Allium oleraceum and *A. vineale* in the Czech Republic: distribution and habitat differentiation

Rozšíření a stanovištní diferenciace *Allium oleraceum* a *A. vineale* v České republice

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The distribution and habitat differentiation of *Allium oleraceum* L. and *Allium vineale* L. in the Czech Republic based on herbarium material is reported. Both species are documented from rather large number of localities all over the Czech Republic and do not show apparently different large-scale pattern of distribution. The altitudinal range of both species in the Czech Republic is very similar. Both species are concentrated from the colline to submontane belts (200–600 m) but rarely occur also in the montane belt, especially *A. oleraceum*. Both species occur in a wide range of habitats ranging from rocks and arable fields to forests. Nevertheless, their relative frequencies within respective habitats significantly differ. *A. oleraceum* frequently occurs in forests (especially in oak-hornbeam forests) and forest edges, on rocks, at field margins, on sunny slopes and in steppe communities. On the other hand, *A. vineale* is common in arable fields (namely in the past), field margins, roadsides, ditch banks and meadows, but rare on rocks, in forests and scrub. Distribution and habitat differentiation of both species in the Czech Republic is compared with data from other parts of their distribution area. The species' habitat differentiation is briefly discussed from the point of view of plant traits.

Keywords: Geophytes, *Allium*, polyploidy, herbarium material, distribution, ecology, Czech Republic

Introduction

Geophytes comprise conspicuous elements of spring flora of alpine and arctic regions (Raunkiaer 1934) and areas with continental (steppe) and Mediterranean climate (Dafni et al. 1981). In the temperate zone they occur mostly in places where they avoid competition with hemicryptophytes, whose leaves, as a rule, last much longer. This is especially the case of deciduous forests on fertile soils where light can reach the ground for sufficient time and in sufficient quantity in the early spring and thus enable geophytes with their low optimum temperature requirements to reach full development (Ellenberg 1986, Grubb & Marks 1989). Less frequently geophytes occur in open, sunny and rather dry sites, e.g. in xerothermic grasslands, forest fringes, vineyards and on rocks (Ellenberg 1986). All these habitats are characterized by seasonal climate with more or less predictable period(s) of unfavourable environmental conditions. Although the stress conditions can comprise various factors, such as drought, frost or shade, geophytes show generally similar life-cycle pattern: (i) during unfavourable period(s) geophytes pass into dormant stage with absence of aboveground parts; (ii) shortly after the beginning of the favourable season geophytes quickly form aboveground structures and rapidly finish their development and reproduction before the arrival of next unfavourable season (Dafni et al. 1981, Grubb & Marks

1989). Their aboveground persistence is thus restricted to relatively short period about one to six months depending on respective habitat conditions and species.

Many geophytes, especially those growing in the temperate deciduous forests, form large colonies of plants that are conspicuous during spring (Ellenberg 1986). Floristic research specialized on distribution mapping of geophytes thus encounters some problems associated especially with less intensive investigation during spring (Slavík 1994). On the other hand, many less conspicuous geophytes with sparse distribution may be overlooked during floristic research. It is common in the situation when vegetative plants with apparently shorter vegetation period in comparison with reproductive ones dominate the populations (Duchoslav 2000). Since flowering is an unusual event in many geophytes growing in unfavourable conditions, only fragmentary data on their distribution and habitat conditions are available.

Only sparse data concerning distribution and habitat requirements in the Czech Republic have been found in published works for two common geophytes, i.e. *Allium oleraceum* L. and *Allium vineale* L. (Duchoslav 2000) although both species are considered the most widespread *Allium* representatives in Europe (Hegi 1939). Moreover, both species are similar in shape and size which causes frequent confusion in their determination (Krahulec 1977). It is therefore dubious to take most of the published data into account when studying their distribution, because both species often occur together.

The aims of the present are to evaluate (i) the distribution and (ii) habitat demands of the species under the study in the area of the Czech Republic and (iii) to compare obtained results with literary data from the other parts of their distribution area.

Methods

The distribution of both species was based on revised material from the following herbaria (abbreviations follow Hradílek et al. 1992): BRNM, BRNU, CB, CHOM, FMM, GM, HR, LIM, LIT, MJ, MP, NJM, OL, OLM, OP, OSM, PL, PR, PRC, ROZ, SUM, VM, VYM, ZMT. Material from several private herbaria (V. Chán, J. Hadinec, A. Roubal) was also revised. In addition, unpublished records of F. Krahulec and the present author were used. In total, 1694 specimens were studied (*A. oleraceum*: 974, *A. vineale*: 720). However, in 185 (10.9%) cases (112 in *A. oleraceum* = 11.5%; 72 in *A. vineale* = 10.0%) the given location was too vague or I was unable to decipher handwriting on labels. These specimens were discarded from the survey. In 23 (1.4%) cases, individuals of both species were mixed together. Literary data were not used in the present study because of frequent interchange between both species (Krahulec 1977).

Since precise description of habitat was not usually given on herbarium labels, I used only rough classification of habitats. The information on habitat type was presented only in 62.5% (*A. oleraceum*) and 71.1% (*A. vineale*) labels of revised specimens. Description of habitat conditions was completed by field observations of F. Krahulec and the present author. Where unavailable from labels, altitude was estimated using the maps.

Results

Distribution

Both *A. oleraceum* and *A. vineale* are documented from rather large number of localities all over the Czech Republic and do not show any apparent large-scale pattern of distribution except of their frequent absence in mountain regions (Fig. 1, 2). Moreover, only sparse data are available for *A. vineale* in some parts of south Moravia. Both species were usually collected in river valleys, especially in colder regions.

Both species are concentrated in the Mesophyticum phytogeographical region (Skalický 1988), i.e. the region of deciduous forests, and are only rarely documented from the Oreophyticum, i.e. the region of mountain flora (Fig. 3). Each species was missing from 23 phytogeographical districts.

Altitudinal range

The altitudinal range of both species in the Czech Republic is very similar (Fig. 4; *A. oleraceum*: $\bar{x} \pm s = 374 \pm 127$ m a.s.l.; *A. vineale*: $\bar{x} \pm s = 382 \pm 121$ m a.s.l.; two-sample t-test, $t = 1.4$, $df = 770$, $P = 0.16$) and species altitudinal distributions do not differ from each other (Kolmogorov-Smirnov test, $D = 0.06$, $P > 0.05$). Both species are concentrated from the hill country to submontane belts (200–600 m) with the most frequent occurrence between 300 and 500 m a.s.l. They also rarely occur in the montane belt, especially *A. oleraceum*. The altitudinal minimum of *A. oleraceum* is 120 m (Labské pískovce phytogeographical district) and that of *A. vineale* 190 m (Všetatské Polabí). The altitudinal maximum of *A. oleraceum* is 908 m (Bílé Karpaty lesní) and that of *A. vineale* 830 m (Krušnohorské podhůří).

Habitat differentiation

Both species occur in a wide range of habitats ranging from rocks and arable land to forests (Fig. 5). Nevertheless, their frequencies within respective habitats significantly differ ($\chi^2 = 234.2$; $df = 12$, $P < 0.001$). *A. oleraceum* frequently occurs in forests (especially in oak-hornbeam forests of the *Carpinion* alliance), forest edges and scrub, on rocks (esp. calcareous), field margins, open sunny slopes and steppe communities (namely those dominated by *Bromus erectus* and/or *Brachypodium pinnatum*, belonging to the *Festuco-Brometea* class). On the other hand, *A. vineale* is common in arable fields (mostly reported from cornfields) and their margins, roadsides, ditch banks, railway embankments and meadows (*Arrhenatheretalia* order) while it is rarely found on rocks, in forests and scrub.

The collectors frequently mentioned the occurrence of *A. vineale* on sandy and dry soils, especially in areas with arable land. In contrast, *A. oleraceum* was often collected on sliding soils (e.g. screes, wall tops) with a high proportion of rubble and detritus, especially of that originating from lime.

Both species are rarely found in wet meadows, alluvial forests and alder forests. Frequent occurrence of both species in the secondary *Robinia pseudacacia*-forests is probably related to the history of those stands which used to be vineyards, pastures, grasslands or steppes in the past and were later afforested. Survival of both species under the changed

conditions is made possible by the delayed foliation of *Robinia* in comparison with that of native tree species.

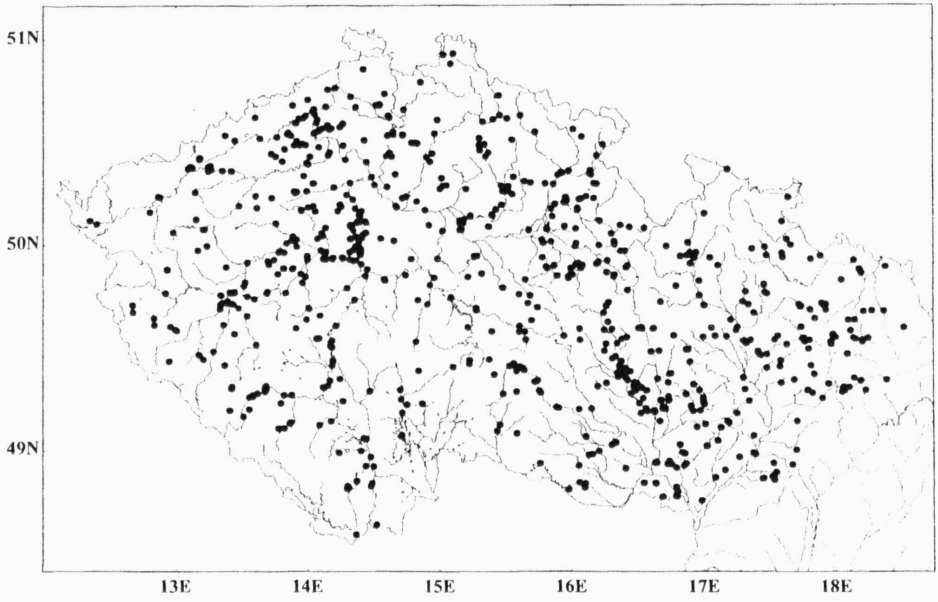

Fig. 1. – Map of the distribution of *Allium oleraceum* in the Czech Republic based on herbarium material.

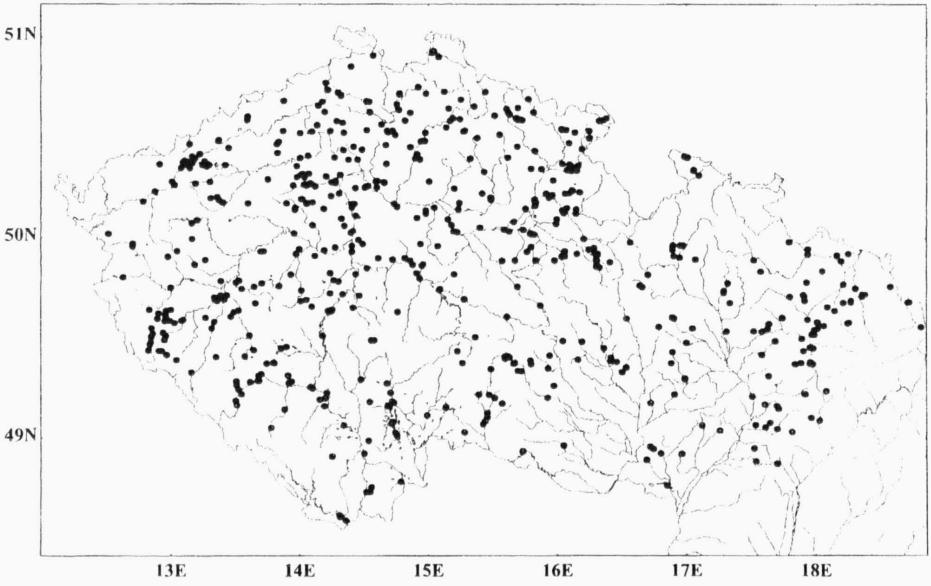

Fig. 2. – Map of the distribution of *Allium vineale* in the Czech Republic based on herbarium material.

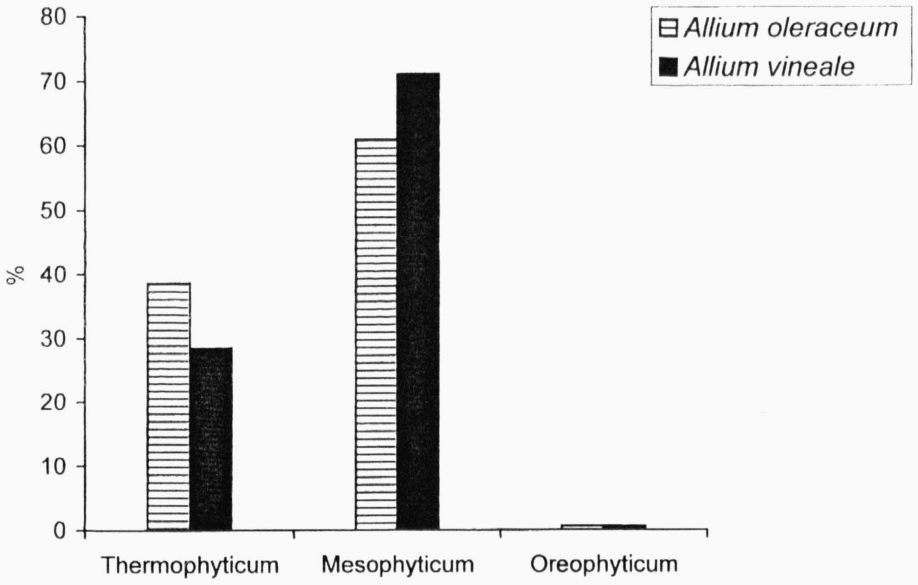

Fig. 3. – Proportional distribution of *Allium oleraceum* and *A. vineale* in phytogeographical regions.

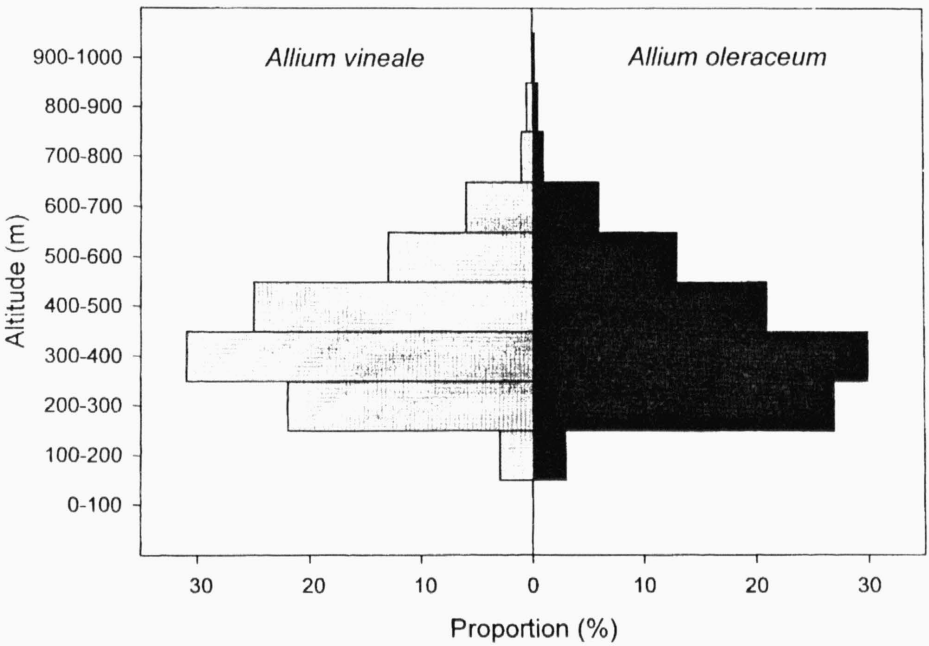

Fig. 4. – Vertical distribution of *Allium oleraceum* and *A. vineale* in the Czech Republic.

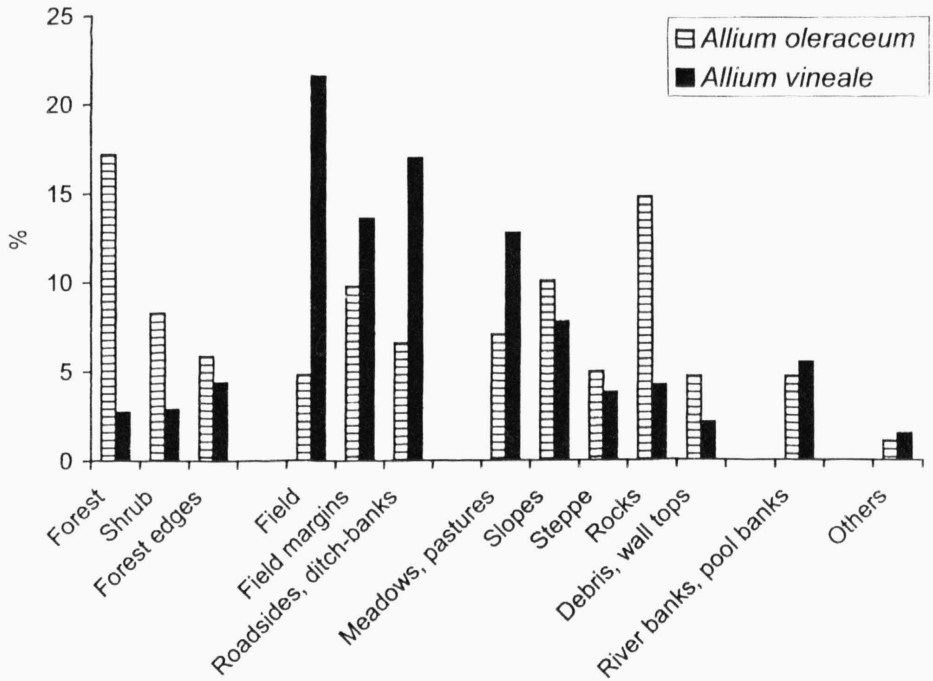

Fig. 5. – Proportional distribution of *Allium oleraceum* and *A. vineale* in various habitat types. Specimens for which the precise description of habitat was not given in the original source were omitted.

Since *A. vineale* was reported as a troublesome weed of arable land from many countries, the proportion of both species in fields in the Czech Republic during the last 150 years was analyzed using 50-years intervals. A significant retreat of both species, especially of *A. vineale*, from arable land in 1900–2000 was documented (Table 1).

Table 1. Proportion of specimens collected in the fields during three successive periods (% of the total number of specimens revised within each of period is given). Specimens for which the precise description of habitat was not given in the original source were omitted.

Period	*Allium oleraceum*	*Allium vineale*
< 1900	18.4	77.8
1900–1949	4.2	41.6
1950–1999	3.4	6.7

Discussion

Distribution and altitudinal range

From the viewpoint of general chorology, the species studied partially differ in their distribution areas. While *A. oleraceum* has the eurassuboceanic (submediteranean) distribution, *A. vineale* has the submediterranean-subatlantic one (Meusel et al. 1965, Oberdorfer

1994). *A. vineale* occurs in most parts of Europe except of N, C and E of Russia. The species further occurs in N Africa, Caucasus and Lebanon (de Wilde-Duyfjes 1976, Hultén & Fries 1986). *A. oleraceum* occurs in Europe from Scandinavia and N Russia to N Spain, Corsica, C Italy, former Yugoslavia, Bulgaria and the Caucasus (Hultén & Fries 1986). Both species were introduced to N America, Australia and New Zealand (Iltis 1947, Håkansson 1963, Meusel et al. 1965, Hultén & Fries 1986).

Near its northern limit (Norway, Sweden, Finland, Denmark), *A. vineale* is a typical lowland plant and most of its localities are situated near the sea-shore (Richens 1947, Faegri 1960, Håkansson 1963, Lid & Lid 1994, Dierssen 1996). In southern regions, the species reaches higher altitudes. In southern Alps it reaches 1000 m a.s.l. (Pitschmann & Reisigl 1965), in Italy 800 m (Sicily: 1900 m) (Pignatti 1982), in Alps of Valais 2 000 m (Kirchner et al. 1934) and in Turkey it is as high as 2650 m (Davis 1984). The altitudinal range of *A. oleraceum* is slightly different from that of *A. vineale* because the former species is frequently noted from higher altitudes. In Norway, *A. oleraceum* grows up to 880 m a.s.l. (Lid & Lid 1994). In the Tyrol and Alps of Valais, respectively, it is ascending to the altitude of about 1200 and 2200 m (Kirchner et al. 1934), in Italy to 1800 m (Pignatti 1982), in Slovakia to 1450 m (Velká Fatra Mts; Krahulec 1977) and in Bulgaria (Valev & Asenov 1964) it occurs also above 1000 m a.s.l.

The present study confirmed that both *A. oleraceum* and *A. vineale* are common species of the Czech flora and the most common species of the genus *Allium* in the area of the Czech Republic (Krahulec 1977, Dostál 1989). Although the species differ in their overall distribution areas, no apparent differences in their distribution pattern within the study area emerged, i.e. none of them prefers any region with specific climatic conditions. Absence of specimens from some regions at lower altitudes is probably caused by less intensive investigation, omission or by avoidance of some "uninteresting" vegetation types (e.g. scrub) where both species occur frequently.

The altitudinal ranges of both species in the Czech Republic are similar to those reported from most European countries where they occur mostly at lower altitudes. Nevertheless, in contrast to most European countries, both species in the Czech Republic occur only below 1000 m. This is probably related to the absence of distinct mountain ridges with rocky habitat and low frequency of lime-rich substratum in higher elevations of the Czech Republic (this holds for *A. oleraceum* in particular), and of low percentage of forest-free or deforested area there (especially *A. vineale*). This view is supported by a narrow habitat range of both species near their altitudinal maximum (above 750 m): *A. oleraceum* is confined to rocks and meadows, and *A. vineale* to meadows and pastures. The occurrence of *A. vineale* at high altitudes could be partly of anthropogenic origin, since many current mountain pastures and meadows could have served as fields in the past. Nevertheless, some observations from the Krkonoše Mts (F. Krahulec, pers. comm.) do not confirm this view.

Habitat differentiation

Habitat differences found between *A. oleraceum* and *A. vineale* in the Czech Republic correspond to the situation reported from other European countries. In N Europe (Sterner 1951, Håkansson 1963, Dierssen 1996, C. A. Haeggstroem in litt.) *A. oleraceum* occurs in deciduous woods (especially in flood-plain forests, e.g. *Ulmo-Fraxinetum*) and bushy

areas, mesic and dry meadows, and on rocky and gravel ground. Furthermore, it is common along field borders, roadsides and ditch-banks. In Great Britain (Clapham et al. 1962, Sell & Murrel 1996) it is confined to habitats including dry grassy, often south-facing slopes over chalk and oolite, banks of floodplain meadows and open sandy riverbanks. In Central Europe (Kirchner et al. 1934, Hegi 1939, Krahulec 1977, Dostál 1989) it is common in sparse light deciduous forests, forest edges and scrub. Furthermore, it occurs in fields, field margins, roadsides and ditch-banks and less frequently in vineyards and pastures. It is also reported from wall tops and steppe communities. In E, SE, SW and S Europe (Vvedensky 1935, Valev & Asenov 1964, Nyárády 1966, Soó 1973, Palhinha 1974, Pignatti 1982, Davis 1984) it is confined to steppe and south-facing slopes, scrub, forest edges, arable land and vineyards with raw soils.

In N European countries (Sweden, Denmark, Norway, Ireland) *A. vineale* is a coastal plant and only rarely occurs farther inland as a field weed (Richens 1947, Faegri 1960, Håkansson 1963). In Finland (C. A. Haeggstroem in litt.) *A. vineale* prefers dry meadows on calcium rich soils. In Britain the species occurs on various types of soils, usually sandy, as a weed of open, cultivated ground as well as of pastureland, on roadsides and only rarely in woods (Richens 1947, Clapham et al. 1962, Sell & Murrell 1996, Stace 1997). In W (Mennema et al. 1985) and C Europe (Kirchner et al. 1934, Hegi 1939, Soó 1973, Wilmanns 1975, 1985, Kotlińska 1999) the species is confined to dry, sandy slopes, fields and field margins, roadsides, meadows and vineyards (*Geranio-Allietum* Tüxen 1950 ass., cf. Wilmanns 1975) and occurs only rarely in forests and scrub. In S, SW and SE Europe *A. vineale* frequently occurs as a weed in vineyards and arable lands, on field-borders, roadsides and ditch-banks and less frequently in meadows and riverbanks (Valev & Asenov 1964, Nyárády 1966, Palhinha 1974, Pignatti 1982, Davis 1984). In Russia and Turkey, the species is also reported from mountain and alpine meadows (Vvedensky 1935, Davis 1984).

Apparently, high frequency of *A. oleraceum* in forests and scrub, in contrast to *A. vineale*, is partly related to plant traits; the former species grows better in the shade (Duchoslav 2000). Moreover, *A. vineale* rarely flowers in forests and scrub and its populations in these vegetation types thus consist mostly of non-reproductive plants, whose spreading is limited to the production of daughter bulbs in the proximity of the mother bulb. On the other hand, *A. oleraceum* often completes reproduction in the shade and produces many bulbils and some seeds on aerial scape (Duchoslav 2000).

Plants of *A. oleraceum* produce one non-dormant daughter bulb aboveground occasionally (Duchoslav 2000). This bulb can spread from the parent plant since the new daughter plant exhibits centrifugal growth up to 5 cm from the parent plant. *A. oleraceum* probably has another advantage, especially on slopes and on rocks, in that the daughter bulbs often fail to pull in the soil, which allows for their movement on the surface to longer distance from the parent plant.

Markedly higher frequency of *A. vineale* as a weed of arable land before 1950, compared to *A. oleraceum*, is closely related to the following plant traits of the former species: (i) massive production of aerial bulbils whose size is similar to barley or wheat corns, (ii) numerous belowground production of dormant daughter bulbs in the proximity of mother plant (Richens 1947, Håkansson 1963, Stritzke & Peters 1972) and (iii) rapid growth which begins during autumn (Håkansson 1963, Duchoslav 2000). These features enabled *A. vineale* to be a troublesome weed in winter sown cereals in N, NW Europe and in N America (e.g. Richens 1947, Iltis 1949, Håkansson 1963) since the cleaning of contami-

nated seeds for sowing from bulbils was not too efficient and dormant daughter bulbs with hard covering leaf were able to withstand cultivation. Moreover, phenology of *A. vineale* is similar to the phenology of crop-plant and part of the bulbils and seeds are able to ripen before the harvest (Duchoslav 2000).

The differences in sprouting and phenology of the daughter bulbs of *A. vineale* and *A. oleraceum* (Duchoslav 2000) could be the main reasons for the less frequent occurrence of the latter species on arable land (cf. Håkansson 1963). Apparent retreat of both species from the fields during the second half of 20th century is related to changes in agricultural management such as subsoil ploughing and use of selective herbicides. Both species were superseded from fields to their margins and roadsides where they are common at present. The above mentioned changes in management were also responsible for extinction of many other bulbous weeds (e.g. *Gagea villosa*, *Ornithogalum* spp., *Muscari* spp.) from vineyards and fields in many European countries (Håkansson 1963, Wilmanns 1975, 1985).

Frequent occurrence of *A. vineale* in meadows and pastures is closely related to its other important features: (i) unpalatability of leaves that decreases the level of herbivory (Håkansson 1963) and (ii) high resistance to cutting, and high competitive ability (Lazenby 1961a, b, 1962). Under such conditions, *A. vineale* shows remarkable small-scale pattern represented by dense clumps of plants originating from daughter bulbs (Duchoslav 2001).

Polyploidy

Both species are formed by polyploid complexes (*A. oleraceum*: 2n = 24, 32, 40, 48; *A. vineale*: 2n = 32, 40; Vachtina & Kudryashova 1985, Májovský & Murín 1987, Měsíček & Jarolímová 1992, Fialová 1996). Within polyploid complexes, the cytotypes can differ in many traits, which influence their geographical, and altitudinal distribution and environmental amplitude (Stebbins 1971, Lewis 1980). Until now, however, only sparse data on karyology, reproduction and distribution of *A. oleraceum* cytotypes has been obtained (Fialová 1996, Duchoslav 2000) and the results are inconsistent. According to preliminary observations, plants of different cytotypes (2n = 4x, 5x) of *A. oleraceum* do not show apparent differences in morphology of vegetative parts and in production of bulbils and flowers (Duchoslav 2000). On the other hand, Fialová (1996) found differences in behaviour during meiosis and in the mean number of produced flowers per plant among cytotypes (2n = 4x, 5x, 6x) of *A. oleraceum*. She also found mixed stands of two cytotypes (15.8% of analysed populations) during her karyological study of *A. oleraceum* in Moravia (Fialová 1996). A more detailed study of cytotypes of both species is therefore needed.

Limitations to the data

Since the length of vegetative season of non-reproductive plants is apparently shorter than that of reproductive ones (Duchoslav 2000), most forest and scrub populations of *A. vineale* are not visible aboveground during summer. Moreover, since both species are very similar in shape and size, especially when sterile plants are compared (Krahulec 1977), they are usually not collected. This is supported by a negligible frequency of sampled sterile plants in revised collections (only 5 and 6 specimens contained entirely sterile

plants in the case of *A. oleraceum* and *A. vineale*, respectively). Thus the habitat preference and altitudinal range of studied species, which is reported in the present study, could be partly biased in favour of sites where flowering plants occur.

Acknowledgement

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Souhrn

Ve střední Evropě a v České republice náleží k nejčastěji se vyskytujícím zástupcům rodu česnek (*Allium* L.) druhy *Allium oleraceum* a *Allium vineale*. Široká a do jisté míry i podobná ekologická amplituda obou druhů uváděná v řadě flór je poměrně vzácným případem v rámci funkční skupiny cibulových geofytů, kam oba druhy náleží. Studium dostupné literatury z původního a druhotného areálu obou druhů přesto ukázalo na jisté rozdíly v jejich rozšíření a stanovištních preferencích. *A. oleraceum* je typický evropský taxon, zatímco rozšíření *A. vineale* má submediterránně-subatlantský charakter. Revize herbářového materiálu z území ČR ukázala, že oba druhy jsou běžnými zástupci naší flóry nižších až středních poloh, ačkoliv výjimečně lze oba druhy nalézt i v oreofytiku. Ačkoliv oba druhy preferují obdobná stanoviště, liší se výrazně v relativních četnostech, s jakými tato stanoviště osídlují. *A. oleraceum* bylo častěji sbíráno v listnatých lesích, křovinách, na skalách a otevřených slunných svazích, *A. vineale* na polích, okrajích cest a silnic, mezích a loukách. Situace zjištěná na území ČR tak velmi dobře odpovídá literárním údajům z dalších oblastí přirozeného areálu obou druhů. Zvláštní pozornost byla věnována výskytu obou druhů jako plevelné složky na polích. Analýza ukázala, že (i) během posledních 100 let došlo k rapidnímu ústupu obou druhů z polí, a že (ii) výskyt *A. oleraceum* na polích byl a je spíše efemérní záležitostí v porovnání s *A. vineale*, které bylo do začátku 20. století sbíráno v ca 78 % případů v polních kulturách.

Častější výskyt *A. oleraceum* v lesích souvisí s jeho schopností úspěšné reprodukce i ve stínu, zatímco stíněné populace *A. vineale* jsou většinou tvořeny pouze sterilními jedinci a druh se v těchto podmínkách jen zřídka reprodukuje prostřednictvím semen a pacibulek. Schopnost *A. vineale* být výrazným plevelem v obilných polích (zvl. v minulosti) souvisí s několika specifickými vlastnostmi druhu: (i) rychlý růst a fenologie obdobná obilninám, (ii) produkce velkého množství pacibulek, jejichž velikost je podobná obilkám plodiny, (iii) produkce velkého počtu dormantních dceřinných cibulí, které jsou schopny přežít orbu. Obdobně tak častější výskyt *A. vineale* na loukách souvisí se: (i) sníženou herbivorií v důsledku „nechutnosti" listů, (ii) výraznou tolerancí ke kosení a (iii) vysokou kompetiční schopností druhu.

Převážnou část revidovaných sběrů (> 99 %) tvořily položky generativních rostlin. Jelikož jsou oba druhy ve sterilním stavu obtížně určitelné a lehce zaměnitelné, sběratelé se pravděpodobně vyhýbali sběru sterilních rostlin. Velmi pravděpodobné je též přehlédnutí sterilních rostlin, protože tyto rostliny jsou při letmějším pohledu lehce zaměnitelné za traviny. Opomíjení či přehlédnutí sterilních rostlin, či spíše celých populací tvořených pouze sterilními rostlinami, však může ovlivnit zjištěné rozdíly ve stanovištních preferencích studovaných druhů. Výsledné stanovištní preference zjištěné na základě studia herbářů by pak byly z části artefaktem daného přístupu při sběru dat a vypovídají především o stanovištích optimálních pro reprodukci obou druhů.

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