Biologia, Bratislava, **56**/1: 57—62, 2001

Small-scale spatial pattern of two common European geophytes *Allium oleraceum* and *A. vineale* in contrasting habitats

Martin DUCHOSLAV

Department of Botany, Faculty of Science, Palacký University, tř. Svobody 26, CZ-77146 Olomouc, Czech Republic; tel.: ++420-68-5241024, fax: ++420-68-5241027, e-mail: duch@risc.upol.cz

DUCHOSLAV M. Small-scale spatial pattern of two common European geophytes *Allium oleraceum* and *A. vineale* in contrasting habitats. Biologia, Bratislava, **56:** 57—62, 2001; ISSN 0006-3088.

The small-scale spatial patterns in *Allium oleraceum* L. and *A. vineale* L. populations, both common European geophytes, were studied in four contrasting habitats (meadow, scree, scrub and forest). Coefficient of dispersion indicated marked clumped distribution of the individuals of both species in all habitats. Pattern analysis revealed considerable differences in pattern both between species studied and among populations of respective species studied. The analyses clearly point at two distinct morphological features of both species concerning dispersion, which affect pattern of their populations – formation of daughter bulbs and that of aerial bulbils. Existence of 'morphological' patches at low block size was a common feature of all *A. vineale* populations studied regardless of habitat; the patchiness was caused by frequent production of many daughter bulbs in close neighbourhood of the parent plant. In contrast, variable and almost no remarkable small 'morphological' patches of *A. oleraceum*, corresponding to clumps of plants originated from daughter bulbs, were detected since daughter bulbs were frequently produced above ground and thus embodied a potential to disperse to the longer distance from the parent plant. Cluster dispersion of bulbils and their restricted dispersal distances were responsible for occurrence of small patches and second-order patches in most populations of both species.

Increase in mean square with increasing block size in the forest and shrub populations of both species studied suggested heterogeneity at higher scales. This heterogeneity was probably related to demography of species, environmental heterogeneity and/or spatial dynamics of the tree and shrub canopy. Disturbance could play important role in dispersal and the spatial structure of populations of both species.

Key words: *Allium*, clumping, density, dispersion, pattern, two term local variance method (TTLQV).

Introduction

Small-scale spatial distribution of individuals is a universal feature of plant populations (GREIG-SMITH, 1979; KERSHAW & LOONEY, 1986). This heterogeneity may be related to intrinsic growth pattern and type of dispersal of the species, to variation in environment, effect of competition with other species, and influence of animals (KERSHAW, 1973). Moreover, pattern of each population is influenced by historical events, which may be difficult to recognise (GREIG-SMITH, 1979).

Studying population ecology of two common European geophytes – *Allium oleraceum* and *Allium vineale* – I found great differences in the stage and size structure, reproduction and propagation among populations from different habitats. Thus, the impression arose that variable performance of species studied under various environmental conditions could affect their small-scale pattern in the field.

Here I report results of pattern analysis that were performed in four contrasting habitats (forest, scrub, scree, meadow) where respective species frequently occur. The analysis focused on the following questions: (1) Do *Allium oleraceum* and *A. vineale* show different small-scale spatial distribution in contrasting habitats? (2) What is the size of the patches/gaps in different habitats? (3) Could the observed pattern be related to the (a) morphology of the species, and (b) various performance of species studied in the field?

Material and methods

Studied species

Allium oleraceum L. (subgen. *Allium*, sect. *Codonoprasum* Reichenb.) is a bulbous herb with 1–4 leaves. Leaves are linear to filiform, fistular in lower part and sheathe the lower half of the scape. Populations consist of single to two-leafed immature plants and three- to four-leafed fertile ones, which usually produce one non-dormant daughter bulb. Sexually mature plants produce a loose lax umbel at the top of a scape with a few of hermaphrodite, protandrous flowers (0–20), a few or many bulbils (10–60) and persistent spathe. Flower can potentially produce six seeds (HÅKANSSON, 1963; STEARN, 1980).

Allium vineale L. (subg. *Allium*, sect. *Allium*) is a bulbous herb with 1–4 leaves. Leaves are subcylindrical, fistular and sheathe the lower third to two thirds of the scape. Like in *A. oleraceum*, the populations contain single to two-leaved immature plants and three- to four-leaved fertile ones. Fertile plants usually produce one to four dormant daughter bulbs. Sexually mature plants produce a compact umbel at the top of a scape with a variable number of hermaphroditic, protandrous flowers (0–30) and bulbils (0–60) ranging from umbels with only flowers to umbels with only bulbils. Flower can potentially produce six seeds. Spathe is deciduous (RICHENS, 1947; STEARN, 1980).

Allium oleraceum and *A. vineale* share many similar features: (a) they are similar in the habit and the size, (b) they possess three modes of propagation – besides sexual reproduction by seeds both species produce aerial bulbils and daughter bulbs, and (c) they occur in wide range of habitats from dry grasslands and rocky ground to scrubs and forests, frequently together.

Study sites

Three populations of *A. oleraceum* from different habitats were selected for this study:

(1) Scree: E Bohemia, Přibylov; a population growing on nutrient-poor dry sliding marl slope in open herb community (cover of herb layer: 25%) dominated by *Sanguisorba minor* and *Salvia verticillata* (*Salvio-Sanguisorbetum* Studnička 1980, *Bromion* Koch 1926) near the village (420 m altitude);
(2) Scrub: E Bohemia, Voletice; a population dominated the understory of *Fraxinus excelsior-Crataegus* spp. semi-dry shrubs (cover of shrub layer: 60%, herb layer: 50 %; *Berberidion* Br.-Bl. 1950) near the village (340 m altitude);
(3) Forest: C Moravia, Slatinice; a population subdominated the understory of a *Robinia pseudacacia* coppice (cover of three layer: 85%, shrub layer: 75%, herb layer: 60%; *Chelidonio-Robinietum* Jurko 1963, *Chelidonio-Robinion* Hadač et Sofron 1980) in the valley of a brook near the village (270 m altitude).

Three populations of *A. vineale* from different habitats were selected for this study:

(1) Meadow: E Bohemia, Štěnec; a population occurring in mesophilous meadow dominated by *Arrhenatherum elatius* (cover of herb layer: 100%; *Arrhenatheretum elatioris* Braun 1915, *Arrhenatherion* J. Braun 1915) near the village (340 m altitude);
(2) Scrub: E Bohemia, Štěnec; a population occurring in the understory of a *Prunus spinosa* scrub (cover of shrub layer: 90%, herb layer: 10%; *Berberidion* Br.-Bl. 1950) near the village (340 m altitude);
(3) Forest: the same locality as (3) in *A. oleraceum*.

Methods

Density was estimated for each population by counting plants in 30 to 120 randomly located quadrates, 0.25 m^2 each. The dispersion pattern was measured by s^2/x (i.e. coefficient of dispersion sensu BLACKMAN, 1942), where s^2 was a variance and x was the respective arithmetical mean (GREIG-SMITH, 1983).

Three to six transects (further referred to as T1 – T6 in the text) of 300 0cm each were established in May 1996 within each site studied. Density of *A. vineale* in each of 300 (1 × 1 cm) quadrates and that of *A. oleraceum* in 150 (2 × 2 cm) quadrates along each transect was recorded. HILL's (HILL, 1973) two term local variance method (TTLQV) was applied for analysing the transect data. An analysis was always stopped at a block size 100 in the case of *A. vineale* and 50 in the case of *A. oleraceum* to avoid decreasing reliability with the decreasing number of averaged terms (LEPŠ, 1990).

Table 1. Density (mean ± s.d.) and coefficient of dispersion of *A. oleraceum* and *A. vineale* populations studied. Difference between the observed ratio and unity was tested by means of a t-test (GREIG-SMITH, 1983).

	A. oleraceum			*A. vineale*		
	Scree $n = 30$	Shrub $n = 30$	Forest $n = 30$	Meadow $n = 120$	Shrub $n = 46$	Forest $n = 30$
Density (ns. per 0.25 m^2)	80.1±61.5	31.7±52.4	10.3±19.3	9.8±52.9	14.3±32.6	81.5±160.2
Coefficient of dispersion	47.3***	86.6***	36.4***	287.3***	74.3***	338.9***

*** $P < 0.001$

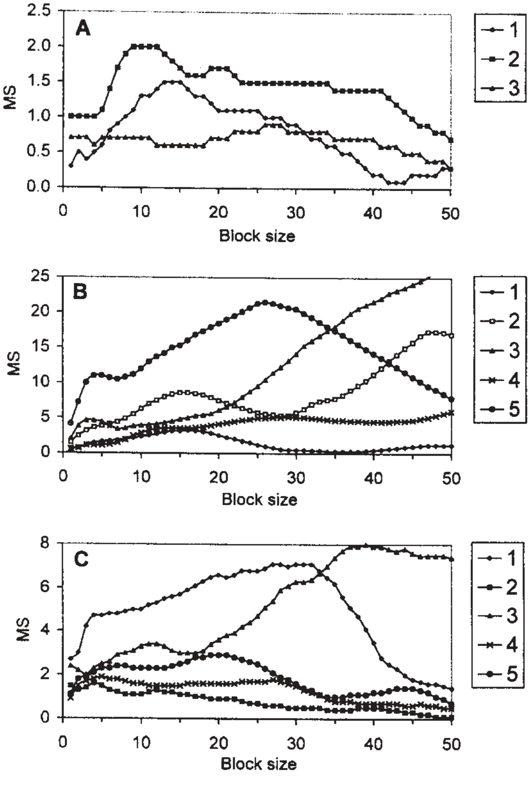

Fig. 1. Pattern analysis of three populations of *A. oleraceum*. A – scree, B – scrub, C – forest. Results of analysis of transects established within respective populations are shown.

Results

Density

Both species showed great variability in their densities at the studied sites. While mean density of *A. oleraceum* decreased in the direction from open to shaded sites, the density of *A. vineale* showed an opposite trend (Tab. 1). Coefficient of dispersion was significantly greater than one in all populations, which indicated clumped distribution of both species in the field (Tab. 1).

Pattern analysis

TTLQV revealed considerable differences in the pattern both between species studied and among populations of the respective species studied (Figs 1, 2).

A. oleraceum. The scree population of A. oleraceum did not show any distinct pattern. While any marked peak was not detected in the T3, plain peaks at block size ranged from 9 to 12 and 15 to 20 were detected in other transects. These peaks correspond to gaps between aggregations of different size of A. oleraceum.

Two scales of aggregation were detected by TTLQV in the scrub and forest populations. The picture (Fig. 1) suggests peak at the block size 3–4 (6–8 cm) in the T3 and T5 of scrub population. The peak corresponds to patches of individuals originated from clusters of bulbils growing on shallow soil. In the forest, the peak at the block size 4–5 (8–10 cm; T1, T2, T4) is not very distinct and corresponds to the basic 'morphological' patches composed of the clusters of plants originating from daughter bulbs. Less distinct peak at the block size 14–18 (28–36 cm) detected in the shrub population and peaks at the block size of about 11–13 units (22–26 cm; T2, T3) and 18–21 units (36–42 cm; T5) detected in the forest population correspond to the second-order patches. Peak at the block size 25 detected by analysis in the scrub (T5) corresponds to gaps between aggregations of *A. oleraceum*.

A. vineale. Existence of 'morphological' patches at low block size was a common feature of all populations studied (Fig. 2). In the meadow, TTLQV suggested distinct peaks at the block size 5, 8,

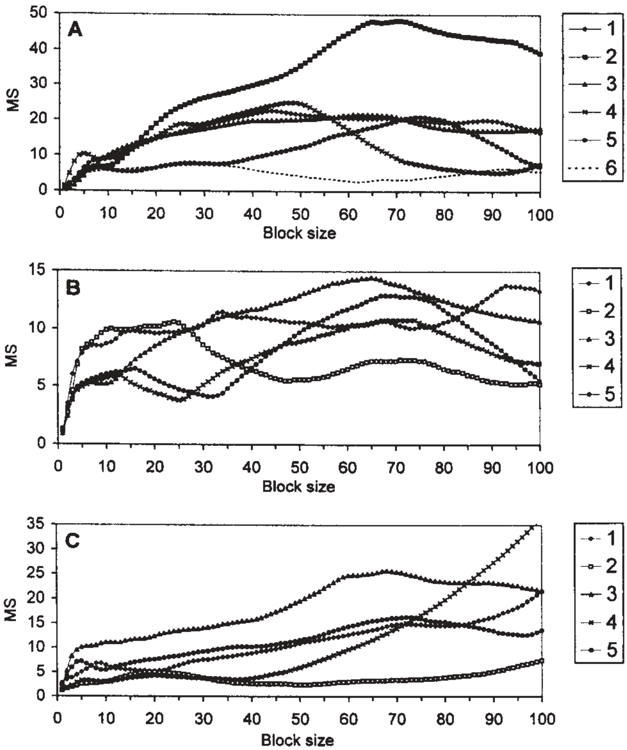

Fig. 2. Pattern analysis of three populations of *A. vineale*. A – meadow, B – scrub, C – forest. Results of analysis of transects established within respective populations are shown.

20 and 26, which correspond to 'morphological' clumps of this species. Less distinct peaks at the block size 44 (T4) and 48 (T6) represent second-order patches formed by closely situated two or three clumps. In most transects, peaks at the block size about 65 (T1), 75 (T1, T5) and 90 (T1, T2, T6) were detected by the analysis and correspond to the gaps between the second-order patches.

The pattern of *A. vineale* in the scrub was very similar to that found in the meadow. TTLQV recognised clear 'morphological' aggregations at the block size 6–16. Pronounced peaks at block size 34 and 24 were recognised in T1 and T2, respectively. The peaks correspond to second-order patches of two – three clumps separated by gaps of the similar size. The peak at the size about 70 corresponds to gaps between the second-order patches.

In the forest, TTLQV recognised pronounced peaks at the block size ranging from 4 to 9 that correspond to 'morphological' clumps of this species. Obscure peak at the block size 70–75 corresponds to gaps between patches variable in size. Increase in the MS suggests heterogeneity at higher scales.

Discussion

Influence of plant traits

Performed analyses clearly pointed to two distinct morphological features of both species studied that were reflected in their dispersion, which in turn affect pattern of their populations: formation of daughter bulbs and that of the aerial bulbils. Both species indeed differ in many characters associated with daughter bulbs. Plants of *A. oleraceum* produce sporadically one non-dormant daughter bulb above(below)ground. Developing daughter bulbs with long axis usually broke the aboveground sheathing bases of the foliage leaves due to the formation of the contractile roots and bulb and elongation of covering leaves. Thus, there is a potential to disperse to longer distances (5–10 cm) from the parent plant since new daughter plant exhibits centrifugal growth. The daughter bulbs frequently fail to pull into the soil. Since the physical connection between the mother plant and daughter bulb decays in the summer, daughter bulbs are dispersed on the soil surface to cover longer distances, especially on slopes. In contrast, *A. vineale* produces up to four dormant daughter bulbs below ground in close vicinity of the parent plant (RICHENS, 1947; HÅKANSSON, 1963). This in part explains why the analysis detected variable and almost non-distinct 'morphological' patches of *A. oleraceum* that would correspond to clumps of the plants that had originated from the daughter bulbs, whereas pronounced clumps of *A. vineale* occurred in all sites studied.

Since the propagation via daughter bulbs allows the plants to spread only short-haul, seeds and bulbils should play dominant role in the dispersion for longer distances. In dispersal experiment with seeds and bulbils of *A. vineale*, RONSHEIM (1994) found out that most of bulbils and seeds (> 90%) had fallen within 50 cm off the parent plant in *A. vineale*. Moreover, clumped dispersal pattern was observed among bulbils in this species (RICHENS, 1947; RONSHEIM, 1994). According to my field observations *A. oleraceum* exhibits similar features although it produces only very low or no seed-set and fewer bulbils than *A. vineale*. Cluster dispersion of the bulbils and their restricted dispersal distances are thus responsible for the occurrence of (i) the small patches and (ii) the second-order patches detected by TTLQV in most of populations in both species. Moreover, occasional setting of many seeds in *A. vineale* (RICHENS, 1947; STEARN, 1980) and ability of the seeds to travel farther than any of the bulbils (> 1 m; RONSHEIM, 1994) allow *A. vineale* effective dispersion to a greater distance.

Effect of species demography, environment and competition

Although both species occur in wide range of habitats (DUCHOSLAV 2000, in press) the light is the most decisive environmental factor influencing their reproduction: *A. vineale* is mostly incapable of flowering under closed canopy in contrast to the (ir)regular sexual reproduction of *A. oleraceum* in the scrubs and forests. That is why populations of *A. oleraceum* differ from those of *A. vineale* in the absence of clear gaps with certain size between the second-order patches. Moreover, bad performance of *A. vineale* at shaded sites affects size of its 'morphological' clumps that were found to be smaller in the scrub and forest compared to those in the meadow.

Nevertheless, higher inequality in bulbil size and apparently low mean dry-mass of bulbils found in *Allium* plants growing in shaded habitats decrease bulbil germination rate (KROCHMAL, 1952) and could give rise to lower probability of establishment of juveniles from small bulbils in the natural stands. Thus, the existence and persistence of patches of *Allium* in forests and scrubs is in part a function of the demography of the species. Similar results were obtained by BARKHAM (1992) in his experiments with *Narcissus pseudonarcissus*.

Increase in MS with increasing block size (Figs 1, 2) in the forest and scrub populations of *A. vineale* and *A. oleraceum* suggests that there is a pattern at higher scales. This heterogeneity is probably related to environmental heterogeneity and/or spatial and/or temporal dynamics of the tree and shrub canopy. Both species usually form large (sparse) patches (ca 4–10 m in diameter) in these habitats (DUCHOSLAV, unpublished observations). The patches probably indicate areas of higher light intensity due to lower cover of canopy at present or in the past. Tree-fall, tree felling or poor local performance of shrubs and trees could be the cause. *Allium* plants respond immediately to increased light and many of them produce bulbils and seeds in the next year following the tree-fall. After canopy closure, population growth is mostly limited to peripheral spreading via daughter bulbs.

Disturbance could play an important role in dispersal and spatial structure of populations of both species. In contrast to other habitats, *A. oleraceum* is patchily distributed in the scree: the size of aggregation is clearly determined by environmental heterogeneity due to variable intensity of erosion that causes movement of skeleton. Moreover, clusters of the bulbils and the daughter bulbs are broken apart and buried in the skeleton, which further increase heterogeneity of the population.

Occasional weak below-ground disturbance in the case of *A. oleraceum* or even strong one (e.g. ploughing, unearthing) in the case of *A. vineale* can allow the populations to spread and cause decreasing of intra- and interspecific competition, which is quite intensive in relatively 'stable' habitats even with above ground disturbance (e.g. in meadow) (LAZENBY, 1961a, b). Remarkable occurrence of *A. vineale* in the neighbourhood of trees in the orchards and plantations is just related to frequent unearthing of bulbs from the ground by voles and to incomplete mowing around trees that allow plants a complete reproduction. In addition, production of many aerial bulbils and dormant daughter bulbs are probably decisive features allowing *A. vineale* to be a troublesome weed in arable land in several parts of the world (RICHENS, 1947; ILTIS, 1949; HÅKANSSON, 1963).

Acknowledgements

I would like to thank to Martin KONVIČKA for the language correction of the manuscript.

References

BARKHAM, J. P. 1992. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). IV. Clumps and gaps. J. Ecol. **80:** 797–808.

BLACKMAN, G. E. 1942. Statistical and ecological studies of the distribution of species in plant communities. I. Dispersion as a factor in the study of changes in plant populations. Ann. Bot. **6:** 351–370.

DUCHOSLAV, M. 2000. *Allium oleraceum* and *Allium vineale* in the Czech Republic: distribution and habitat differentiation. Preslia **73:** (in press).

GREIG-SMITH, P. 1979. Pattern in vegetation. J. Ecol. **67:** 755–779.

GREIG-SMITH, P. 1983. Quantitative plant ecology. 3rd ed. Blackwell, Oxford.

HÅKANSSON, S. 1963. *Allium vineale* L. as a weed. Plant Husbandry **19:** 1–208.

HILL, M. O. 1973. The intensity of spatial pattern in plant communities. J. Ecol. **61:** 225–235.

ILTIS, H. 1949. An immigrant conquers a continent: the story of the wild garlic. Sci. Month. **68:** 122–128.

KERSHAW, K. A. 1973. Quantitative and dynamics plant ecology. Edward Arnold, London.

KERSHAW, K. A. & LOONEY, J. H. H. 1986. Quantitative and dynamic plant ecology. 3rd ed. Edward Arnold, London.

KROCHMAL, A. 1952. Germination studies of aerial bulblets of *Allium vineale* L. and *A. canadense* L. Am. Midl. Nat. **63:** 497–508.

LAZENBY, A. 1961a. Studies on *Allium vineale* L. I. The effects of soils fertilisers and competition on establishment and growth of plants from aerial bulbils. J. Ecol. **49:** 519–541.

LAZENBY, A. 1961b. Studies on *Allium vineale* L. II. Establishment and growth in different intensities of competition. J. Ecol. **49:** 543–558.

LEPŠ, J. 1990. Comparison of transect methods for the analysis of spatial pattern, pp. 71–82. In: KRAHULEC, F., AGNEW, A. D. Q., AGNEW, S. & WILLEMS, J. H. (eds), Spatial processes in plant communities, Academia, Praha.

RICHENS, R. H. 1947. Biological flora of the British Isles. *Allium vineale* L. J. Ecol. **34:** 209–227.

RONSHEIM, M. L. 1994. Dispersal distances and predation rates of sexual and asexual propagules of *Allium vineale* L. Am. Midl. Nat. **131:** 55–64.

STEARN, W. T. 1980. *Allium* L., pp. 49–69. In: TUTIN T. G., HEYWOOD V. H., RURGESS N. A., MOORE, D. M., VALENTINE, D. H., WALTERS, S. M. & WEBB D. A. (eds), Flora Europaea. Vol. 10, Cambridge Univ. Press, Cambridge.

Received December 15, 1999
Accepted November 8, 2000