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Morphological-developmental properties as an agent forming spatial structure of *Adonis vernalis* (L.) populations

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Abstract

Aggregated and group-aggregated spatial structure of two *Adonis vernalis* (L.) populations in xerothermic grasslands are presented. It has been found that different disturbances (grazing, fire), which affect each population, modify morphological properties and developmental potential of individuals. This is followed by differentation in spatial and age structure of both populations. Comparative analysis of above- and below-ground plant organs of *Adonis vernalis* has enabled to present hierarchical spatial structure of aggregations and clumps as a result of modular structure of individuals and populations.

Key words: Adonis vernalis, morphological properties, spatial structure, grazing, fire

INTRODUCTION

The way in which single individuals occupy space is a crucial characteristics of each plant population. Under natural conditions most plant species tend to form distinct aggregations within a phytocoenose. The causes of this commonly encountered phenomenon have been analysed by many workers (e.a. Snaydon 1962, Harper et al. 1965, Ross and Harper 1972, Collinson 1977, Kershaw 1978, Andrzejewski and Falińska 1986).

Habitat conditions have been fairly often considered as main agents affecting aggregated type of spatial organization (cf. Andrzejewski and Symonides 1986). Whilst biological properties of a species, especially the modes of growth and reproduction, have been rarely mentioned as those which determine the size and structure of aggregation zones (Kershaw 1978, Falińska 1982, 1985, Czarnecka 1986). It has been frequently stressed that the reproduction mode governs the distribution of individuals. Especially vegetative propagation favours the formation of aggregations with their sizes only partly dependent on time and reproductive potential of a population (Harper 1977). In plants that reproduce mainly generatively the dissemination mode plays essential role in the formation of aggregations. For example in *Sarothamnus scoparius* ballistochory and myrmecochory determine non-random spatial distribution of individuals (Nieckuła 1987).

However, spatial structure is neither static, nor independent of population developmental phase or dynamic state of biocoenose. Kershaw (1978) shows that many populations at early colonization stages only slightly tend to aggregate, the tendency increases with the establishment of a population and finally decreases till individuals are distributed at random. Faliński (1986) finds similar tendencies in the secondary succession of woody species.

The studies on the biology and ecology of *Adonis vernalis* populations, conducted for a number of years, aim to elucidate demographic processes in this species. The results here presented are only a part of wider studies and illustrate relations between morphological-developmental properties of individuals and the spatial structure of a population.

STUDY SUBJECT

Due to its properties, *Adonis vernalis* has been the subject of many studies of botanists and pharmacologists, some of them started already in the previous century (Dieudonne 1876, Turesson 1933, Stary 1952, Kulpa 1960, and others). As an element of lowland south-east-European steppes, in Poland it is restricted to xerothermic grasslands, located extrazonally, in the south in gypsum and loess outcrops, in the north along valley margins (Gawłowska 1956, Kornaś and Medwecka-Kornaś 1986).

Adonis vernalis is a perennial that reproduces mainly generatively. It starts its growth very early, and flowers after mid-April, as one of the first within xerothermic grassland. In respect of morphological-developmental properties it is a rhizomatous caulophyte (Łukasiewicz 1962). Adult individuals form big clumps with a few to teens of flowers (Fig. 1.) Its fruit, a reticulate-wrinkled achene has a hooked apex (Kulpa 1960). This perennial possesses short, in older individuals thickened, rhizome, which is several cm long, and forms dark-brown adventitious roots (Fig. 2). Above-ground shoots branch sympodially and at the bottom are covered with brown scale leaves. They are either vegetative or generative with one flower. Fruits mature from the end of June till July. They fall down near a mother plant or are dispersed by ants (Gawłowska 1956). The shoots do not elongate in summer and already in early autumn above-ground organs of *Adonis* die. Seedlings are of two cohorts, autumn and summer.

The species has been analysed in the phytosociologically homogeneous phytocoenoses of xerothermic grasslands, located on southern slopes in the Skowronno Dolne reserve (near Pińczów), and in the neighbourhood of Wola Chroberska (near Chrobrze). Each of the populations studies has a different spatial structure.

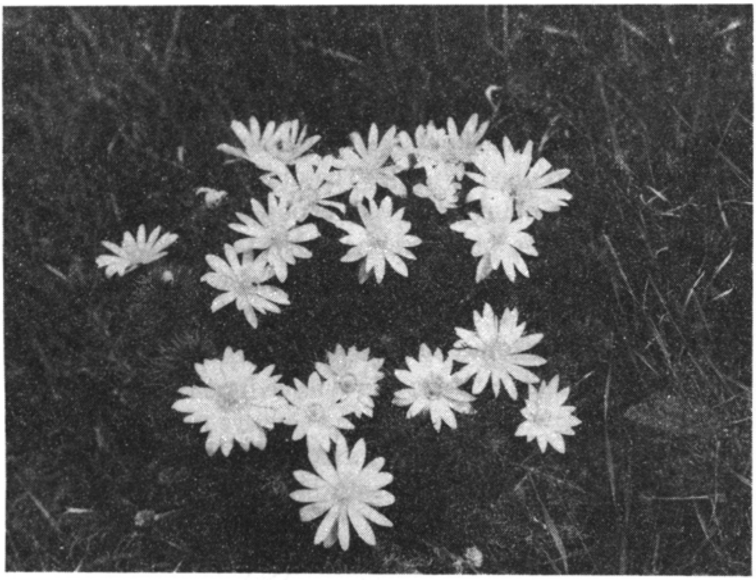

Fig. 1. Multiyear clump of *Adonis vernalis* (Phot. A. Błaszczuk)

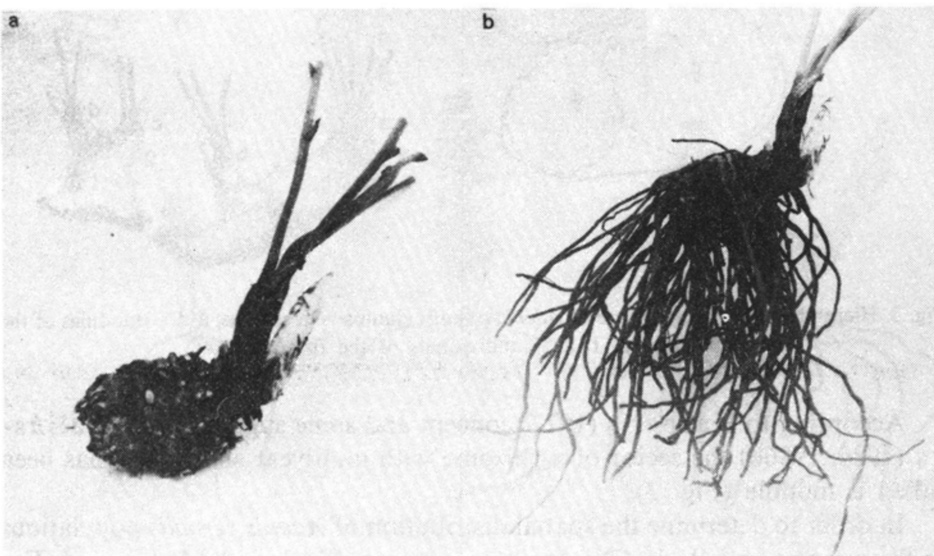

Fig. 2. Subterranean organs of *Adonis vernalis* (Phot. A. Błaszczuk), a – rhizome without adventitious roots, b – rhizome with adventitious roots

METHODS

In order to analyse the properties of the morphological structure of *Adonis* organs 30 clumps (58 individuals), dug out from natural habitats were compared. Also morphology of root systems and above-ground shoots of seedlings, and of one-, two-, and three-years-old juvenile individuals were studied. The sample size was low due to the protection of the species which is fairly rare in Poland. The studies were conducted in the second half of August when individuals form regenerative buds on their rhizomes. In laboratory the morphology of above-ground shoots, as well as clump area and distribution of shoot groups were determined (Fig. 3). The dug-out clumps were washed, the earth and roots of other plants removed, exposed rhizomes with adventitious roots were then drawn or photographed. Next, all advetitious roots were removed while the shape and size of the rhizome itself was determined (Fig. 2). From the crossection analysis the rhizome age was found, with the accuracy of 2-3 years. In the case of rhizomes older than 15 years the error could be bigger.

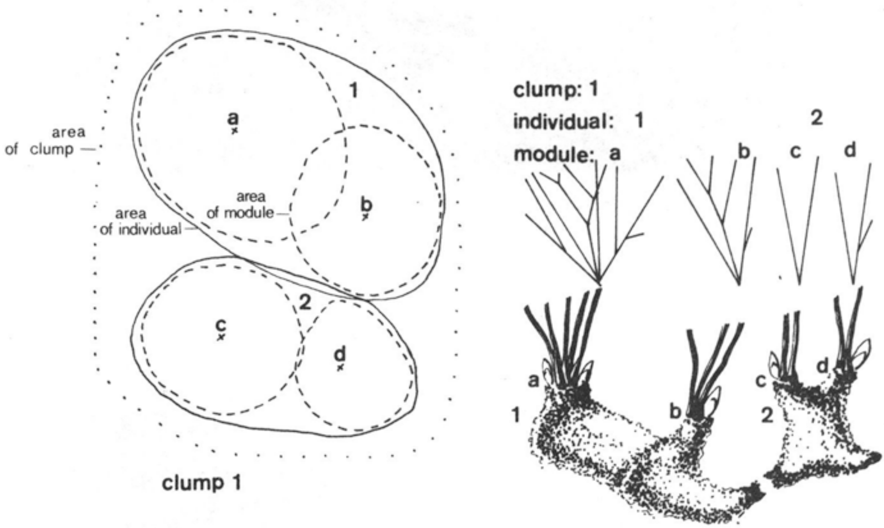

Fig. 3. Hierarchical spatial structure of *Adonis vernalis* clumps — a scheme; a-d — modules of the first clump, 1, 2 — individuals of the first clump

According to Harper's (1977) concept and some suggestions of Falińska (1984, 1986b) the sector of a rhizome with multiyear shoot base has been called a module (Fig. 3).

In order to determine the spatial distribution of *Adonis vernalis* populations in Skowronno and Wola Chroberska a cartographical method was used. For the area of 100 m² the plan of plant distribution at 1:10 scale was made. The areas of individuals, and where it was impossible those of clumps or bigger shoot aggregations, were marked. The morphological properties of individuals and clumps were contrasted with the spatial structure of the populations studied.

RESULTS

MORPHOLOGY AND DEVELOPMENT OF *ADONIS* INDIVIDUALS

It has been found that seedlings, which germinate in late autumn or early spring, form large bright green cotyledons. In the case of autumn cohort the cotyledons last through winter till spring. Occasionally, the first small leaf already originates in autumn. The root system of seedlings is well-formed. For the autumn cohort it may attain some teens cms (Fig. 4). In the first year in summer the plants develop regenerative buds at the base of primary shoot. From these buds, in next spring the regenerative shoots are formed. The bases of first and later regenerative shoots originate slightly above their mother shoots. The primary root system, well developed in seedlings, disappears in 2-3 year of plant lifer (Fig. 4). It has been observed that young 2-3 years-old plants form small, slightly thickened rhizome with developed adventitious roots. In

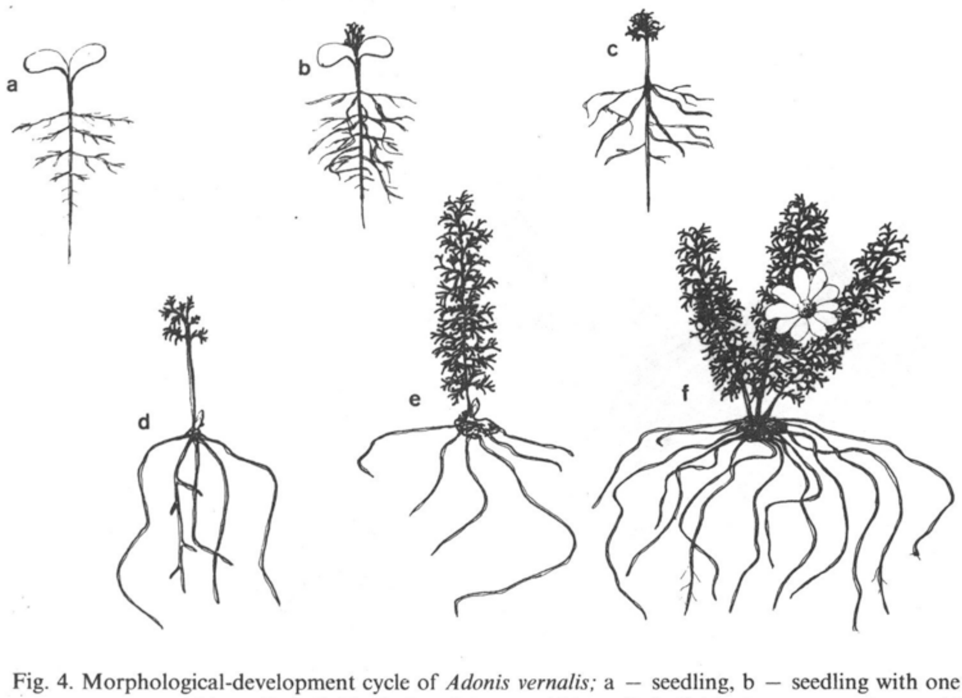

Fig. 4. Morphological-development cycle of *Adonis vernalis;* a — seedling, b — seedling with one leaf, c — 1-year-old juvenile individual, d — 2-4-year-old juvenile individual, c — several-year-old virginile individual, f — mature generative individual

mature individuals short, thick rhizome with multiyear shoot bases is a main perennating subterranean organ (Fig. 2). Rhizomes form very numerous, black-brown adventitious roots and are either slightly skewed or horizontal towards the soil surface. At the base of a shoot, annually in July or August, regenerative bud develops which in next spring gives new shoots. The number of shoots originating from one bud increases with time, hence the shoot base and rhizome grow.

The individuals with one regenerative bud have tubulliformovate unbranched much shortened rhizomes. Such individuals may develop 5-6 above-ground shoots. However, it has been observed that at this stage the second regenerative bud often develops, also at the bottom of multiyear shoot bases. In next year two shoot groups, originating from two buds, grow near each other. The above-ground shoots of one individual form a compact, multishoot clump. Annual development of shoots originating from two regenerative buds distinguishes two independent, perennating shoot bases. The rhizome growth increases the distance between the bases, hence also that between regenerative buds produced annually. Such individuals give clumps within which shoot groups derived from single regenerative buds can be easily distinguished. With further rhizome growth its middle part ages and dies. These processes lead to the division of multiyear, developed rhizome into two sectors which grow later independently. The adventitious roots of both sectors are stongly intertwined, but morphologically distinct (Fig. 5).

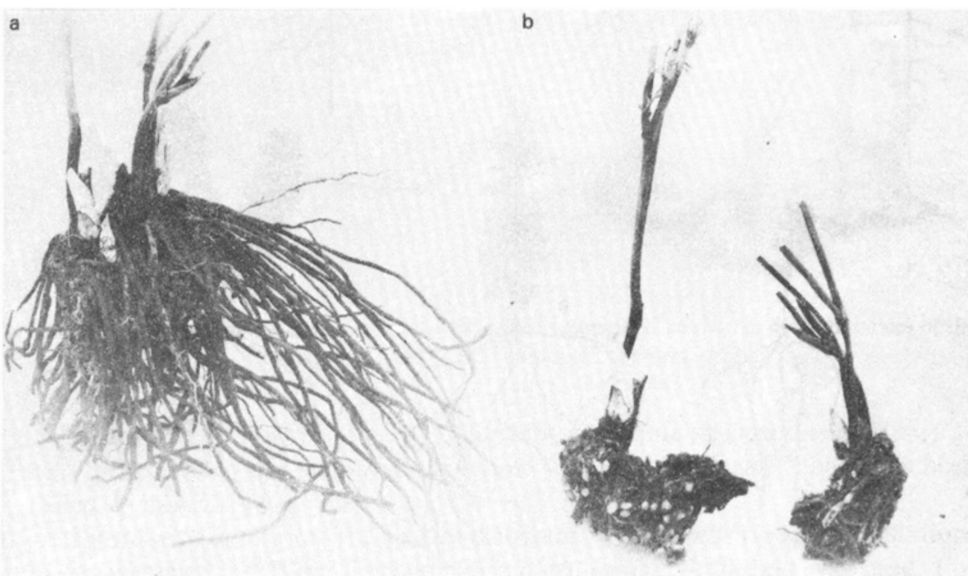

Fig. 5. Vegetative reproduction of *Adonis vernalis*; a – individuals with adventitious roots, b – individuals devoid of adventitious roots (Phot. A. Błaszczuk)

The model for rhizome development in *Adonis vernalis*, presented in Fig. 6, illustrates successive phases of the process. Observed morphological diversity of dug-out rhizomes (Fig. 7) suggests the effect of several external agents which affect e.a. the degree of rhizome branching or its size. Rhizome deformations probably result from various damages like crushed regenerative buds, and biten or burned upper shoot bases. In response to damaging agents plants develop regenerative buds in another undamaged part of a rhizome (Fig. 7).

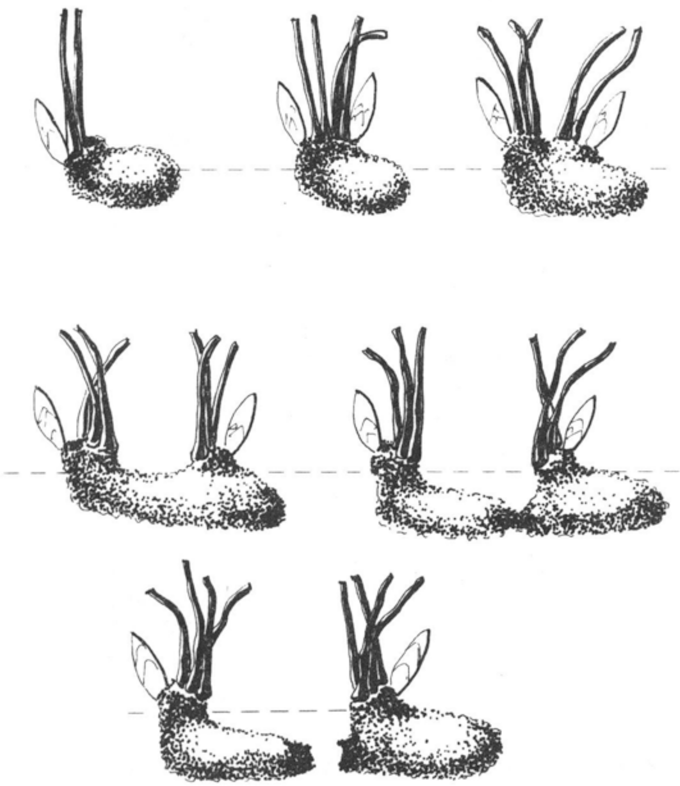

Fig. 6. Rhizome development in *Adonis vernalis* – a scheme

The analysis of the observed results enables to distinguish three morphological-developmental phases of *Adonis* organs:

Phase I – Only primary root system develops, no rhizome and adventitious roots, above-ground shoots usually single, unbranched, 5-7 cm high (seedlings and juvenile individuals) (Fig. 4).

Phase II – Rhizome well-development, with one, more rarely several regenerative buds located at the single multiyear shoot base, shoot numbers vary from one in younger (virginile) to many in older (mature) individuals (Figs. 2, 4).

Phase III – Rhizomes with at least two distinct multiyear shoot bases with regenerative buds, two or more distinct shoot groups develop, usually strongly branched, most shoots generative (mature individuals) (Figs. 1, 4).

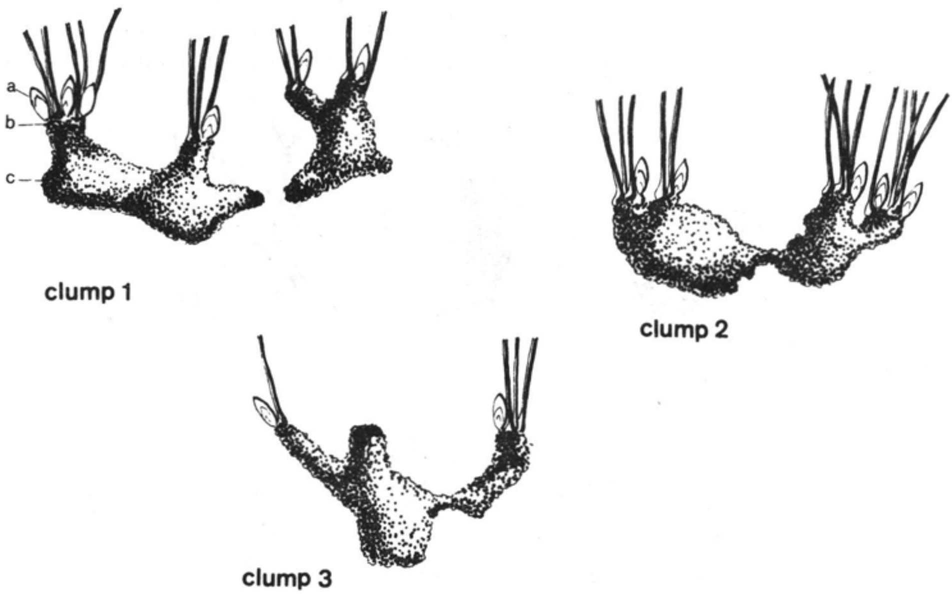

Fig. 7. Morphological differentiation of subterranean organs in *Adonis vernalis* individuals; a – regnerative bud, b – perennating shoot base, c – rhizome, clump 1 – 16-18 years, clump 2 – 12-14 years, clump 3 – 18-20 years, the age estimated from rhizome morphology

MODULAR SPATIAL STRUCTURE OF INDIVIDUALS AND POPULATIONS OF *ADONIS VERNALIS*

Spatial structure of perennials consists of single compact shoot groups, here called modules, that originate from multiyear common shoot base. Undoubtly, the distribution of modules determines spatial organization of a whole population. The area and structure of a module is connected with the number of component shoots and reflects a particular phase of rhizome development (Fig. 3).

Within high-density zones (aggregations) individual clumps are often undistinguishable, whereas within clumps the limit age of individuals cannot be determined. Hence, description of spatial structure of *Adonis vernalis* has to be based upon the analysis of the distribution of seedlings and juvenile individuals (phase I), and the modules of virginile and mature individuals (phase I and II). In phase I there is no rhizome so in fact there are no modules. For that reason an individual is the only demographic unit applied to describe this part of a population.

Older individuals of *Adonis vernalis* which belong to phase II are unimodular, therefore the increase in their area is connected with the increase in the number and branching of shoots. The development dynamics in this group of individuals is determined by the dynamics of shoot number. Unimodular, multishoot individuals with a big area form usually more than one regnerative bud, which is followed by a division of multiyear shoot bases and formation of two distinct shoot groups, i.e. modules.

Teenage individuals of the species are multimodular plants which tend to separate single modules from a mother organism. The process affects directly both the age structure and the dynamics of the observed population.

SPATIAL-AGE STRUCTURE OF POPULATIONS

The analysis of *Adonis vernalis* in the Skowronno reserve clearly indicates the highly aggregated spatial organization of the population (Fig. 8). High-density areas are separated with those where the species grows only occassionally (Fig. 8). Thorough inventarization of the population on 100 m² enables to determine the type of the distribution of individuals in each age group. The plants in phase I (seedlings and juvenile individuals), aggregate into groups with 2-4 individuals, and are located in the margins of aggregations or single clumps (Fig. 8). Within clumps seedlings are fairly rare and usually single. The distribution of older age groups in a population (virginile and generative modules), presented in Fig. 8, indicates diversified age structure of aggregations. In loose aggregations virginile modules prevail. Between them single generative modules grow. The areas of these modules do not overlap. Seedlings and juvenile individuals are numerous within the whole high-density zone. Hence, it may be assumed that modules are individuals in the second developmental phase. Therefore, loose aggregations are young and only recently formed.

Spatial-age relationships within compact aggregations are different (Fig. 8). They consist mainly of numerous generative modules with numerous branched shoots, whose areas overlap and which form uniform shoot "thicket". Within such aggregations seedlings and juvenile individuals are occassional, whereas in their margins they constitute distinct groups. High density of modules (mostly generative) and their size (shoots are high and branched) indicate that probably teenage individuals prevail, which are mature, and have complex multimodular structure (III phase).

Within the population area also those individuals which are single, located at random, and not connected with any aggregation are found. These are seedlings, and juvenile, virginile and generative individuals. However, it is

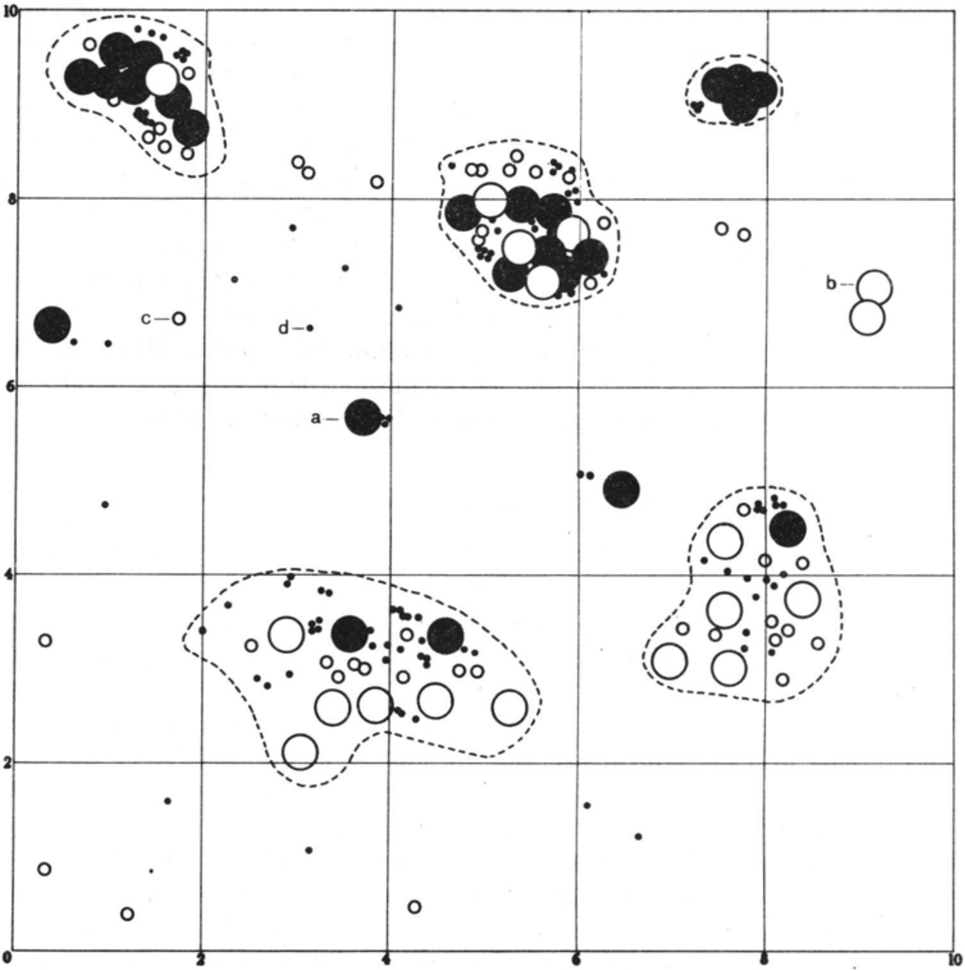

Fig. 8. Aggregated-group spatial structure of *Adonis vernalis* population in xerothermic grassland (Skowronno reserve); a — generative modules, b — vegetative modules, c — virginile individuals, d — seedlings and juvenile individuals

worth mentioning that around single flowering plants more or less numerous seedlings grow.

The spatial structure of the population located on xerothermic slope in Wola Chroberska is different (Fig. 9). There are no high- and low-density zones (aggregations and thinnings) while single individuals are scattered at random within the area. *Adonis* clumps in Wola Chroberska significantly differ in size and spatial structure from those in Skowronno reserve. Mostly single individuals are smaller, have shorter and less branched shoots, and are unimodular. Also seedlings and juvenile individulas are single, although they may form several-individuals-groups in the margin of some clumps.

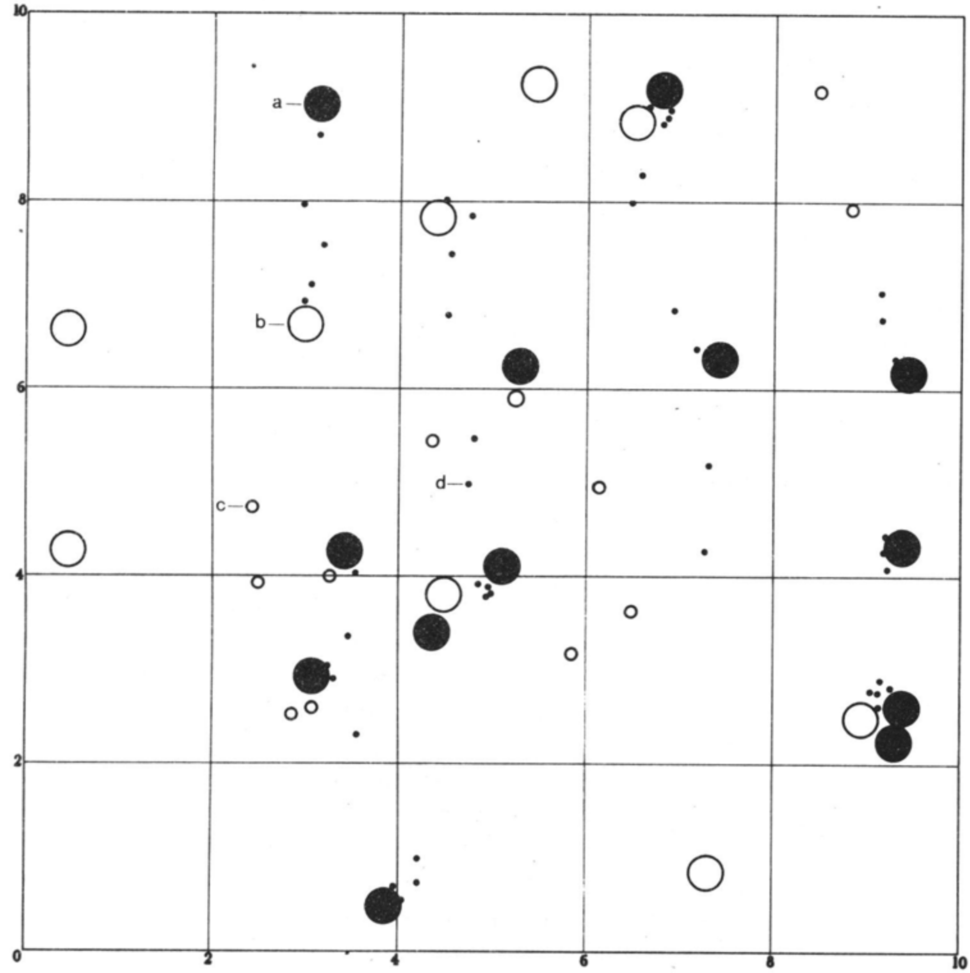

Fig. 9. Aggregated spatial structure of *Adonis vernalis* population in xerothermic grassland subjected to intense grazing (Wola Chroberska); a-d – see Fig. 8.

DISCUSSION

The studies which not only do describe the type of spatial structure of a population, but also its origin require the complex analysis both of a number of phytocoenotic and habitat agents, and biological properties of a species. Kershaw (1978), discussing the correlations in species co-occurrance, emphasises the role of microtopography, especially water conditions at microscale. He considers the latter to determine the distribution of nutrients and directly cause aggregated spatial organization of plant populations. Also Harper

(1977, 1980) stresses the role of ecological factors (light, water, soil, microstructure) in the formation of safe germination sites, which, on the other hand, mark high-density areas. Wilkoń-Michalska (1976) considers the aggregated spatial structure of an annual *Salicornia patula* to be directly related to the microstructure of its habitat. Collinson (1977) finds such agents as: location of available water, inclination, exposition as related to sun and wind, and structure and chemistry of soil, to be responsible for aggregated spatial structre, highly common in plant populations. Krebs (1972) represents similar approach to the problem.

The age-spatial structure of the populations presented in this paper is a result of agents affecting single individuals. The studies on morphological-developmental properties of *Adonis vernalis* have enabled to find one of the crucial factors that make possible the interpretation of the origin of this type of spatial structure of a population. Environment conditions (soil, microclimate, phytocoenose type) have been additionally studied.

The area of the Skowronno reserve, although not subjected to agriculture, is regularly (twice an year) burned out, in 1987 even at the height of growing season of *Adonis vernalis*. Xerothermic slope in Wola Chroberska is not protected, and serves as a pasture for cattle and sheep. However, it is not burned. Hence, it may be inferred that these two forms of disturbance, affect with different intensity the development of individuals, followed by a differentiation of a spatial structure of both populations.

Under the conditions of intense grazing the individuals of *Adonis vernalis* cannot achieve their complete life cycle – no divisions of multimodular rhizomes occur, neither do compact clump aggregations, clumps are mostly unimodular, with 2-3 shoots only. Therefore, one cannot call the spatial structure hierarchical, as was that in Skowronno (Błaszczuk, unpublished).

Grime (1979) has distinguished in the ontogenesis of plant organisms two phases (Fig. 10). He has also stressed that in order to understand fundamental properties of the species ecology it is necessary to know life strategies of individuals in these two phases. The paper does not even attempt to answer the question to what degree disturbances mentioned about affect the life strategy of successive ontogenesis stages. It is, however, undoubted that intense grazing changes significantly morphological properties of *Adonis* individuals, which is followed by the alternation in age-spatial structure of a population.

The studies on the populations of perennials (Falińska 1978, 1979, 1982, 1985, Symonides 1979, Czarnecka 1986, Nieckuła 1987) show very close relationship between morphological-developmental properties of individuals and age-spatial structure of a population. Inner spatial structure of shoot aggregations depends upon the phase of ontogenic development, hence indicates a special age structure of a population. Falińska (1986a) in her growth analysis of the polycormones of *Iris pseudoacorus* describes changes in their spatial structure. She has found that within the area of several-year-old

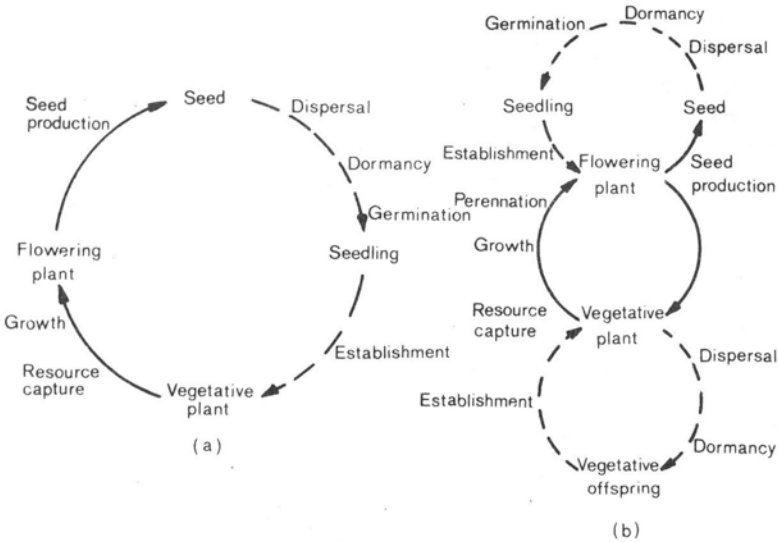

Fig. 10. Schemes illustrating the activities associated with the regenerative (— — —) and established (————) phases in the life-cycles of an annual flowering plant (a) and a perennial plant producing both seeds and vegetative offspring (b). (After Grime 1979)

polycormones the gaps appear due to dying of senile fragments. In available sites seedlings establish.

Czarnecka (1986) in her studies on biological properties of polycormones of *Majanthemum bifolium* shows that the size structure of shoots within single polycormones, polycormone size and their inner spatial structure are interrelated. Again, significant differences in the aggregation size between two *Milium effusum* populations, growing under different habitat conditions have been found (Towpasz and Szymska 1983).

Adonis vernalis, even though does not form large-area polycormones and reproduces mainly generatively, it under vourable conditions builds aggregations characteristic of most perennials; their age-spatial structure reflects morphological-developmental properties of the species. According to Grime (1979) the formation of subterranean storage organs, like *Adonis* rhizomes, is one of the crucial characteristics of life strategy in a mature phase of life cycle. For, it affects competitive ability of a species and its resistance to various stresses. The differentiation of rhizome structure observed here results not only from steady stress associated with habitat conditions (periodical drought), but also occasional disturbances (grazing, fire). The individuals of the populations studied show different morphological properties, which is followed by a different type of age-spatial structure. Hence, one may infer that the ability of response and adaptation of individuals to various conditions in this species lies at the organism level in diversified rhizome structure, whereas at the population level in different age-spatial structure.

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Własności morfologiczno-rozwojowe jako czynnik kształtowania struktury przestrzennej populacji Adonis vernalis (L)

Streszczenie

Analizowano właściwości struktury morfologicznej organów *Adonis vernalis*. Porównywano morfologię systemu korzeniowego i pędów nadziemnych osobników w różnym wieku (siewki, osobniki juvenilne, wirginilne, generatywne). Na podstawie analizy porównawczej przedstawiono model rozwoju kłącza i trwałej nasady pędów. Stwierdzono, że na pewnym etapie rozwoju kłącze dzieli się — dwa nowe, powstałe w wyniku podziału osobniki wykazują pełną odrębność morfologiczną. Analiza wyników obserwacji pozwoliła na wyodrębnienie trzech faz morfologiczno-rozwojowych organów *Adonis vernalis* oraz na określenie modułowej budowy wieloletnich osobników tego gatunku. Przedstawiono dwie zróżnicowane pod względem struktury przestrzennej populacje miłka. Populacja w rezerwacie Skowronno pod Pińczowem wykazywała typowo skupiskowo-grupowy charakter organizacji przestrzennej, natomiast druga w Woli Chroberskiej — skupiskowy. Zauważono, że zróżnicowane warunki wzrostu (w Skowronnie częste wypalanie, a w Woli Chroberskiej intensywny wypas) spowodowały istotne różnice w budowie morfologicznej osobników obu populacji, pociągnęło to za sobą istotne różnice w ich strukturze przestrzenno-wiekowej. Stwierdzono, że zdolność reakcji i przystosowania się osobników tego gatunku do różnych warunków objawia się na poziomie organizmu zróżnicowaną budową morfologiczną kłączy, a na poziomie populacji odmienną strukturą przestrzenno-wiekową.