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Life cycle and morphological features of *Allium* species in connection with geographical distribution

Abstract

Kamenetsky, R.: Life cycle and morphological features of *Allium* species in connection with geographical distribution. – Bocconea 5: 251-257. 1996. – ISSN 1120-4060.

The life cycle and morphological features of about 30 *Allium* species from the Mediterranean region and Central Asia have been studied in their natural populations and under the conditions of introduction. Six main biomorphological types have been defined within the genus, according to the presence of rhizomes or bulbs, and also based on root system structure. Annual cycle and underground organ features are related to the geographical spread of the genus from zones with a moderate climate to arid regions. Life form evolution in the genus leads to an extreme, "geoephemeroid" biomorphological type.

Introduction

From the time of Linnaeus, classification of flowering plants has been based on the peculiarities of the structure of the generative sphere. Nowadays anatomical, cytological and biochemical methods are largely used for improving our knowledge of the relationships between species and genera. A further important criterion of such relations is DNA structure.

However, we still do not have enough information on plant phylogenesis. A key position in this respect is held by palaeontology and biomorphological analysis. The latter helps identify a connection between morphological features and environmental conditions, which are a driving force of evolutionary transformation (Hohrjakov 1975).

That variable and widespread genus, *Allium*, is an interesting subject for biomorphological analysis. Its c. 600 species are distributed in the northern hemisphere, mainly in central Asia, the Mediterranean area and western North America (Hanelt 1990). The ancient Mediterranean territory is usually considered to be the hearth of formation of the genus (Kamelin 1973). The geographical range of *Allium* embraces regions with a mesic, semi-arid and arid climate. Its great morphological diversity and wide geographical distribution gave grounds for Vvedenskij (1935) to consider this genus an "unnatural miscellaneous group with artificial division into sections".

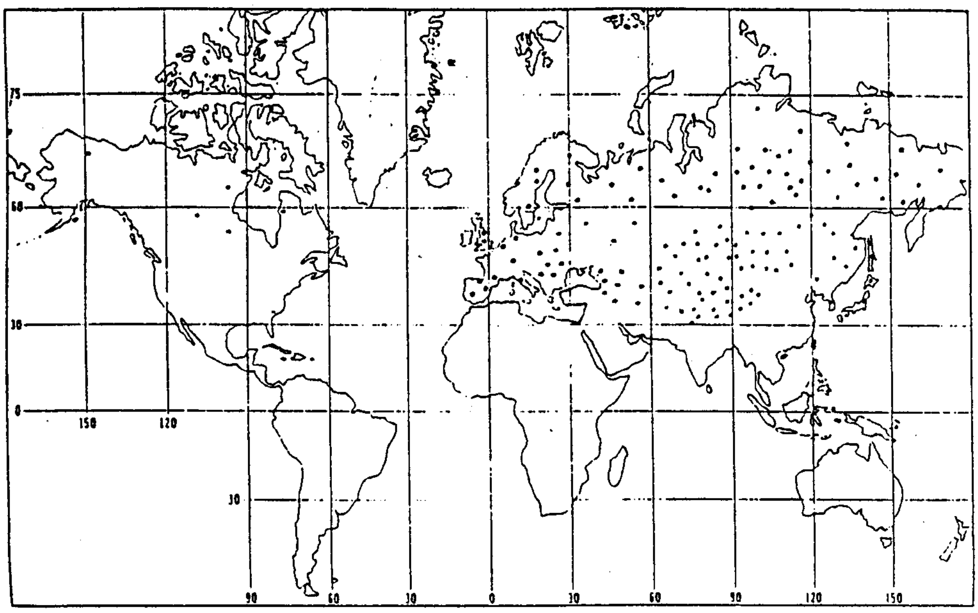

Fig. 1. The world distribution of rhizomatous *Allium* species.

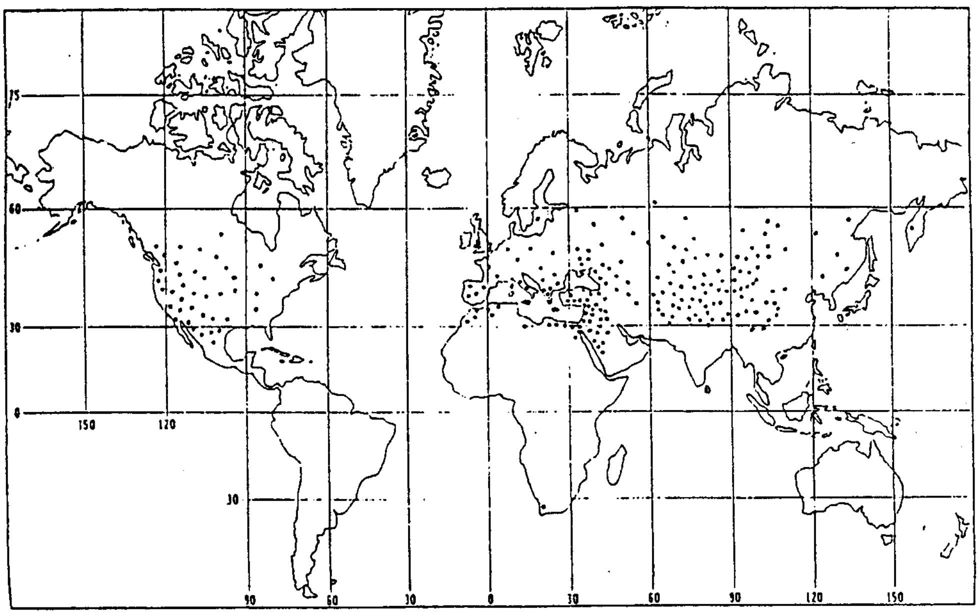

Fig. 2. The world distribution of bulbous *Allium* species.

Many different classifications of *Allium* have been proposed. One of the most detailed is the compendium of Kamelin (1973), who distinguished 6 subgenera and 30 sections within the genus. The last survey to date, of Hanelt & al. (1992), recognizes 46 sections within 6 subgenera.

Currently it is recognized that in the genus *Allium* there is a relatively strong correlation between the taxonomic position of species, its geographical distribution, and its underground morphological structure (Cheremushkina 1985, 1992, Kamenetsky 1989, 1992 a). Vegetative propagation may also provide an important clue as to the phylogenetic position of a species (Kamenetsky 1992b).

Results and discussion

Life cycle and morphological features of about 30 *Allium* species have been studied in connection with their geographical distribution. These studies were carried out in Kazakhstan from 1982 to 1990, and in Israel from 1991 to 1993. The genus is well represented in the flora of both regions. The native flora of Kazakhstan, a large republic in the south-east of the former Soviet Union, includes more than 100 *Allium* species (Pavlov & Poljakov 1958). In Israel, 29 species have been found (Kollmann 1986).

The traditional methods of morphological analysis have been used to study the structure of underground organs and the life cycles. A survey of the geographical distribution of *Allium* has been performed, using regional floristic literature (Frizen 1987, Goloskokov 1984, Gorčakovskij 1966, Grubov 1982, Hanelt 1985, Hultén 1968, Kitamura 1960, Pavlov & Poljakov 1958, Prohanov 1930, Vvedenskij 1935, Wendelbo 1971, Xu & al. 1990).

Allium species are geophytes or hemicryptophytes, and the morphology of their underground shoots is highly variable. Roughly, two large groups of species can be distinguished.

Species of *Allium* subg. *Rhiziridium* and subg. *Amerallium* belong to the rhizomatous group. Fleshy rhizomes of *Allium* species, which function primarily as storage organs, usually result from successive accrescence of basal plates through several years. However in some cases rhizomes are formed in other ways. Horizontally, obliquely and vertically growing rhizomes can be distinguished. Bulbs, in these species, are composed of leaf sheaths of varying thickness.

Species *Allium* subg. *Allium*, subg. *Melanocrommyum*, subg. *Caloscordum* and, partly, subg. *Amerallium* belong to the bulbous group. A bulb is a subterranean or partly subterranean storage organ that consists of a longitudinally compressed stem – the basal plate, which is usually vertically oriented – and fleshy, succulent leaf bases, or specialized scales, that assume the storage function.

The different geographical distribution of rhizomatous and bulbous species is shown in Fig. 1 and 2, respectively. The main pool of rhizomatous species is distributed in the temperate climate zone of Siberia, Europe and Canada. Some are also found in arid areas, but in that cases in the subalpine and alpine belt of mountains. In contrast, bulbous species are mainly found in semi-desert and desert territories. In Israel for example, with its rather severe desert conditions, only bulbous *Allium* species are found.

The maps in Fig. 1-2 are to some extent approximations, because no monograph of *Allium* exists, and regional floras are often repetitive and inaccurate. However, the basic geographical differences between the groups are evident.

The division of the genus into rhizomatous and bulbous species is rather fundamental. Careful analysis shows that, based on the structure of underground organs, at least 6 biomorphological types can be distinguished.

The rhizomatous group can be divided into four types:

Species with horizontally growing rhizomes. – This type includes the hemicryptophytic *Allium senescens* L., *A. ramosum* L., *A. subtilissimum* Ledeb., and *A. nutans* L. Besides the thickened rhizome, their underground system includes false bulbs, composed of slightly thickened leaf sheaths. The root system is perennial, adventitious, and generally includes roots of the first and second order.

Species with horizontally long-growing rhizomes. – This type is represented by a single species, *Allium caespitosum* Siev. ex Bong. & C. A. Mey. An obligate psammophyte from western Kazakhstan, its underground sphere has a long branching, thread-like rhizome that forms regular nodules during its development. Scale-sheathed reproductive buds and roots are located at these nodules. The bulb is quite indistinct, the shoot is sheathed by the joint bases of 2-3 leaves. The perennial root system is of a diffuse, filamentous type not found in other *Allium* species, and includes roots of the first order.

Species with oblique and obliquely to vertically growing rhizomes. – The false bulb is weakly formed and covered by numerous tunics, corresponding to the dead sheaths of the previous years' leaves. The root system is usually perennial and includes roots of the first order. *Allium strictum* Schrad., *A. oreoprasum* Schrenk, and *A. rubens* Schrad. ex Willd. belong to this type.

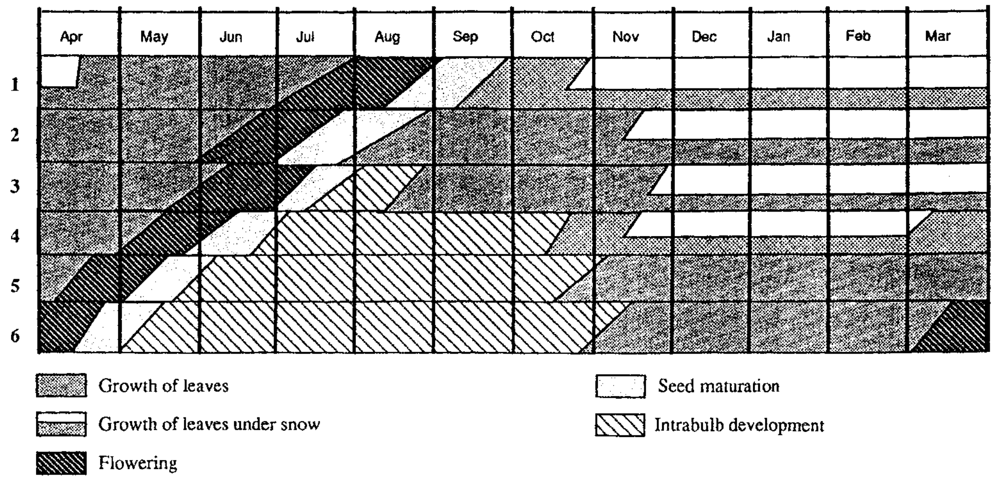

Fig. 3. Annual cycles of some *Allium* species. – 1, *A. nutans* (mountains, Siberia); 2, *A. pskemense* (mountains, Kazakhstan); 3, *A. caeruleum* (steppes, Russia); 4, *A. karataviense* (semi-desert, Kazakhstan); 5, *A. ampeloprasum* (semi-desert, Mediterranean); 6, *A. rothii* (desert, Israel).

Species with vertically growing rhizomes. – From the morphological point of view, this type is probably intermediate between the rhizomatous and bulbous species. A largish group of wild relatives of the onion, e.g. *Allium galanthum* Kar. & Kir., *A. altaicum* Pall., and *A. pskemense* B. Fedtsch. belong to this type. They have short rhizomes, the large false bulbs consist of thickened leaf sheaths, the root system is annual and includes roots of the first order.

The bulbous species are less variable in their underground structure:

Species with true bulbs. – There is a miscellaneous group of species with bulbs which consist of specialized scales and 1-5 thickened leaf sheaths. The root system is annual, includes roots of the first order, and its arrangement is diffuse or semi-diffuse. Examples of this type are *Allium caeruleum* Pall., *A. delicatulum* Schult. & Schult. f., *A. ampeloprasum* L., *A. dictyoprasum* C. A. Mey., and *A. phanerantherum* Boiss. & Hausskn.

The specialized, ephemeroid plants. – The true bulbs of these species consist of specialized scales up to 2 cm thick. The leaf sheath dries up after the vegetation season and only fulfils a cover function. The root system is annual and frequently ephemeral, non-branching and diffuse. The number of roots per plant is very high and may reach 200, which permits intense, rapid absorption. This type includes *Allium karataviense* Regel, *A. altissimum* Regel, *A. sergii* Vved., *A. oreophilum* C.A. Mey., *A. rothii* Zucc., *A. tel-avivense* Eig, etc.

Study of the life cycle and morphogenesis of each monocarpic shoot generation of different *Allium* species has shown significant variation. Flowering time depends on the climatic cycle, since before they flower the plants usually need a certain amount of low temperatures. Seed maturation is a quite rapid process in all species. Once the seeds havee ripened, development may continue in either of two directions.

Rhizomatous species have no dormancy period (Fig 3: 1-2). New leaves are formed throughout the year, and low winter temperatures only slow down leaf growth. Because the false bulb of these species consists of leaf sheaths, renewal of the bulb is also a more or less permanent process. Typical rhizomatous species like *Allium nutans* and *A. senescens* can form 20-22 leaves during one year. In intermediate, rhizomatous-bulbous species like *A. pskemense, A. galanthum,* and *A. vavilovii* Popov & Vved. the number of leaves is limited to 6-7 per vegetation cycle. Generative shoot formation of rhizomatous species occurs in the spring that precedes flowering. Inflorescences develop very quickly and do not need cold to trigger their development. First results of the introduction of rhizomatous *Allium* species from Siberia and eastern Kazakhstan to the Negev desert highlands in Israel show that under the conditions of a winter without snow and frost these species complete their full annual cycle and produce normal flowers, fruits and seeds.

Bulbous species, after seed maturation, lose their roots and above-ground organs (Fig. 3: 3-6). During this time, which we call the "intrabulb development period", vegetative and generative organs are formed. The duration of the Intrabulb development period definitely depends on environmental conditions and varies geographically. Thus, *A. karataviense,* which grows on stony slopes in the middle mountain belt of South Kazakhstan, remains in this stage for 4 months, *A. rothii,* from the Negev desert highlands of Israel, for about 6 months. Both species have a very similar morphology and belong to the same taxonomic group.

Even such a rough, morphologically based grouping allows to evaluate the adaptation process of representatives of this genus to increasingly severe conditions, to changes of climate and seasonality. Cheremushkina (1985), in our opinion, has valid reasons for considering a possible origin of all rhizomatous *Allium* species from an ancestral type with a rhizome and a slightly thickened shoot composed of leaf sheaths. Through a complex process of divergent evolution, the horizontally, obliquely and vertically growing rhizomes have subsequently been formed. The long vegetation period and winter-green habit of most rhizomatous species is indicative of their lack of adaptation to extreme conditions and of their wide ecological amplitude (Cheremushkina, 1992). The successful introduction of many rhizomatous species from temperate zones to arid regions and, in particular, to Israel (Kamenetsky 1992c) confirm this hypothesis.

The switch to bulb formation is a cardinal point in the history of the genus, the beginning of a new epoch with its spread into and conquest of arid territories. Bulbous *Allium* plants are much better adapted to the severe climatic rhythm of the desert: the vegetation period of above-ground organs and of the root system is reduced, and the intrabulb development period increases. Within the genus, the bulbous species can be arranged in various phylogenetic lines, each representing an independent response to increasing soil dryness (*A.* sect. *Cepa,* sect. *Oreiprason,* sect. *Petroprason,* sect. *Rhiziridium*) or decreasing soil temperature *A.* sect. *Schoenoprasum).*

Life form evolution leads further to the formation of an extreme biomorphological type, the geoephemeroid (Kamenetsky 1992a). The annual alteration processes in geoephemeroids are fairly quick. The previous year's shoot dies during development of the next shoot generation. Thus, the cycle of one module of the true geoephemeroid lasts little more than one year.

The important criterion of ephemeroidization is the seasonal correlation of the vegetative and generative periods of development: the vegetation of a majority of the species stops before the fruits are fully mature. From a physiological point of view, geoephemeroids are typical mesophytes because they usually grow in conditions of sufficient water supply, if only during the vegetation period (Hohrjakov 1975). The Mediterranean type of climate, with its alternation of cool winters and hot, dry summers, is very suitable for the evolution of geoephemeroids.

The scarcity of life resources and the strong climatic rhythm, under desert conditions, trigger adaptation processes within different monocotyledonous groups. The genus *Allium* is a good example, showing considerable structural changes correlated with geographical distribution and natural environmental conditions.

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