

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	57	1	15–32	2009
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Regular research paper

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EFFECTS OF CONTRASTING HABITATS ON THE PHENOLOGY, SEASONAL GROWTH, AND DRY-MASS ALLOCATION PATTERN OF TWO BULBOUS GEOPHYTES (ALLIACEAE) WITH PARTLY DIFFERENT GEOGRAPHIC RANGES

ABSTRACT: *Allium oleraceum* L. and *A. vineale* L. are two related bulbous geophytes with an annual storage organ that coexist in a wide range of habitats but show both partly different geographic ranges and habitat preferences in Europe. To explore whether ecological and distributional differences between species can be related to expected variation in some key life-history traits between them, research was undertaken to compare the phenology, seasonal growth, and dry-mass allocation of vegetative and reproductive plants of the species at successional gradient comprising three sites with contrasting environmental conditions (steppe, scrub, forest), where populations of the study species coexist (the Czech Republic). The results showed, in general, partly different timing of phenophases between species and different responses of species to contrasting environmental conditions. *A. vineale* displayed an annual life cycle similar to that observed in many Mediterranean geophytes, i.e. regularly sprouting above ground before the arrival of winter, its growth was concentrated into early and mid-spring and started to wither after a temperature increase and several short-term drought events in early summer, though its flowering was delayed until late June. *A. oleraceum* showed high year-on-year variation in the onset of shoot elongation above-ground; its growth was concentrated into mid- and late spring and its flowering was delayed until July. The patterns of phenology observed between the study spe-

cies thus partly reflect selection under different environmental conditions of their origin. The total duration of the green above-ground period of reproductive plants in both species continued about 1.5–2 months beyond that of the vegetative ones. Over main growth period, mean relative growth rates (*RGR*) of *A. oleraceum* and *A. vineale* ranged from 20 to 22 and from 6 to 28 mg g⁻¹dw day⁻¹, respectively. *A. vineale* showed significantly higher *RGR* than *A. oleraceum* only in steppe conditions while at shaded sites the reverse pattern was found. The *RGR* of both vegetative and reproductive plants of *A. oleraceum* did not differ from one site to another. On the other hand, both vegetative and reproductive *A. vineale* plants showed lower *RGR* at shaded sites than at steppe one. Shading increased allocation into leaves in both species, caused complete abortion of developing scapes in *A. vineale* but only reduced reproductive allocation in *A. oleraceum*. *A. oleraceum* was able to maintain fitness-related traits more stably across the environments studied than *A. vineale* that fit well into the pattern of habitat differentiation observed between them in Central Europe. Data concerning growth of and allocation into new bulb in both species also support the hypothesis that allocating reserves for the coming year is the first priority in geophytes with an annual storage organ.

KEY WORDS: geophytes, allocation, canopy closure, growth dynamics, phenology, storage

1. INTRODUCTION

When attempting to understand the environmental control of plant development, the origin of particular species must be taken into account (Meusel and Jäger 1992). Thus, species with different geographic ranges can respond differently to similar environmental conditions (Rychnovská and Úlehlová 1975, Kawano 1985). On a landscape level, a correlation has been found between the performance of particular range types and certain types of environments (Nimis and Bolghini 1993, Chytrý 1995). From this point of view, geophytes are ideal study subjects. Geophytes are a highly specialised life form with renewal buds located underground and are associated with large storage organs such as bulbs, corms, rhizomes, etc. This specialisation is related to their adaptations to environmental extremes, especially strong seasonal climate variation (Rees 1972, Dafni *et al.* 1981, Debussche *et al.* 2004) or disturbances (Iwasa and Kubo 1997), and is manifested by distinct periodicity in their growth and flowering.

The objective of this study was to compare variation in selected life-history traits of two congeneric bulbous geophytes, *Allium oleraceum* and *A. vineale* (Alliaceae). The study species are structurally and morphologically similar (Duchoslav 2000), their life cycle is characterized by the successive development of leaves and flowers during the growing season and by an annually renewed storage organ, and they inhabit a wide and similar range of habitats from rocky ground to deciduous forests (Duchoslav 2001a). On the other hand, the species differ in their geographic pattern of distribution and in habitat preferences. Although their distribution areas overlap strongly in Central and Western Europe, *A. oleraceum* has a eurasuboceanic-submediterranean pattern of distribution while *A. vineale* has a submediterranean-subatlantic pattern (Meusel *et al.* 1965, Oberdorfer 1994). The former inhabits both exposed and shaded habitats while the latter rather prefers exposed and often disturbed habitats in Europe (Duchoslav 2001a, Hægström and Åström 2005).

To examine whether ecological and distributional differences between species can be related to expected variation in some key life-history traits between them, research was undertaken to compare the phenology, seasonal dynamics of growth, and dry-mass allocation of the species at three sites with contrasting environmental conditions representing successional gradient from open grassland to closed forest, where populations of the study species coexist. Specifically, the following questions were addressed: (i) Do the study species show different overall patterns of phenology, growth, and dry-mass allocation?; (ii) To what extent are the growth, phenology, and the dry-mass allocation of the species altered by contrasting habitats? Since it was observed in many geophytes that smaller plants differ in responses to climate and local environmental conditions from larger ones (Barkham 1980, Nault and Gagnon 1988, Eggert 1992), I made separate observations on vegetative and reproductive plants.

The study species have an annually renewed storage organ; hence it is predicted that allocating reserves for the coming year is their first priority (Rees 1966, Dafni *et al.* 1981). Nevertheless, model studies of the growth of perennial plants predict that in undisturbed, strictly seasonal environments with a predictable pattern of variation in growing conditions selection will operate for the optimal time to switch from growth to storage (Iwasa and Cohen 1989) and sexual reproduction (Iwasa and Roughgarden 1984). In contrast, unpredictable temporal variability in the environment selects for resources being stored at all times (Iwasa and Kubo 1997). Therefore, I addressed an additional question: (iii) What is the timing of reserve allocation in these species?

2. MATERIAL AND METHODS

2.1. Study species

Allium oleraceum L. is a bulbous herb with 1–5 leaves. The leaves are linear to filiform, fistular in the lower part and sheath on the lower half of the scape. The terminal bulb in the vegetative plants and the major offset bulb in the reproductive plants replace the

parent bulb annually. In addition, plants can form laterally non-dormant daughter bulbs. Reproductive plants produce a loose lax umbel with a few hermaphroditic flowers (0–20) and a few or many bulbils (5–60) at the top of a scape. Each flower can potentially produce six seeds (Stearn 1980, Duchoslav 2000).

Allium vineale L. is a bulbous herb with 1–4 leaves. The leaves are sub-cylindrical, fistular and sheathe the lower third to two thirds of the scape. The terminal bulb in the vegetative plants and the major offset bulb in the reproductive plants replace the parent bulb annually. Plants can form lateral daughter bulbs with a heavily cuticularised, waxy covering leaf. At the top of the scape, reproductive plants produce a compact umbel with a variable number of hermaphroditic flowers (0–30) and bulbils (0–60) ranging from umbels with only flowers to umbels with only bulbils. Each of the flowers can potentially produce six seeds (Richens 1947, Duchoslav 2000).

2.2. Study sites

One site for each of the three contrasting habitats that are typical of the study species in Central Europe (forest, scrub, and steppe; Duchoslav 2001a) was selected for the study. The first (**forest**) was near the village of Slatinice, Czech Republic (49°33'39"N, 17°05'20"E; 270 m a.s.l.) with an overstory mainly of alien *Robinia pseudacacia* L. (cover of tree layer: 85%; cover of shrub layer: 75%; cover of herb layer: 60%; *Chelidonio-Robinion* alliance in phytosociological classification). The second site (**scrub**), near the village of Voletice, Czech Republic (49°54'27"N, 16°02'09"E; 340 m a.s.l.) had an overstory of *Fraxinus excelsior* L. and *Prunus spinosa* L. shrubs (cover of shrub layer: 80%; cover of herb layer: 40%; *Berberidion*). The third site (**steppe**) was near the village of Štěnec, Czech Republic (49°56'01"N, 16°03'30"E; 340 m a.s.l.) and represents semidry grassland dominated by *Bromus erectus* Hudson and *Arrhenatherum elatius* (L.) Beauv. ex J. Presl et C. Presl (cover of herb layer 90%; transient type between *Arrhenatherion* and *Cirsio-Brachypodion*). Sparse populations of the study species occur at all the sites studied.

2.3. Study of phenology

All populations were monitored during the years 1995–1998. Two ontogenetic stages were studied at all sites: adult vegetative plants (V) usually bearing two or three leaves, and reproductive plants (R). Observation of at least 25 randomly located individuals of each ontogenetic stage was carried out every second week during the spring and summer and once monthly during the autumn and winter. When necessary, plants were carefully dug up and their phenologic status was determined in the laboratory. The phenologic phases are described in Fig. 2. The respective phenophase was assigned to each stage if at least 50% of the observed individuals entered the phenophase.

2.4. Seasonal growth and allocation

During 1995, eight harvests were carried out at intervals of approximately three weeks throughout the growing season and as a single shot in the winter (i.e. 10 January, 20 March, 10 April, 2 May, 22 May, 15 June, 17 July and 6 August). At each site all individuals of the study species were dug up from five to seven randomly located quadrates of 20 × 20 cm. In late summer (6 August), a different sampling method was used: only reproductive plants of the study species were randomly sampled within each population. Except for the July and August samplings, the sample size for each combination of species, period, habitat and stage always exceeded 12 plants. In the laboratory, all plants were excavated from the soil, washed in the washing bath, and classified into appropriate stage categories (V, R; other individuals were excluded from the analysis). Plant height (i.e. distance from the top of the bulb to the tip of the longest leaf or the top of scape) was measured in each plant. The plants were then divided into leaves (blades and sheaths above the bulb), scape, basal leaf sheaths (i.e. base of the dead and live leaves covering storage leaf and bulb axis), bulb (incl. bulb axis), flowers, bulbils and spathe. All samples were weighed after oven drying at 85°C for 48 hrs. The relative allocation into component parts was expressed as the ratio of the plant

mass of the respective part to the total plant mass (in %). Because of the rare occurrence of plants bearing new daughter bulbs, those plants were excluded from the analysis. Roots were eliminated from the collections because they were not all removed from the soil. Data on dry mass were used to calculate relative growth rate (*RGR*) according to Hoffmann and Poorter (2002):

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \text{ (day}^{-1}\text{)} \quad (1)$$

where $\ln(W_1)$, $\ln(W_2)$ were the mean of the \ln -transformed dry mass of each stage (mg) in the respective t_1 and t_2 , i.e. dates of sampling.

2.5. Irradiance

On each visit in growing season 1995, irradiance was measured with double METRA LUX PU 150 photometers comparing the open plain field and beneath the canopy (5 cm above the ground; $n = 15$ at each visit) at the study sites. Measurements were carried out during uniform weather conditions. The course of the relative irradiance (RI) during 1995 at the sites studied is shown in Fig. 1. While high solar radiation reached the soil

surface of the steppe throughout the year, great changes in RI were found at the other sites (ANOVA; habitat, time, habitat \times time interaction, all $P < 0.001$). During late April and May, a decrease in RI occurred in the scrub and forest because of buds bursting in some trees and shrubs and quick growth in some herbs. An apparent decrease in RI occurred at both shaded sites at the beginning of June. The low RI continued beneath the canopy in forest and scrub throughout summer.

2.6. Climatic conditions

The study sites are characterised by a mean annual temperature of about 8.5°C and mean annual precipitation of about 600 mm (Hradec Králové and Olomouc climatic stations; long-term averages from 1960 to 1990). The course of precipitation and temperature in the spring and summer of 1995 did not markedly differ from the long-term course, except for February and July, which were warmer than the long-term averages. Low precipitation and temperatures occurred during the autumn in both regions. Very low temperatures and low precipitation were typical of the winter and early spring

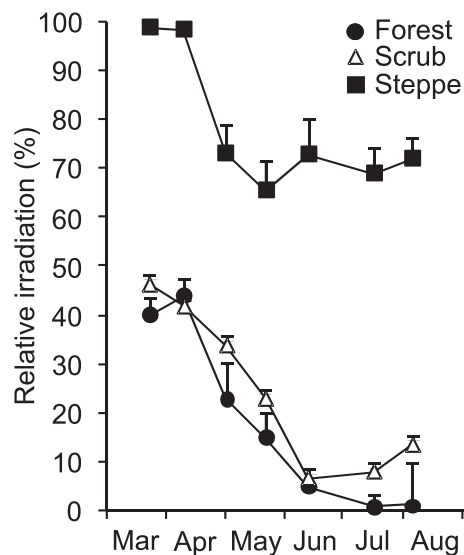


Fig. 1. The course of the relative irradiation (mean + SE) in the study sites during the 1995 growing season.

(March) of 1996. The course of temperature and precipitation during the rest of the year was similar to the long-term averages. The course of temperature and precipitation in 1997 did not differ markedly from the long-term course, except for extremely high rainfall in July.

2.7. Statistical analysis

A general linear model (GLM) was performed on the plant mass and height of the species with species (S), habitat (H), and time of harvest (T) as crossed, fixed factors. Possible factor effects on RGR were analysed by testing the factor \times time interactions, using the \ln -transformed dry-mass data (Poorter and Lewis 1986). Tests were separately performed for vegetative and reproductive plants and were restricted to the period 20 March–15 June to meet the restrictive conditions of the analyses and reasonable sample sizes. Before the analyses, plant mass was \ln -transformed and the height was square root-transformed to meet normality requirements. Post-hoc multiple comparisons were made by means of the Tukey test (Zar 1996).

The plant mass allocation pattern expressed as a ratio of dry-mass of each component to the total dry-mass (in %) was first analysed using MANOVA, with species, time, and habitat as crossed, fixed factors. Tests were performed separately for vegetative and reproductive plants and restricted to the period 20 March–15 June. Pillai's trace was used as a test statistic because it is more robust regarding departures from assumptions than the other statistics (Hintze 2004). Once a multivariate test had found a term significant, a univariate ANOVA was used to determine which of the variables and factors were responsible for the significant effects (data not shown).

3. RESULTS

3.1. Phenology

The study species differed from each other in the timing of their phenophases within the year (Fig. 2). Generally, *A. vineale* began

and finished each phenophase earlier than *A. oleraceum*. The timing of some vegetative phenophases was stage-specific.

Shoots of vegetative and reproductive *A. vineale* plants started to sprout from September to November and plants usually overwintered with one or two leaves above ground. *A. oleraceum* sprouted slowly from October to December and usually grew just close to the soil surface before winter. *A. oleraceum* plants showed, however, higher year-on-year variation in the onset of shoot elongation above ground than those of *A. vineale* (Fig. 2). Shoot sprouting of both species was retarded by cold and dry autumns and cold winters (e.g. in 1995–96), when especially the *A. oleraceum* plants did not appear above ground until February. On the other hand, plants of both species had green leaves present above ground before the arrival of winter in years with a warm and wet autumn (e.g. in 1994). The duration of the phase of green leaves took about 1–1.5 months longer in *A. vineale* plants than in *A. oleraceum*.

Vegetative *A. vineale* plants usually entered the phase of leaves withering from the second half of May till the beginning of June, *A. oleraceum* two-three weeks later. Shoots of vegetative *A. vineale* plants died out by the end of June while those of *A. oleraceum* died out, on average, in the middle of July (Fig. 2). The green leaves persisted in reproductive plants of both species for a longer time span than those in the vegetative ones. During summer, the leaves of reproductive plants of both species continually senesced with usually the last (*A. oleraceum*) or no (*A. vineale*) leaf being green during the full flowering. The initiation and subsequent development of the scape and reproductive structures both started and terminated earlier in *A. vineale* than in *A. oleraceum* (Fig. 2).

Modifications of phenologic development by contrasting habitats were observed in plants of both species but the responses of the species to identical environmental conditions were not always similar. In general, plants of both species growing in steppe conditions entered most of their phenophases (i.e. sprouting to reproduction) earlier but they passed into withering and shoot dormancy phases later than those in shaded sites (Fig. 2). The vegetative *A.*

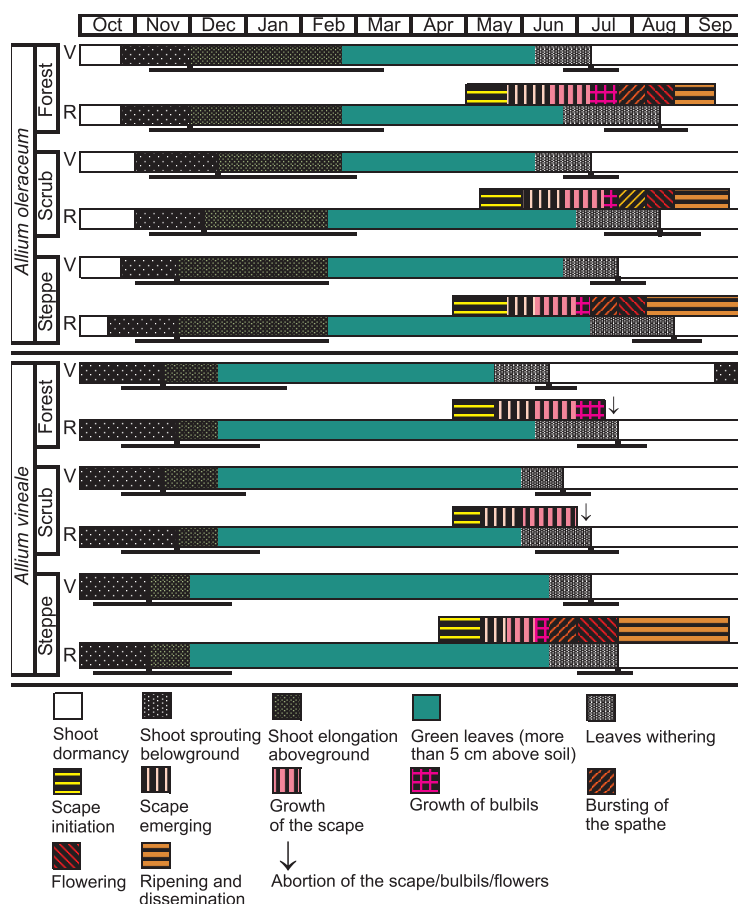


Fig. 2. Phenology of vegetative (V) and reproductive (R) *Allium oleraceum* and *A. vineale* plants in three contrasting habitats (steppe, scrub, forest). The beginning of the respective phenophase represents the median of the dates when at least 50% of the individuals observed entered the respective phenophase during 4 years of monitoring (1995–1998). A horizontal line below selected phenophases (elongation of shoot above ground; complete senescence of leaves) represents the range of observed medians during the 4 years of monitoring.

vineale plants responded immediately to canopy closure in forest and scrub conditions at the end of May (Fig. 1) and switched over to withering and afterwards died out apparently faster than those of *A. oleraceum*. Reproductive plants of both species growing in steppe conditions finished reproduction successfully. On the other hand, reproductive *A. vineale* plants, in contrast to those of *A. oleraceum*, usually failed in the composition of either scape or generative organs at shaded sites (Fig. 2).

3.2. Seasonal changes in plant height

All factors and their interactions significantly affected the plant height of both vegetative and reproductive plants (Table 1, Fig. 3).

Vegetative plants. In January, *A. vineale* was higher than *A. oleraceum* at all sites. During late March and April, the height of both species increased rapidly in shrub and steppe conditions but *A. vineale* increased in height even faster than *A. oleraceum* there. Apparent differences in height between species occurred in forest conditions, where the increase in the height of *A. vineale* slowed down in the second half of April while *A. oleraceum* increased steadily in height (Fig. 3). *A. oleraceum* had reached its maximal height at all sites by the end of May while *A. vineale* reached its maximal height either at the beginning of May in forest conditions or by the end of May in steppe and in scrub conditions. Except for *A. vineale* in forest conditions, the maximal height of both species increased

Table 1. General linear models of the time course of the plant height and dry mass of *A. oleraceum* and *A. vineale*: effects of species, habitat, time, and their interactions. Vegetative and reproductive plants are tested separately. Tests are restricted to the period 20 March–15 June.

Source of variation	Height				Dry mass				
	Vegetative plants		Reproductive plants		Vegetative plants		Reproductive plants		
	DF	F	P	F	P	F	P		
Species (S)	1	18.1	<0.001	42.7	<0.001	16.2	<0.001	30.7	<0.001
Habitat (H)	2	17.5	<0.001	32.9	<0.001	82.8	<0.001	155.7	<0.001
Time (T)	4	279.9	<0.001	462.0	<0.001	128.3	<0.001	164.5	<0.001
S × H	2	43.1	<0.001	4.4	0.013	77.2	<0.001	63.3	<0.001
S × T	4	10.4	<0.001	15.0	<0.001	7.3	<0.001	8.6	<0.001
H × T	8	5.5	<0.001	8.8	<0.001	5.6	<0.001	11.7	<0.001
S × H × T	8	16.3	<0.001	25.0	<0.001	16.3	<0.001	14.6	<0.001
Total DF			836		786		836		786

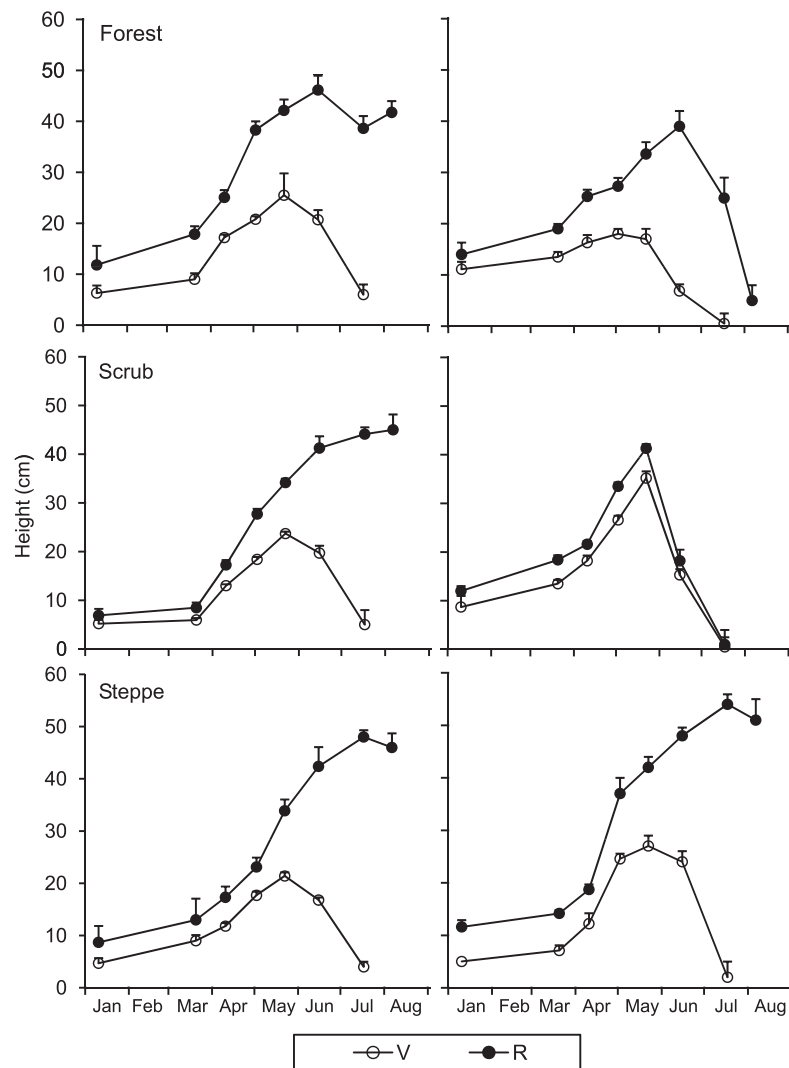


Fig. 3. Seasonal changes in the plant height (mean + SE) in vegetative (V) and reproductive (R) *Allium oleraceum* plants (left column) and *A. vineale* plants (right column) in three contrasting habitats (steppe, scrub, forest) during 1995.

in more shaded sites, with *A. vineale* being higher than *A. oleraceum* within scrub and steppe. The maximal height of *A. vineale* was lower than that of *A. oleraceum* in the forest and it was even the lowest of all sites (all $P < 0.05$). After the peak in height, vegetative plants of both species started to decrease in height as a result of the onset of senescence but the process was more rapid in *A. vineale* than in *A. oleraceum*.

Reproductive plants. During the winter and early spring, height changes in reproductive plants of both species were similar to those observed in vegetative plants at all sites (Fig. 3). During the second half of April and in May, the height of *A. oleraceum* increased rapidly at all sites while that of *A. vineale* increased, either slowly in the forest or rapidly at other sites. Both species reached their maximal height one month earlier in the forest (mid-June) than in the steppe (mid-July). In scrub, *A. oleraceum* reached its maximal height in mid-July, while *A. vineale* had done so by the end of May, and then it rapidly decreased in height because of failing to develop a scape. Except for on the steppe ($P = 0.12$), the maximal height of *A. oleraceum* was higher than that of *A. vineale* within the forest and scrub (all $P < 0.05$). The maximal height reached by both species was significantly higher in steppe conditions than in shaded populations ($P = 0.02$).

3.3. Seasonal changes in dry mass and RGR

All factors and their interactions affected the plant mass of vegetative and reproductive plants significantly (Table 1, Fig. 4).

Vegetative plants. During the winter, plants of both species lost reserves and showed negative RGR at all sites. Both species reached their lowest plant mass at all sites in March. A rapid increase in plant mass occurred in both species at all sites during April. No significant differences in RGR were observed between species in shaded sites during April (all $P > 0.1$). On the other hand, the RGR of *A. vineale* was significantly higher than that of *A. oleraceum* in steppe conditions at the same time ($P = 0.001$). During May and the first half of June, the increase in the plant mass of *A. vineale*, but not of *A. oleraceum*, slowed down and later stopped at

shaded sites. Hence, the RGR of *A. oleraceum* was significantly higher than the RGR of *A. vineale* in shaded sites during this period (all $P < 0.05$). On the other hand, no differences in RGR were found between species growing in steppe conditions during May and the first half of June ($P = 0.79$). *A. oleraceum* at all sites and *A. vineale* at the steppe site reached their highest mass during the middle of June. *A. vineale* at the forest and shrub sites reached its maximal mass in late May (Fig. 4). The maximal mass of both species decreased in more shaded sites, with *A. oleraceum* being heavier than *A. vineale* within each site (all $P < 0.05$).

Reproductive plants. During the winter and early spring (March, April), changes in mass in the reproductive plants of the study species were very similar to those observed in the vegetative plants at all sites (Fig. 4). In May, June, and the first half of July, the increase in plant mass of *A. vineale*, but not that of *A. oleraceum*, slowed down and later decreased at shaded sites. Hence, the RGR of *A. oleraceum* was significantly higher than the RGR of *A. vineale* in shaded sites during this period (all $P < 0.05$). On the other hand, both species increased in mass and no differences in RGR were found between them at the steppe site during the same period ($P = 0.12$). *A. oleraceum* at all sites and *A. vineale* at the steppe site reached their highest mass during the middle of July, while *A. vineale* in forest and shrub conditions reached its maximal mass in mid-June and late May, respectively. The maximal mass of both species decreased in more shaded sites, with *A. oleraceum* being heavier than *A. vineale* within scrub and forest conditions (all $P < 0.05$). No difference in maximal mass was found between species growing in steppe conditions ($P = 0.19$).

3.4. RGR over main growth period

The daily RGR of the vegetative and reproductive plants of the study species over the main growth period is summarised in Table 2. Vegetative and reproductive *A. vineale* plants showed significantly higher RGR than those of *A. oleraceum* only in steppe conditions, while at the other sites the

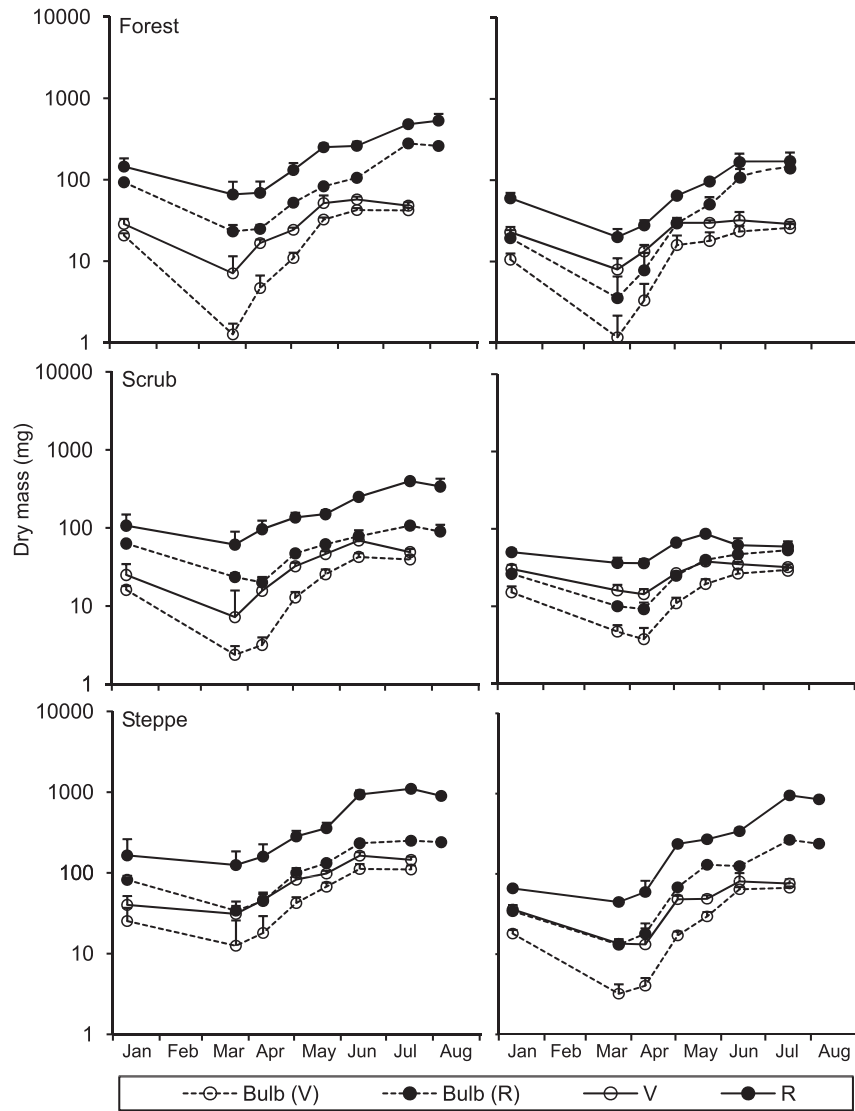


Fig. 4. Seasonal changes in the total plant dry mass (mean + SE; solid line) and bulb dry mass (dashed line) in the vegetative (V) and reproductive (R) *Allium oleraceum* plants (left column) and *A. vineale* plants (right column) in three contrasting habitats (steppe, scrub, forest) during 1995. Note the log-scale of plant dry mass.

reverse pattern was found. The *RGR* of both the vegetative and reproductive *A. oleraceum* plants did not differ from site to site. On the other hand, both the vegetative and reproductive *A. vineale* plants showed lower *RGR* at shaded sites than at the steppe one.

3.5. Allocation

MANOVA revealed the significant influence of all factors and their interactions on the pattern of mass allocation of vegetative and reproductive plants (Table 3).

Vegetative plants. A comparison of the pattern of mass allocation clearly showed time asynchrony between species (Fig. 5). *A. vineale* allocated significantly more percentage of mass to leaves than *A. oleraceum* during the majority of the growing period. Leaf allocation was greater in both species in the shade than in the steppe but under shade *A. vineale* allocated even more to leaves than *A. oleraceum* (all $P < 0.05$). At all sites, the mass of the bulb in both species started to increase in size immediately after its exhaustion and the allocation to the

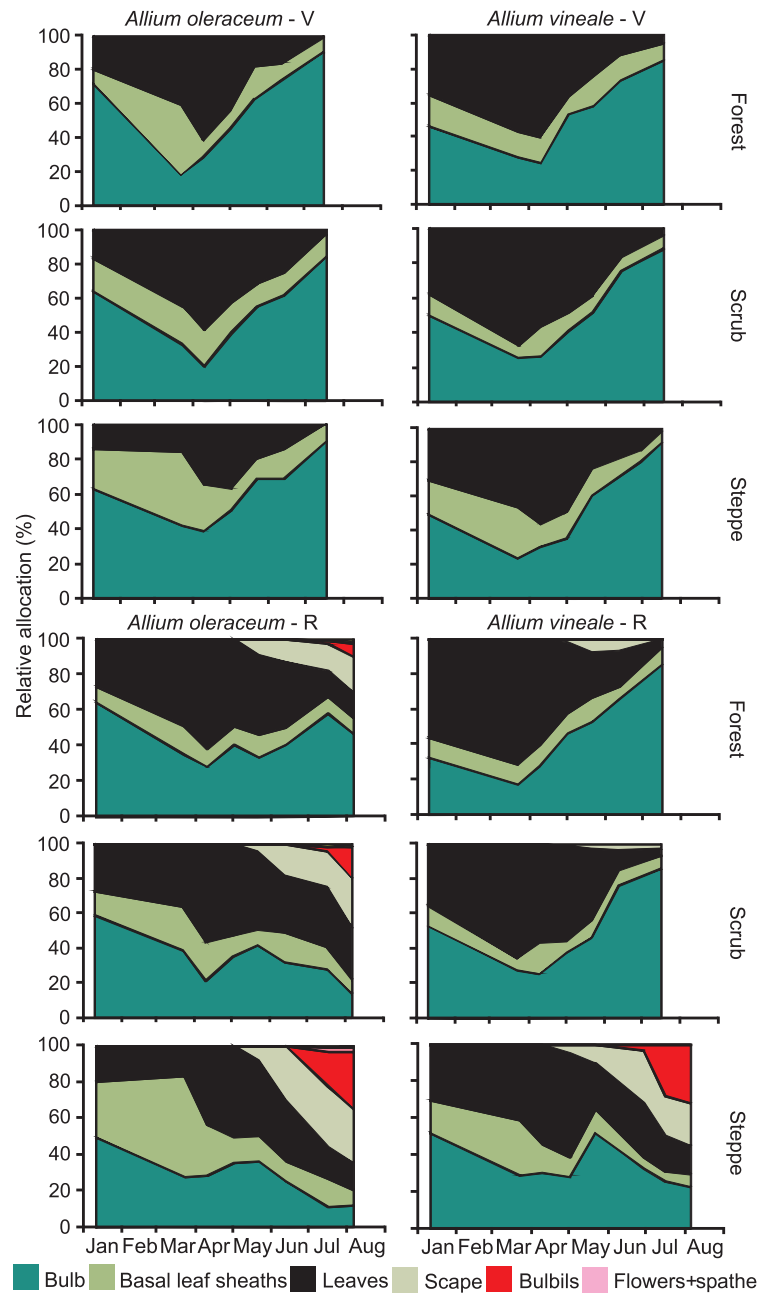


Fig. 5. Changes in relative distribution of the dry mass (%) in the vegetative (V) and reproductive (R) *Allium oleraceum* and *A. vineale* plants in three contrasting habitats (steppe, scrub, forest) during 1995.

bulb increased gradually during the season (Figs 3, 5).

Reproductive plants. During the winter and early spring (March, April), the pattern of mass allocation in the reproductive plants of the study species was very similar to that observed in the vegetative plants (Fig. 5). Dramatic changes in mass allocation occurred in both species in the phase of scape

elongation. *A. vineale* growing at the shaded sites aborted scape development very early (May) and therefore the allocation into and growth of the bulb increased gradually during plant maturation (Figs 3, 5). In *A. vineale* growing at the steppe site and in *A. oleraceum* growing at all sites, scape elongation initially caused short-time stagnation and then deceleration of the growth of the bulb.

Table 2. Relative growth rates (*RGR*, formulae (1); ($\text{mg g}^{-1}\text{dw day}^{-1}$); (mean \pm standard error) of vegetative and reproductive *A. oleraceum* and *A. vineale* plants at three studied sites during the main growth period of 1995. The *RGR* of vegetative plants was estimated for the period 20 March–15 June, that of reproductive plants for the period 20 March–17 July. All tests were performed separately for vegetative and reproductive plants, respectively.

Significantly different relative growth rates (at $P < 0.05$) between the species within each respective site are indicated by different upper-case letters row-wise. Significantly different relative growth rates (at $P < 0.05$) of plants between the different sites are indicated by different lower-case letters column-wise separately for *A. oleraceum* and *A. vineale*, respectively.

Site	Vegetative plants		Reproductive plants	
	<i>A. oleraceum</i>	<i>A. vineale</i>	<i>A. oleraceum</i>	<i>A. vineale</i>
Forest	22.97 \pm 1.61 ^{aA}	16.75 \pm 1.45 ^{aB}	20.27 \pm 1.02 ^{aA}	16.71 \pm 1.20 ^{aB}
Scrub	23.30 \pm 2.32 ^{aA}	12.11 \pm 1.22 ^{aB}	19.81 \pm 2.49 ^{aA}	6.51 \pm 2.32 ^{bB}
Steppe	20.61 \pm 1.18 ^{aA}	23.62 \pm 2.01 ^{bB}	20.54 \pm 1.37 ^{aA}	27.87 \pm 2.17 ^{cB}

Table 3. MANOVA of the time course of the plant mass allocation pattern: the effect of species, time and habitat. Tests were restricted to the period 20 March–15 June 1995. The test values of Pillai's trace are shown. All tests were performed separately for vegetative and reproductive plants, respectively.

Source of variation	Vegetative plants					Reproductive plants				
	Test value	DF1	DF2	F	<i>P</i>	Test value	DF1	DF2	F	<i>P</i>
Species (S)	0.962	3	828	10.85	<0.001	0.124	4	499	17.61	<0.001
Time (T)	0.615	12	2191	36.79	<0.001	1.057	16	2008	44.72	<0.001
Habitat (H)	0.695	6	1656	55.08	<0.001	0.674	8	1000	63.46	<0.001
S×T	0.961	12	2191	2.76	<0.001	0.148	16	2008	4.83	<0.001
S×H	0.946	6	1656	7.75	<0.001	0.043	8	1000	2.77	0.006
T×H	0.608	24	2402	18.75	<0.001	1.043	32	2008	22.14	<0.001
S×T×H	0.866	24	2402	5.07	<0.001	0.236	32	2008	3.94	<0.001

At the shaded sites, *A. vineale* did not reproduce and even reproductive structures in *A. oleraceum* were suppressed. At the steppe site, reproductive allocation did not differ between the species (percent allocation to bulbils and flowers during the flowering phase, mean \pm SE.; *A. oleraceum*, steppe: 30.3 \pm 5.6%^a; scrub: 18.0 \pm 3.6%^b; forest: 5.4 \pm 2.3%^c; *A. vineale*, steppe: 32.5 \pm 6.2%^a; ANOVA, $P = 0.02$; Fig. 5).

4. DISCUSSION AND CONCLUSIONS

4.1. General pattern of phenology and growth

The results demonstrate a difference in phenologic development between the species. Both species showed the late summer rest period which is typical for most mem-

bers of the subgenus *Allium* (Pistrick 1992) and is related to the adaptation of the members of the subgenus to hot and dry habitats (Hanelt *et al.* 1992). On the other hand, the species differed in the appearance of winter growth. *A. vineale* regularly emerged above ground during early autumn and grew above ground before the arrival of winter. Identical behaviour on the part of *A. vineale* has been reported from most parts of its distribution, including areas of adventitious distribution (Richens 1947, Hakansson 1963, Ronsheim 1996). On the other hand, the development of *A. oleraceum* was delayed until mid-autumn and its leaves usually have stopped growth and remained sheltered underground or even failed to grow out of the bulb. It implies the occurrence of winter rest period, as reported for this species

by Hanelt *et al.* (1992). Nevertheless, the above-ground growth of *A. oleraceum* during a warm autumn/winter which has been reported from various parts of Europe (Bremer 1999, Åström and Haegström 2004, this study) rather supports the idea of an environmentally forced rest period in *A. oleraceum*.

Seasonal thermoperiodicity is regarded as the major factor controlling seasonal development, flowering, and yield in most geophytes (Hartsema 1961, Halevy 1990, De Hertogh and Le Nard 1993). A warm spring allowing faster and earlier expansion, and subsequent cool and wet weather delaying leaf senescence maximise the length of the growing season and lead to high storage of reserves (Rees 1972, van der Valk and Timmer 1974, Nault and Gagnon 1993). The above-ground presence of leaves early in the season should be advantageous since plants can immediately begin assimilation with increasing temperature (Goryshina 1972, Kawano and Nagai 1975). It might be, however, less advantageous to keep photosynthetic organs under the conditions of cold continental winters because low temperatures restrict or disable photosynthetic rates during this period. It was clearly demonstrated by negative *RGR* in both species during the “normal course” of winter, even though *A. vineale* had markedly more dry mass allocated to leaves than *A. oleraceum* over the winter. Therefore, low winter temperatures reduce the potential advantage of winter growth in *A. vineale*.

The presence of leaves in early spring, however, allows *A. vineale* to start rapid growth even at lower mean temperatures and that is why *A. vineale* showed more intensive growth than *A. oleraceum* during April at one (steppe) of the three sites where the temperatures at the beginning of April 1995 exceeded 5–7°C because of full irradiance. The development of *A. oleraceum*, although similar to that of *A. vineale*, is shifted a little bit in season, and its temperature optima for the start of exponential phase of growth are slightly higher than those of *A. vineale*. That is why the reverse pattern of *RGR* between species was observed during May and June as compared to the April data.

The results support the idea that different patterns of growth and phenology between the study species may be a result of selection under different environmental conditions of their origin (Halevy 1990). *A. oleraceum* shows a more variable inter-annual phenological pattern that may reduce the potential cost of reduced survival, growth, and flowering (Vaughton and Ramsey 2001) and is predicted to be typical of geophytes growing in a less predictable (e.g. temperate) climate. On the other hand, *A. vineale* displays rather the annual life cycle typical of many Mediterranean geophytes (Cheryomushkina 2004), which grow actively under strong predictable seasonal oscillations during mild, rainy winters and quickly senesce either after several short-term drought events (Pastor and Valdes 1985, Pantis *et al.* 1994, Kamenetsky 1994) or with increasing temperature (Spano *et al.* 1999) in summer. The effect of season shortening may also explain the absence of *A. vineale* in the more continental parts of Europe (Meusel *et al.* 1965).

4.2. Growth in contrasting habitats

Both species failed to thrive and reached a lower dry mass under shade than at the exposed site. In response to shading, both species modified their phenologic development, increased either leaf length or leaf numbers (forest population of *A. vineale*; Duchoslav, unpubl. results), and allocated more mass to leaves and less mass to reproduction. Such morphological-physiological changes induced by shading have been commonly reported for perennial herbs (Grime 1965, Rees 1972, Grime 1979, Björkman 1981) and increase the probability of survival.

Both species began to grow early in the season, which partly allowed them to avoid competing for light with the surrounding vegetation. During the open canopy period (~ seven weeks) both species reached their highest *RGR* and those resources which they gained, especially in the case of *A. vineale*, because of its quick development, are probably sufficient for their survival and next year's growth as has been observed in some understory plants (Seiwa 1998, Routhier and Lapointe 2002). In contrast to *A. olera-*

ceum, the growth of *A. vineale* at the forest and scrub sites was, however, hampered even before full canopy closure, probably because of its lower efficiency in utilizing the lower irradiation penetrating through the leafless overstory canopy. Particularly, the shaded leaves of *A. vineale* were thin and beaten down in the course of season and were thus more susceptible to shading from the surrounding vegetation.

The species differed from each other in their subsequent growth after full canopy closure at the shaded sites: while *A. oleraceum* continued to increase in mass, the growth of *A. vineale* usually stopped – plants were etiolated, which is a typical response to light stress (Salisbury and Ross 1978). Such behaviour suggests limited shade acclimation in *A. vineale*. The data on *RGR* over the main growth period support these observations. This is at variance with Ellenberg *et al.* (1991), who reported higher demands on the part of *A. oleraceum* for light than was the case with *A. vineale*.

At the exposed site, *A. vineale* showed higher *RGR* than *A. oleraceum* over the main growth season. This contradiction is not caused by lower adaptation of *A. oleraceum* to sunlit conditions but can be explained by microsite differentiation between species at the steppe site with patches of *A. oleraceum* occurring frequently at more dry and nutrient-poorer microsites than those of *A. vineale* (Duchoslav, pers. observations). Plants respond to lower nutrient availability by shifting the allocation of carbohydrates to below-ground organs, i.e. roots (Bazzaz and Grace 1997). *A. oleraceum* plants growing at the steppe site had strongly developed root systems (data not shown) and a large percentage of their dry mass allocated in sheaths even at the beginning of the season. Microsite differentiation between species at the steppe site may also partly explain why *A. oleraceum* plants at the exposed site showed *RGR* similar to those from shaded sites over the main growth period.

The different growth capacity of the species observed in various habitats has a fundamental effect on their performance and population dynamics. In general, plants growing under suboptimal conditions (shade) persist many years in the same stage and a marked

increase in mass is strongly dependent on favorable climatic and light conditions during the season caused by the creation of gaps, e.g. by trees falling (Duchoslav 2001b, 2005). Similar population dynamics were observed in *Narcissus pseudonarcissus* L. (Barkham 1992). Consequently, shaded *A. vineale* populations showed a population structure with a prevalence of immature plants and an extremely low proportion of reproductive plants (Duchoslav 2000). Such populations are maintained only by means of vegetative propagation via daughter bulbs and they can eventually become extinct from the vegetation, as was shown for highly shaded patches of *Corydalis cava* (L.) Schweigger et Koerte and *C. intermedia* (L.) Mérat (Olesen 1994, Ehlers and Olesen 2004). On the other hand, populations of *A. oleraceum* occurring in the same shaded sites showed a unimodal stage structure with a prevalence of middle and large-sized vegetative plants and a higher proportion of reproductive plants and seedlings (Duchoslav 2000), though their reproductive output was reduced.

The data showed that *A. oleraceum* was able to maintain fitness-related traits more stably across the environments studied than *A. vineale* that fit well into the pattern of habitat differentiation observed between them in Central Europe (Duchoslav 2001a), i.e. scarcer occurrence of *A. vineale*, in contrast to *A. oleraceum*, in later successional communities, i.e. natural deciduous forests. There is, however, one exception to this pattern: secondary forests dominated by alien *Robinia pseudacacia* (Duchoslav 2001a), planted on abandoned grasslands, tracks, and field margins or in place of natural forests. This study showed that the survival of *A. vineale* populations in the understory of *Robinia* forests, though poor, is made possible by the one-month delayed foliation of *Robinia* trees in comparison with native tree species. The delayed foliation of *Robinia pseudoacacia* trees may also partially explain why many other, often endangered, geophytes with quick spring growth (e.g. representatives of the genera *Muscari*, *Ornithogalum*, and *Gagea*) frequently survive under a *Robinia* canopy. *Robinia* stands can therefore function as an important refuge for geophytes in an agricultural landscape.

4.3. Differences between ontogenetic stages

Although the vegetative and reproductive plants of both species showed similar *RGR* until May, their subsequent growth differed strongly: the vegetative plants matured one-two months earlier than the reproductive ones. There may be several explanations for this pattern. First, the phenology of vegetative plants is more influenced by weather conditions than is that of reproductive plants. Smaller plants live partly in micro-environments different from those of larger reproductive ones. Their bulbs are placed shallowly in the soil (Duchoslav 2000) and are thus exposed to increased temperature and humidity variations later in the season. Short-term drought regularly occurs during the early summer and could cause the onset of senescence. Such behaviour has been mentioned in many bulbous geophytes (Jones and Mann 1963, Rees 1972, van der Valk and Timmer 1974, Barkham 1980, Kawano *et al.* 1982, Nault and Gagnon 1988, Eggert 1992). Secondly, vegetative plants suffer more than reproductive ones from increased shading caused by closure of the herb canopy at the end of May because of their inability to overgrow surrounding vegetation. Thirdly, the initiation of flowering buds implies a fundamental change in the developmental programme of the study species. The new bulb of vegetative plants represents a principle sink during most of the season. As hypothesised for spring ephemerals (Lapointe 2001), leaf senescence is induced by a reduction in sink demand once carbohydrate reserves have been filled. In contrast to vegetative plants, reproductive plants have a two-compartment system with bulb and growing scape as sinks which delay their maturation. The prolonged development of reproductive plants was also observed in other geophytes, e.g. *Dactylorhiza lapponica* (Laest. ex Hartm.) Soó (Øien and Pedersen 2005) and *Cypripedium calceolus* L. (Kull 1998).

All stages showed a decrease in *RGR* during late spring/early summer that was partially caused by leaf age effect, an increase in maintenance respiration resulting from increasing temperatures, and by allocating an increasingly larger fraction to the bulb (Tis-

sue *et al.* 1995). In reproductive plants, however, this allocation pattern was modified by the partial reallocation of carbohydrates into the photosynthetically less active tissue of the quickly growing scape. This phase of plant development is probably critical since it can reduce the resources stored in the bulb and strongly affects the success of generative reproduction. Competition between the bulb and scape for assimilates has been reported in some geophytes (Pate and Dixon 1982, Snow and Whigham 1989, Ruiters and McKenzie 1994, Rosen and Tong 2001). Rosen and Tong (2001) state that scape removal in the curled stage from *Allium sativum* L. plants resulted in a 15% increase in bulb yield and an increase in bulb size compared with leaving scapes on until harvest at a low organic matter site. On the other hand, scape removal increased bulb yield by 5% at a high organic matter site (Rosen and Tong 2001). On the other hand, Lapointe (1998) observed that the stem serves as a temporal carbohydrate reservoir for supporting full fruit development in a spring geophyte *Trillium erectum* L. and that carbohydrate accumulation in the stem did not compete with rhizome carbohydrate storage because the leaves were capable of replenishing rhizome reserves within 3 weeks when the plants were still flowering. The study species did not differ in either plant mass or the allocation pattern of reproductive plants growing in steppe conditions, but it did in shaded sites. In general, shading increased the scape abortion rate, and reduced plant size and allocation to reproductive structures. All parameters were more influenced in *A. vineale* than in *A. oleraceum*. Scape abortion in the early stage is probably caused by an insufficient amount of carbohydrates captured by the reproductive plants during spring and was previously observed in several species of the genera *Lilium*, *Iris*, *Freesia*, and *Gladiolus* (De Hertogh and Le Nard 1993). After early scape abortion, 'reproductive' plants usually switch over to 'vegetative' mode, and carbohydrates temporarily stored in the "transient bulb", i.e. the thickened leaf bases around the new bulb, are released and translocated into the new bulb. Hence, no marked decrease in bulb growth was observed in these plants. On the other hand, a decrease in bulb growth

was recorded in reproductive plants of both study species that continued in scape growth, which supports the hypothesis of competition between bulb and scape for assimilates. In fact, reproductive plants of both species growing at the exposed site had a lower or only slightly higher bulb dry mass than those growing at shaded sites, though they had a total dry mass up to two times higher during the flowering period.

The importance of leaves later in the season for successful reproduction and bulb growth differs in the study species. In *A. vineale*, leaves usually withered away during stem maturation and, therefore, they could not directly support the flowering and filling of the bulb. In *A. oleraceum*, leaves senesced slowly during flowering and a possibility of support for flowering or the accumulation of reserves into the bulb, therefore, exists, as has been shown for the geophyte *Arum italicum* Mill. (Méndez 1999). Moreover, *A. oleraceum* has a green and persistent spathe that can support growing reproductive structures as well (Antlfinger and Wendel 1997). It is important to consider that even scapes in both species can provide partial self-sufficiency to the reproductive structures since they contain functional chlorophyll (Nault and Gagnon 1988).

In summary, the decision to flower (i.e. initiation of generative parts within the bulb) is probably predetermined in the study species either by the size of the apical meristem within the bulb (Halevy 1990), i.e. the size of the old “mother” bulb (Rees 1972, De Hertogh and Le Nard 1993, Pantis 1993) or by the amount of carbohydrates captured by the plants during the early spring (Cheryomushkina 2004); the results however showed that reproductive success depends on production during the whole growing season and, therefore, is more variable from year to year, especially under stress conditions (Hæggström and Åström 2005). Although models of perennial plants’ growth (Iwasa and Cohen 1989) predicted different patterns of switching from growth to storage in the study species, the patterns observed in the study species are similar: allocating reserves for the coming year is the first priority as a mechanism for guarding against plant death resulting from insufficient re-

sources for survival, and support the hypothesis of Dafni *et al.* (1981) concerning the growth and allocation patterns of synanthous geophytes with an annual storage organ.

ACKNOWLEDGEMENTS: I am grateful to F. Krahulec and an anonymous reviewer for comments and suggestions on the manuscript at various stages. Fieldwork assistance of Z. Duchoslavová, J. Duchoslavová and A. Kočárková was appreciated very much. S. Gill kindly revised the English. The research was supported by grants No. 206/01/P097, No. 206/07/0706 and No. 206/04/P115 from the Grant Agency of the Czech Republic.

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Received after revising August 2008