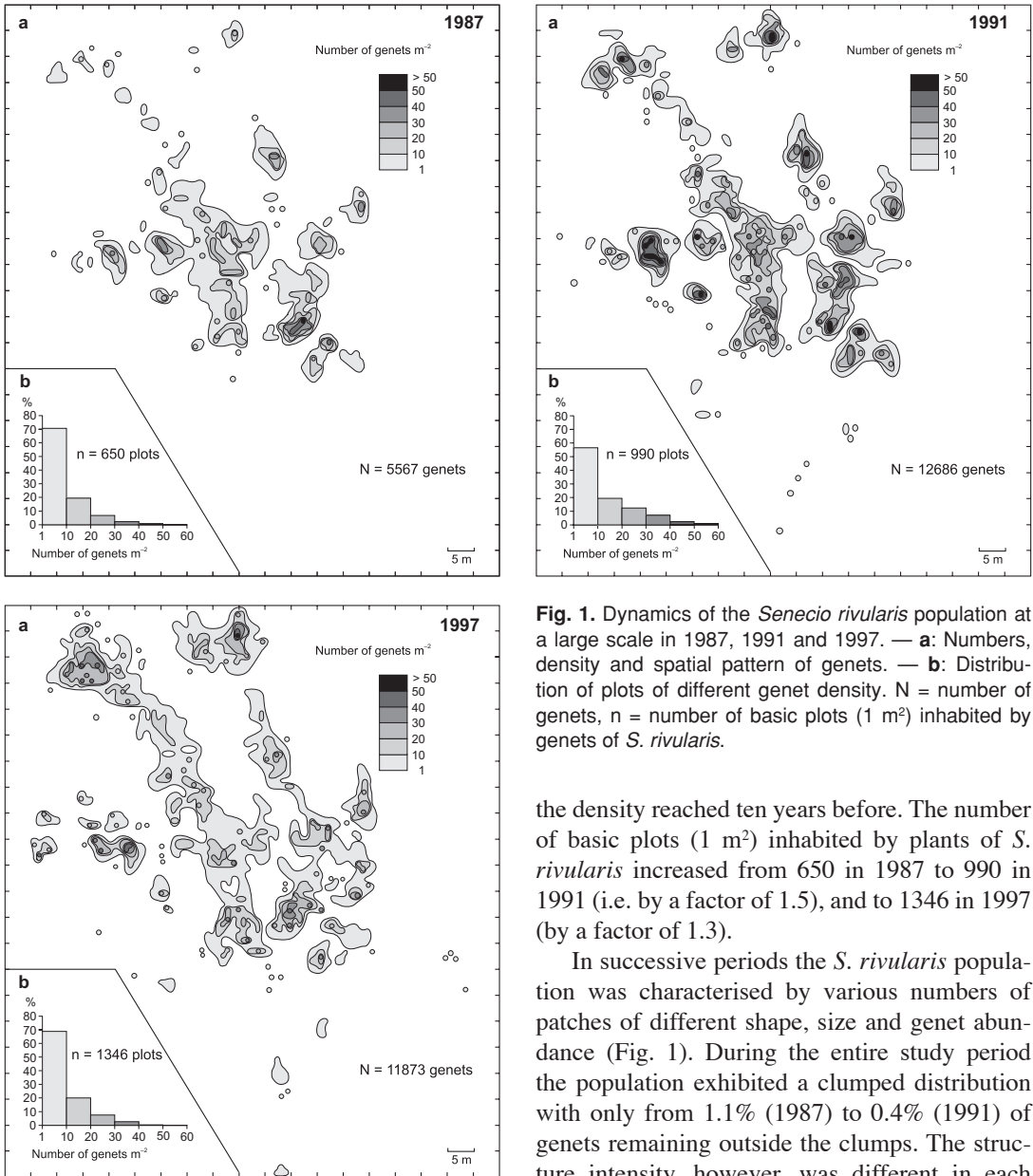
A selected patch (5 × 5 m = 25 m<sup>2</sup>) in the centre of the greatest clump was divided into permanent 1 × 1-m plots. I marked all the genets on the maps at 1:10 scale, with the description of the developmental stages of all the ramets, during the flowering period in five consecutive years (1987–1991) and the mapping was repeated in 1997.

I converted the mapping of the spatial distribution of genets and ramets, done during the field study, into isarithmic maps using the interpolation method. For the estimation of the population density on the level of genets within a whole population I took into consideration only the basic plots overgrown with the genets of *S. rivularis*, which is a measure of the actual use of the resources in the heterogeneous environment (so-called 'ecological density', cf. Robinson & Redford 1986, Gaston 1991). For the estimation of the spatial patterns on the level of genets and ramets I used the aggregation coefficient called Leksis' index (Steinhaus 1947). The Kruskal-Wallis test was used to check the significance of differences among the mean densities of genets and ramets calculated for successive study years, and for both spatial scales utilized. I analysed the proportion of unitary and iterative genets and ramets by means of the test of significance of differences between two fractions, i.e. the *U*-test.

## Results

### Patterns of genet dynamics

The examined population of *Senecio rivularis* exhibited considerable dynamics in the number, density and dispersal of genets, at a large scale (Table 1 and Fig. 1) and at a small scale (Table 2). In the first study period (1987–1991), the entire population abundance increased by 2.3 times and the average ecological density by 1.5 times. In the next period (1991–1997), I observed a small decrease in the number of genets (by 8%), but the average density was 1.4 times lower and reached the value comparable to



**Fig. 1.** Dynamics of the *Senecio rivularis* population at a large scale in 1987, 1991 and 1997. — **a:** Numbers, density and spatial pattern of genets. — **b:** Distribution of plots of different genet density. N = number of genets, n = number of basic plots (1  $m^2$ ) inhabited by genets of *S. rivularis*.

the density reached ten years before. The number of basic plots (1  $m^2$ ) inhabited by plants of *S. rivularis* increased from 650 in 1987 to 990 in 1991 (i.e. by a factor of 1.5), and to 1346 in 1997 (by a factor of 1.3).

In successive periods the *S. rivularis* population was characterised by various numbers of patches of different shape, size and genet abundance (Fig. 1). During the entire study period the population exhibited a clumped distribution with only from 1.1% (1987) to 0.4% (1991) of genets remaining outside the clumps. The structure intensity, however, was different in each of the analysed periods. In 1987 the population

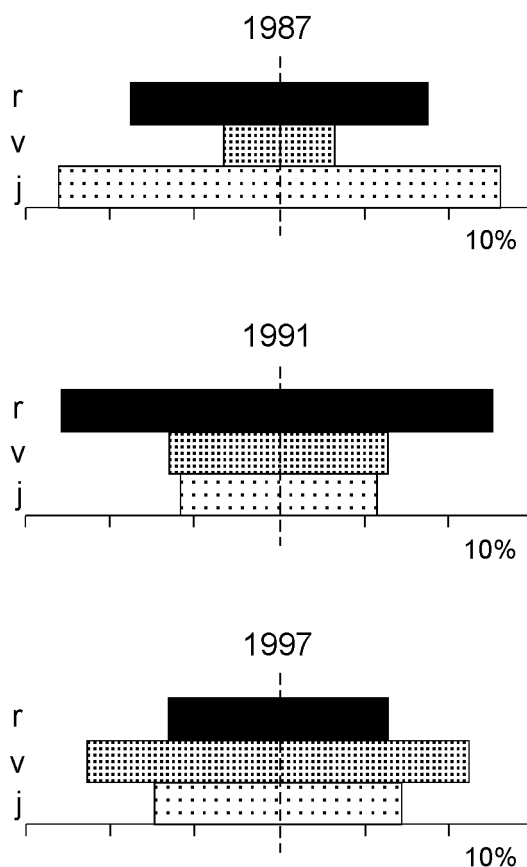
**Table 1.** Successive changes of abundance, density and dispersion of genets in the *Senecio rivularis* population.

Year	Area ( $m^2$ )	Abundance	Genets per $m^2$		Leksis' index $I = \frac{s^2}{\bar{x}}$
			mean $\pm$ SD	max	
1987	650	5567	8.6 $\pm$ 9.4	58	10.1
1991	990	12686	12.8 $\pm$ 17.7	71	24.3
1997	1346	11873	8.8 $\pm$ 8.9	55	8.9

$I < 1$  tendency to uniform distribution,  $I = 1$  random distribution,  $I > 1$  clumped distribution.

consisted of 22 clumps, with the biggest, central one occupying an area of 295 m<sup>2</sup> (45.5% of the whole population area) and having 2648 genets (47.6% of the total number of genets). In the whole population I observed very few basic plots with high density (more than 30 genets m<sup>-2</sup>). In 1991, the genets of *S. rivularis* were grouped into 26 clumps. On the area margins there developed numerous new aggregations. The majority of the clumps had been present since the beginning of the research, yet they were very dynamic: the bigger clumps ‘devoured’ the smaller ones, or they divided themselves into parts. More numerous clumps became the centres of high genet density. All these facts contributed to the doubling of the aggregation coefficient of the population ( $I = 10.1$  and  $I = 24.3$ , respectively). During the following six years new patches of *S. rivularis* continued to appear at a considerable distance from the ‘original’ area and the peripheral also increased in size. Meanwhile, in the centre of the area I observed a gradual unification of genet density, or even a decline of the number of the genets in some parts of the population. In 1997 the population consisted of several widespread patches of a polycentric character. The proportion of the basic plots with the lowest density (1–10 genets m<sup>-2</sup>) returned to the state noted ten years before (Fig. 1: 1987, 1997). All these facts resulted in the lowering of the aggregation coefficient of the population to the value formerly seen in 1987 (Table 1). Genet density significantly varied among some time periods (the Kruskal-Wallis test;  $H = 314.30$ ;  $P < 0.0001$ ). A much smaller intensity fluctuation in genet density occurred within some particular patches of *S. rivularis* (Table 2) ranging from 14 to 17 genets m<sup>-2</sup>.

‘Thickening’ and ‘thinning’ of the genets’ spatial distribution occurred in 1987, 1991 and 1997 (Fig. 1). These fluctuations demonstrate, apart from taking over new habitats mainly in the periphery of the area, that a gradual filling of the space within the already existing clumps also took place. In the clumps consisting of up to 20–30 genets the density was usually low and the distribution quite uniform or close to random. In clumps consisting of up to 100 individuals the aggregation coefficient took the values  $1 < I < 10$ .

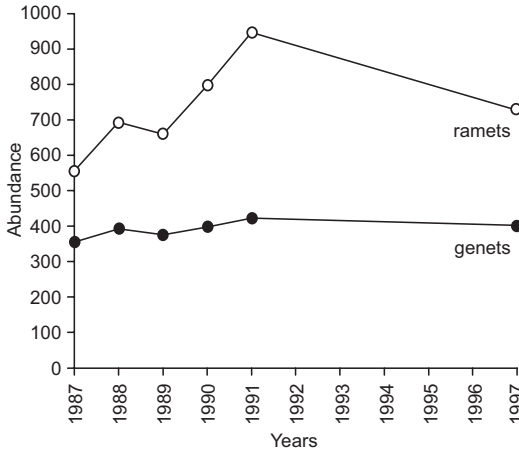


**Fig. 2.** The life-stage structure dynamics of genets in the *Senecio rivularis* population. j = juvenile genets, v = vegetative genets, r = reproductive genets.

In each of the study periods the population of *S. rivularis* exhibited a different life-stage structure of genets (Fig. 2). In 1987 the population consisted of almost 52% of juvenile individuals; four years later their percentage dropped to only

**Table 2.** Spatial distribution of *Senecio rivularis* genets in a 5 × 5-m plot in 1987–1991 and 1997.  $I^*$  = Leksis’ index; for other explanations see Table 1.

Year	Total number of genets	Genets per m <sup>2</sup>			$I^*$
		mean ± SD	min	max	
1987	357	14.3 ± 1.6	0	32	4.69
1988	388	15.5 ± 1.7	0	32	4.56
1989	375	15.0 ± 1.6	0	29	4.42
1990	392	15.7 ± 1.6	0	29	4.29
1991	422	16.9 ± 1.8	0	30	4.63
1997	407	16.3 ± 1.1	0	31	2.03

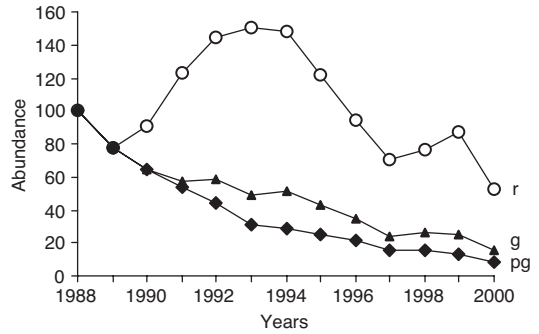


**Fig. 3.** Genet (dots) vs. ramet (circles) dynamics in the *Senecio rivularis* population. Data collected from a 5 × 5-m plot.

23%, while 51% of the population consisted of genets in the reproductive stage. In 1997 the stage structure was more balanced with the greatest percentage (45%) of genets in the vegetative stage. In the analysed three periods the ratio of juvenile and mature genets (both in the flowering and non-flowering phase) was 1:0.92, 1:3.35, 1:2.45, respectively. The proportion both of juveniles and reproductive plants were significantly different (*U*-test: *P* < 0.001).

**Patterns of ramet dynamics**

In 1987–1991, the number of ramets of *Senecio rivularis* increased by a factor of 1.7, and the ratio of the number of genets and ramets changed from 1:1.55 to 1:2.23 (Table 3 and Fig. 3). Until

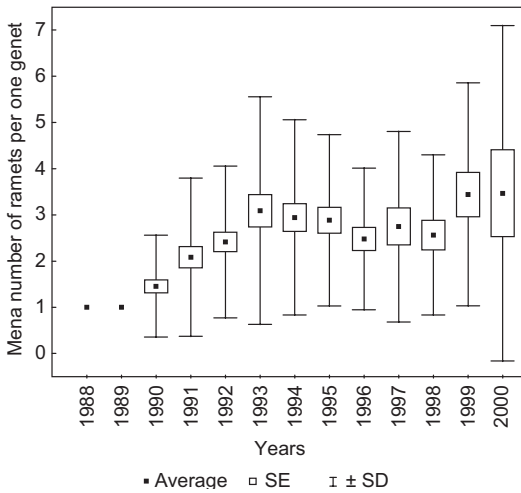


**Fig. 4.** Survival of 100 plants of *Senecio rivularis* in 1988–2000. pg = number of ‘primary’ genets (i.e. labelled in spring 1988), g = total number of genets (i.e. ‘primary’ and ‘descendant’ ones), r = number of ramets.

1997 the number of genets decreased by only 3.5%, while the number of ramets dropped by 23%. On average, one genet corresponded to 1.79 ramets. I observed that individual genets formed usually two or three (maximum eight) daughter rosettes (Figs. 4 and 5). The disintegration of ‘primary’ genets took place after the second or third flowering (in 6–7-year-old plants) and in exceptional cases in younger genets, that is, after the first flowering. Genets fall into two or three, and less frequently four, units (‘descendant’ genets), which differ from each other in size and the development stage, thus affecting the population abundance and spatial pattern in different ways. The units, which as a result of genet division came into younger fragments of rhizomes, were growing intensely and even producing a few ramets in the subsequent years. It seems that disintegration has a rejuvenating effect on the ‘descendant’ genets. Older frag-

**Table 3.** Distribution of *Senecio rivularis* ramets in different spatial scales. Data collected from a 5 × 5-m (25 m<sup>2</sup>) plot in 1987–1991 and 1997. *I*\* = Leksis’ index; for other explanations see Table 1.

Year	Total number of ramets	Ramets per m <sup>2</sup>			<i>I</i> *	Ramets per 0.25 m <sup>2</sup>			<i>I</i> *
		mean ± SD	min	max		mean ± SD	min	max	
1987	553	22.1 ± 11.7	0	41	6.18	5.5 ± 4.4	0	19	3.48
1988	685	27.4 ± 14.1	0	54	7.28	6.8 ± 5.2	0	19	3.95
1989	659	25.9 ± 13.2	0	45	6.68	6.6 ± 5.0	0	21	3.93
1990	795	31.8 ± 15.6	3	54	7.68	7.9 ± 5.6	0	24	4.00
1991	942	37.7 ± 20.1	4	67	10.73	9.4 ± 6.8	0	26	4.88
1997	729	29.2 ± 14.2	10	62	6.89	7.3 ± 6.1	0	28	5.12

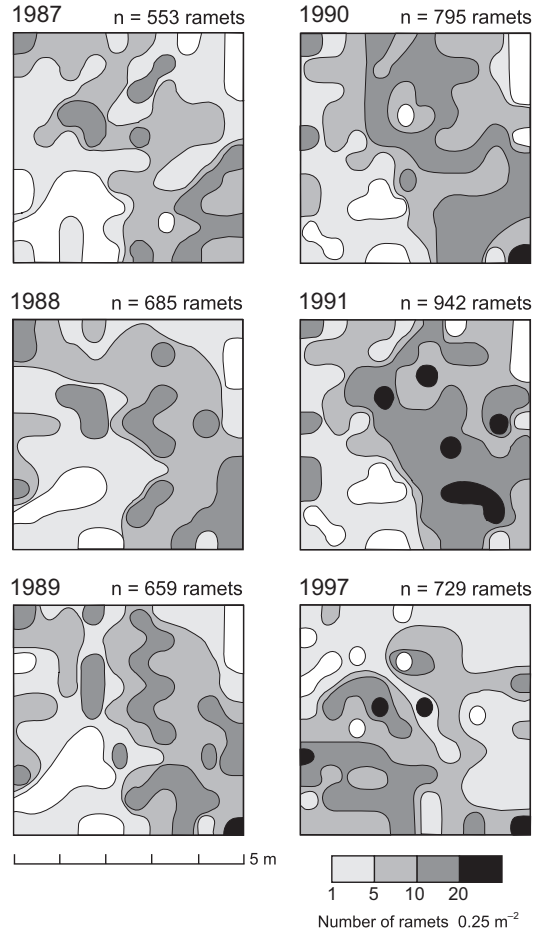


**Fig. 5.** Changes in numbers of ramets per one genet of *Senecio rivularis* in 1988–2000.

ments of rhizomes produce usually a decreasing number of ramets, sometimes only single above-ground shoots.

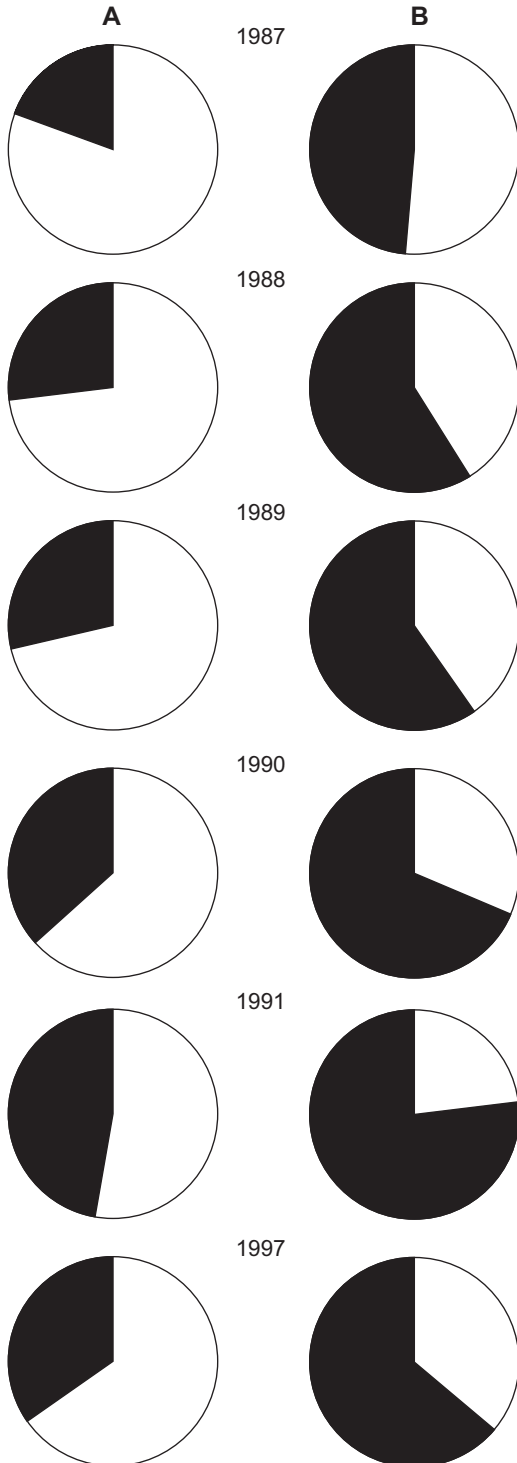
The spatial structure of ramets had a clumped character, irrespective of the scale adopted: 1 m<sup>2</sup> or 0.25 m<sup>2</sup> (Table 3). The maximum density was over 60 ramets m<sup>-2</sup> (or was close to 30 ramets per 0.25 m<sup>2</sup>). The increase in the ramet density was accompanied by a rise of the aggregation coefficient (at 1 m<sup>2</sup> scale  $I = 10.73$  in 1991). In the following period, I observed reduction of the spatial pattern intensity: in 1997 the value of the coefficient dropped to the level reached eight and ten years before. By contrast, the aggregation coefficient in the 0.25-m<sup>2</sup> scale increased (Table 3). In the successive years the differences in density at both scales were significant (Kruskal-Wallis test: at 1 m<sup>2</sup>:  $H = 20.86$ ,  $P < 0.001$ ; at 0.25 m<sup>2</sup>:  $H = 11.27$ ,  $P < 0.05$ ).

With the passage of time the spatial pattern of ramets changed too (Fig. 6). The genets present already at the onset of the research spread out and filled the space. Already in 1989 the plots reached densities of 20 or more ramets per 0.25 m<sup>2</sup>, and the intensity of the pattern continued to increase steadily until 1991, accompanied by the increase in the number of ramets (Table 3 and Fig. 3). On the other hand, the sites without genets of *S. rivularis* at the beginning of the study were gradually colonised and in 1997 exhibited a greater density of ramets than the sites initially occupied.



**Fig. 6.** Dynamics of ramet numbers (n), density and spatial pattern at a small scale. Data collected from a 5 × 5-m plot.

The spatiotemporal pattern of ramets was accompanied by two phenomena: (i) changes in the proportion of genets of unitary and iterative growth (Fig. 7A), and (ii) by the contribution of both of those categories to the total number of ramets in the population (Fig. 7B). The proportion of the iterative genets increased consistently from barely 20% in 1987 to 47% in 1991, while their contribution to the ramet production reached 48% and 76%, respectively. In 1997 the percentage of genets belonging to the two categories was back at the state of 1990. Proportions of unitary and iterative genets were significantly different ( $U$ -test:  $0.001 < P < 0.05$ ) except the years: 1988–1989 as well as 1989–1997 and 1990–1997. However, the contribution of ramets



**Fig. 7.** The share of unitary (white fields) and iterative (black fields) genets (**A**) and ramets originated from unitary and iterative genets (**B**). Data collected from a 5 × 5-m plot.

produced by iterative genets were not always statistically significant.

The transformation of the spatial pattern was reflected in the changing stage structure of ramets (Fig. 8). In 1987, I observed a balanced proportion of ramets belonging to all categories. In the following years, however, the proportion of juvenile ramets decreased gradually, thus confirming the decrease of the unitary genet share, which reached its lowest value in 1991 (Fig. 7A). Hence a reversed pyramid was present with only 12% of juvenile plants and 57% of reproductive ones until 1997 when the rejuvenation of the stage structure of ramets took place, connected with the increasing proportion of ramets originating from unitary genets. The differences in the proportion of reproductive ramets were significant between 1991 and all remaining study years ( $U$ -test;  $0.001 < P < 0.05$ ). The contribution of juvenile ramets was significantly different only between 1987 and other years ( $0.001 < P < 0.01$ ) as well as between 1988 and 1991 ( $P < 0.05$ ).

## Discussion

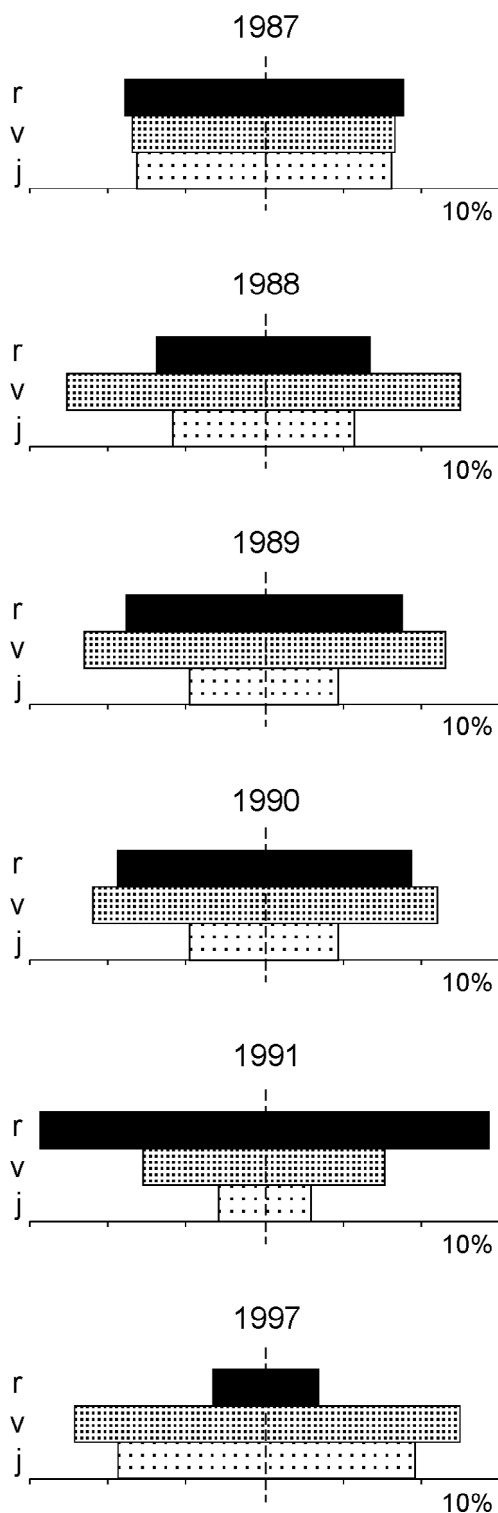
### Temporal arrangement of abundance and spatial structure of a population

After a successful colonisation event within a given habitat, populations usually exhibit considerable growth (e.g. Hartnett & Bazzaz 1985, Falińska 1986, 1995, Adamowski 1998, Meyer & Schmid 1999). The total lifetime of the study population of *Senecio rivularis* is unknown, yet already at the beginning of the 1970s it covered an area of ca. 800 m<sup>2</sup> and consisted of six dense clumps and some groups consisted of several distinct individuals (Izdebski 1972). In 1987–1991, the genet abundance increased 2.3 times, while the mean density and the area actually used by the population increased by a factor of 1.5. These numbers prove that the population of *S. rivularis* was still in an expansive phase, and its abundance and large-scale spatial pattern were regulated mainly by the number and diversity of clumps. The latter originated quite rapidly around separate genets in the reproductive stage, especially along the population margins where the genera-



tive reproduction effectiveness and the juvenile genet survival were significantly higher than in the centre (Czarnecka 1995, 1998a, 1998b). It seems that in this period favourable habitat conditions were most decisive for the population dynamics. Sufficient 'safe sites' for seed germination and seedling establishment (*sensu* Harper & Sagar 1953) and adequate nutrient availability appear to have been available.

Abiotic structure of the environment, that is, environmental heterogeneity in terms of geomorphology-related gradients, bedrock composition, soil depth and texture, etc., tends to produce patterns that do not change over time. In contrast, biotically generated heterogeneity both of below-ground (nutrients, water) and above-ground (space, light) resources, tends to be dynamic (Herben *et al.* 2001). The degree of heterogeneity in the biotic environment depends on hierarchical selection of plant individuals and on differences in competitive ability among them (Eriksson & Jerling 1990). Competitive ability varies as a function of plant age or life-stage, particularly in clonal species (Grubb 1977, Grace 1985, Howard & Goldberg 2001, Weiner 2004, Lamb & Cahill 2006). The dominant process of competition is occupation of horizontal space, called spatial expansion (Herben & Hara 1997), expansion in space (Czarnecka 1998c) or horizontal competition (Grubb 1986). Together with the increase in the density of genets within particular patches, and with the changes in the stage structure of genets (from the dominance of juvenile genets and/or the unitary adult genets to the dominance of adult genets of iterative growth), the intrapopulation relationships become more and more important for the abundance regulation of the number of clumps. It results from the fact that together with the depletion of nutrients, the competition between genets becomes stronger generating 'self-thinning' within a given clump (e.g. White & Harper 1970, Weiner 1988, 1995, Silvertown & Lovett Doust 1993, Hutchings 1997, Gersani *et al.* 1998, Falińska 1998, 2002, Day *et al.* 2003). The genets which appeared earlier increased their 'biological space' (Ross & Harper 1972) by vegetative growth (sprouting), which is a conspicuous link between dynamics at the level of ramets and the level of individual plants or genets (Harper 1977). The foraging



**Fig. 8.** The life-stage structure dynamics of ramets. j = juvenile ramets, v = vegetative ramets, r = reproductive ramets. Data collected from a 5 × 5-m plot.

ability of older genets in heterogeneous environments increases due to their expansion over the younger genets established later (Grime *et al.* 1986, Grime 1988, Silvertown & Lovett Doust 1993, Hutchings & de Kroon 1994, Kleijn & van Groenendael 1999, van Kleunen & Fischer 2001). My observations confirm the statement that the success of an individual genet is a function of 'available area', which has been convincingly documented for numerous species (Harper 1977, Mithen *et al.* 1984, Hartnett & Bazzaz 1985, Klinkhamer & de Jong 1988, and others).

The insufficiency of resources in a given part of a biotope, that is, within a given clump, results in self-thinning of a population (White & Harper 1970, Harper 1977, Hutchings & Budd 1981, Hutchings 1997), and the increased growth of the genets intensifies the process (e.g. Lovett Doust 1981, Goldberg 1988, Weiner 1988, 1995, Clark 1990, Silvertown & Lovett Doust 1993). After the first period (1987–1991) when the average density of the *S. rivularis* population increased from 8.6 to 12.8 genets m<sup>-2</sup>, and its maximum density increased from 58 to 71 genets m<sup>-2</sup>, I predicted that the density could not keep on growing because of the size of adult plants and their space and nutrient demands (Czarnecka 1995). For example, in 1987 and 1991 the average diameter of a leaf rosette of genets was almost 29 cm and 21 cm, respectively; in the next study period it decreased to ca. 17 cm. Simultaneously, the mean stem height for genets in the reproductive stage exceeded 73, 71 and 63 cm (Czarnecka 2006b). At least in the central part of the area, that was occupied first, the population had already filled the available space and had reached a relative balance with habitat resources. It can be assumed, then, that it entered the phase of stable growth and that its abundance was shaped according to the oscillation type (May 1975, Silvertown & Lovett Doust 1993, Falińska 1998, 2002), with some abundance fluctuations. A small decrease in the number of genets (by 8%) in 1991–1997 shows that the intensive recruitment of new genets and the formation of new clumps along the margins of the population area were not able to compensate for the losses in the centre caused by various factors, such as habitat structure and intrapopulation competition.

Some researches maintain that long-lived

herbaceous perennials are characteristic of a stable type of population dynamics, or that it is impossible to characterize what kind of dynamics (if any) their populations exhibit (e.g. Crawley 1990). According to Eriksson (1993) this statement may be a consequence of too short a period of observation or covering too small a part of a population. In my study the conclusions concerning the abundance dynamics and spatial patterns seem to be justified: they were drawn on the basis of eleven seasons of research during which time the whole population was investigated three times.

### **Genet vs. ramet dynamics: changes in the numbers and spatial patterns**

The population dynamics of clonal plants may be considered at two different levels: dynamics of genets, that is, units composed of all tissue originating from one zygote, and the dynamics of ramets, that is, potentially independent parts of a genet (Harper & White 1974, Harper 1977, Eriksson 1993, Watkinson 1997). Changes in the numbers of genets may have different consequences than changes in the numbers of ramets. The birth and death schedules of genets affect the genet population size and genetic composition and are evolutionarily relevant, while the birth and death rates of ramets affect the size and fitness of individual genets (Hartnett & Bazzaz 1985). There may also be an interaction between genets and how many ramets they are composed of that may affect fitness differentiation among individuals within a population.

Various plant features are of great importance in population dynamics, filling and keeping the occupied space and in relations with neighbours, that is, the number of ramets per a single genet, the inner spatial-stage structure, size of underground and above-ground parts, persistence of morphological ties and exchange rate of ramets within a genet (Czarnecka 1998c). In the study period the relationship between the numbers of genets and ramets in the population of *Senecio rivularis* was relatively stable with the values ranging from 1.58 to 2.12 ramets per genet. This was a result of the variable presence of genets of unitary and iterative growth, lifespan

of genets, and the intensity of the genet division. A similar pattern in the number of genets and ramets was observed in the two other species of the Asteraceae, *Cirsium rivulare* and *C. oleraceum* (Kotańska 1986), comparable to *S. rivularis* in terms of the genet size and rhizome persistence, and inhabiting moist and wet places. A completely different pattern of the genet and ramet dynamics occurred, when the recruitment of seedlings is limited in a population, as well as when the plants increase their biomass at an exceptionally high speed and have a high capacity for vegetative growth to fill the physical space with both biomass and necromass; in other words, when they are characteristic of high competitive abilities (*sensu* Grime 1973). In populations of many clonal species, for example, *Asarum europaeum* (Czarnecka 1996), *A. canadense* (Cain & Damman 1997), *Mercurialis perennis* (Falińska 1982), *Narcissus pseudonacissus* (Barkham 1980b), *Iris pseudacorus* (Falińska 1986), *I. aphylla* (Czarnecka 2000), *Filipendula ulmaria* (Falińska 1995), *Typha angustifolia*, *T. latifolia* and *Phragmites australis* (Fiala 1976, 1978) the increase in numbers of genets follows a logistic model while that of ramets follows an exponential model. Genet and ramet dynamics of invasive species of *Solidago* spp. also follows an exponential model (Hartnett & Bazzaz 1985, Meyer & Schmid 1999) such that the genets recruited in first seasons after the abandonment of arable fields had the highest survival and expanded rapidly *via* daughter ramet production.

The dispersion type of ramets of *S. rivularis* was always clumpy ( $I > 1$ ) both at 1-m<sup>2</sup> and 0.25-m<sup>2</sup> scales, but at the same time it was subject to some fluctuations: the ‘thickening’ areas became, after some time, the ‘thinning’ ones and *vice versa*. The observation of ramet dynamics shows that this cycle can last from several to ten or more years, which reflects the established lifespan of *S. rivularis* genets within the study population. In gaps left by dying old plants recruitment of new genets commonly took place. This cyclic replacement of older genets by younger ones foster the degree of heterogeneity in the biotic environment and is commonly recognized as a vital factor impacting the spatial dynamics of populations and communities

(Grubb 1977, 1986, Grime 1978, 1979, White 1979, Grubb *et al.* 1982, Pickett & White 1985, Begon *et al.* 1990, Watkinson 1997, Day *et al.* 2003, Wijesinghe *et al.* 2005).

## Conclusions

1. In the expansion phase the spatial structure and the population abundance is affected by the number and size of particular clumps, and in the fluctuation phase its growth is manifested mainly by dynamics within the clumps themselves. Thus, the null hypothesis was confirmed.
2. In each of the study years there existed clumps differing in their area, number, density and mode of genet dispersion. Smaller clumps were usually characteristic of monocentric density distribution and exhibited random or uniform spatial patterns. Large clumps, consisting of several hundreds or even thousands of genets, exhibited a polycentric distribution of genet density.
3. It cannot be said that long-lived clonal plants exhibited a stable type of population dynamics. In the expansion phase of the population, i.e. the situation when sufficient habitat resources are present (mainly space and soil nutrients), regardless of the species character (invasive or non-invasive), the genet dynamics exhibited a logistic model of growth, while that of ramets exhibited an exponential growth pattern. In the phase of stable resource dynamics an oscillation type of growth was found at the genet and ramet levels alike.
4. Different factors seem to be important for the population dynamics in the phases of expansion and fluctuation, respectively: environmental conditions, plant features, and intrapopulation relations.
5. The spatial pattern of the whole *Senecio rivularis* population, that is, on the level of genets and their clumps, was variable at all times. However, on the level of ramets within particular patches the spatial pattern concerning ‘structure scale’ and ‘structure intensity’ may be regenerated in the period representing the mean lifespan of genets, i.e. in about ten years.

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