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VARIATION IN REPRODUCTIVE MODES OF *ALLIUM OLERACEUM*, *A. SCORODOPRASUM* AND *A. VINEALE* IN FIELD COLLECTION

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The interspecific and infraspecific variation of reproductive modes in three *Allium* species were studied under similar growing conditions. The number of flowers per plant was the feature in which the interspecific and infraspecific differences were the highest. The real seed production in studied species was rather low. Only 0.9 % of ovules developed into seed in *A. oleraceum* and 4.8 – in *A. vineale* while all *A. scorodoprasum* plants did not set any seeds at all. Great interspecific variation was observed in production of daughter bulbs and aerial bulbils. *A. oleraceum* plants produced 0.1, *A. scorodoprasum* – 2.3 and *A. vineale* – 3.2 daughter bulbs on average. The number of bulbils in one inflorescence of *A. oleraceum* was 46.0, *A. scorodoprasum* – 78.4 and *A. vineale* – 40.0.

Key words: *Allium oleraceum, Allium scorodoprasum, Allium vineale*, seed productivity, vegetative reproduction,

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INTRODUCTION

Genus *Allium* L. consists of about 750 species (Stearn 1992) widely distributed over the holarctic region from the dry subtropics to the boreal zone (Fritsch & Friesen 2002). The genus shows an extraordinary large amount of anatomical, morphological, karyological, chemical as well as ecological variations. Due to such variability the genus *Allium* is divided into 6 (Hanelt et al. 1992) or even 15 subgenera (Friesen et al. 2006). The largest of them, the subgenus *Allium* exclusively originates from the Old World (Fritsch & Friesen 2002). It consists of about 300 species whereas in Lithuania occur only three of them: *A. oleraceum* L., *A. scorodoprasum* L. and *A. vineale* L. *A. oleraceum* is the most common of all *Allium* species (Karpavičienė 2004), while *A. scorodoprasum* and *A. vineale* are enlisted in the Red Data Book of Lithuania (Karpavičienė 2007 b, c).

A. oleraceum, *A. scorodoprasum* and *A. vineale* are very closed in their modes of vegetative reproduction – plants form underground daughter bulbs and aerial bulbils in inflorescences. The daughter bulbs remain and sprout in a close vicinity of the parent plant, whereas aerial bulbils are dispersed like large seeds. A significant genetic variation in allocation to different reproductive modes has been reported for *A. vineale* (Ronscheim & Bever 2000), however, the variation in reproductive modes has been studied neither in *A. oleraceum* nor in *A. scorodoprasum*. Whereas heritable characters reveal more visibly under similar growing condition, the plant samples of *A. oleraceum*, *A. scorodoprasum* and *A. vineale* were transferred from natural populations into the field collection. After the adaptation of plants in new growing conditions their visible morphological and reproductive variations were observed. The objective of the current study was to clarify the interspecific and infraspecific variations of the reproductive modes in three *Allium* species under similar growing condition.

METHODS

Modes of reproduction were studied in 12 accessions (4 accessions of each species) which have been growing in field collection of medicinal and aromatic plants of the Institute of Botany not less than for four years. The accession in this study is meant a group of plants transferred from one population and grown on a separate collection plot. 30 mature individuals of each accession were labelled and used for the measurements of both sexual and asexual reproductive features as well as vegetative plant characteristics over the course of one growth season. Those included leaves, flowers, fruits, seeds, daughter bulbs and bulbils numbers per plant, stem as well as bulb height and diameter, length and width of the second uppermost leaf, mass of bulbs and bulbils . The potential seed productivity (the number of ovules produced) and a real seed productivity were estimated in milky or wax stages of seeds. The ratio of seed productivity was defined as the potential seed productivity divided by the real seed productivity and expressed in percent.

In order to obtain the data on the effect of cross polination for seed setting 15 inflorescences in each accession were isolated before the opening of floral buds. For this purpose each inflorescence was enclosed in a spunbond fabric bag and sealed.

For data analyses the correlation, analysis of variance and other techniques of the Statistica 8.0 software package (StatSoft, 2008) were used with the employment of Fisher‘s criterion (F) and probability level p=0.05

RESULTS

Flowers of studied *Allium* species contain 3-locular ovary, with two ovules in each locule. Some studied flowers consisted of two or four locules. In those cases, correspondingly, there were less or more than six ovules in an ovary. However, such cases were rare and made less than one per cent of the whole amount of ovaries. In spite of these insignificant deviations, the number of ovules in an ovary can be interpreted as constant, therefore, the potential seed productivity depends exceptionally upon the number of flowers in the inflorescence.

In the studied accessions the inflorescences of *A. oleraceum* contained on average 4.0–19.8, *A. scorodoprasum* – 4.9–20.6 and *A. vineale* – 0–6.9 flowers (Table 1). Floral development without bulbils formation was not recorded while plants with bulbils and without flower are common in all species studied. Even 74.5 % of mature *A. vineale* plants were without flowers (Fig. 1). Two accessions of *A. vineale* consisted of flowerless plants entirely. These accessions were transferred into the collection from populations where only plants without flowers occurred. However, some plants produced considerable amount of flowers in 2003 and 2006. In *A. oleraceum* plants with aerial bulbils but without flowers amounted to 7.5 %, in *A. scorodoprasum* – 1.9 % (Fig. 1). The statistically significant correlations between the number of flowers and almost all the other studied characters were observed in *A. oleraceum*, whereas in *A. vineale*

Table 1. Comparison of reproductive characters of three *Allium* species as estimated per plant (F_1) and four accessions in each species (F) in field collection in 2008. M – arithmetic mean, s – standard deviation, M_{min} – minimum value of M of four accessions, M_{max} – maximum value of M of four accessions

Features	*A.oleraceum*		*A.scorodoprasum*		*A.vineale*		F_1
	M±s M_{min}–M_{max}	F	M±s M_{min}–M_{max}	F	M±s M_{min}–M_{max}	F	
Number of flowers	13.2±10.7 4.0–19.8	22.8*	11.1±10.7 4.9–20.6	26.0*	2.0±5.2 0–6.9	18.4*	46.5*
Ratio of seed productivity %	0.9±2.6 0.3–1.3	1.0	0	–	4.8±8.1 0–5.6	0.4	5.9*
Number of fruits	0.8±2.1 0.1–1.3	2.8	0	–	0.4±1.7 0–1.3	4.1*	8.2*
Number of seeds	1.2±2.8 0.3–2.2	3.2*	0	–	0.7±3.5 0–1.2	3.1*	4.5*
Number of aerial bulbils	46.0±34.8 30.1–61.9	4.5	78.4±42.0 62.1–89.7	2.3	40.0±29.7 30.0–56.2	3.7*	31.3*
Mass of aerial bulbils g	1.5±1.5 0.7–2.9	15.4*	2.6±1.7 1.2–3.3	7.2*	1.2±1.0 0.5–1.7	3.9*	25.9*
Mass of 1 bulbil mg	33.5±17.3 21.1–47.7	16.4*	37.2±22.6 19.3–50.3	14.1*	32.5±21.4 14.4–43.3	13.8*	1.4
Number of daughter bulbs	0.1±0.3 0–0.2	0.1	2.3±0.2 1.9–3.4	5.2*	3.2±0.3 2.2–4.4	10.5*	73.4*

*– effects are significant, $p<0.05$

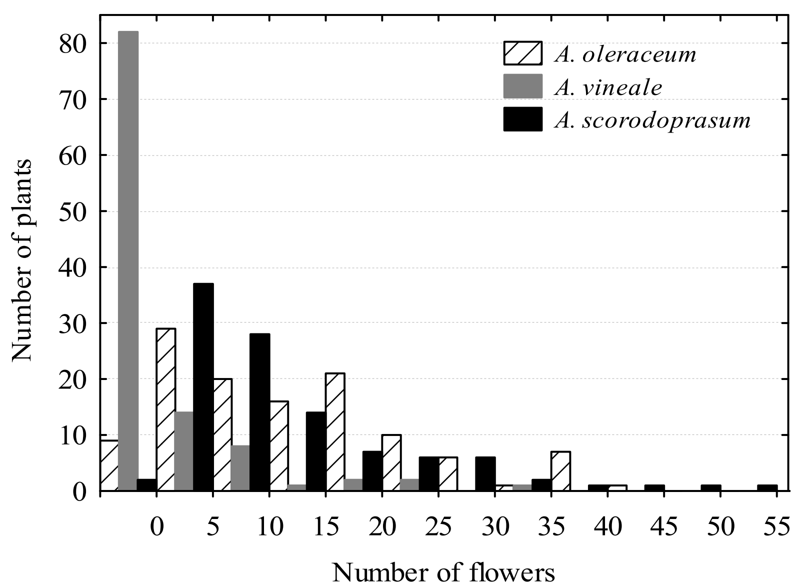

Fig. 1. Number of flowers in mature *Allium* plants studied

these features showed no significant correlation (Table 2). However, significant differences were established between *A. vineale* plants with and without flowers in renewal bulb size and mass, daughter bulbs number and mass as well as mass of aerial bulbils. Plants with flowers had bigger bulbs (F=9.1, $p<0.05$) and aerial bulbils (F=4.3, $p<0.05$), but less daughter bulbils (F=12.5, $p<0.05$) than plants with bulbils only. The number of flowers in *A. scorodoprasum* showed direct correlation with some vegetative characteristics and significant negative correlation with mean mass of aerial bulbils (Table 3).

The ratio of seed productivity shows what part of ovules develops into the seeds. This ratio was extremely low in all *Allium* species (Table 1). In *A. oleraceum* accessions it was on average 0.3–1.3 %, *A. vineale* – 0–5.6 % wile all *A. scorodoprasum* plants did not set any seeds at all. In the studied accessions the number of seeds matured up by a single individual was: *A. oleraceum* – 0–16 and *A. vineale* – 0–23. No fruits with all six seeds matured were found. The statistically significant correlation between flowers and seed number were found in *A. vineale* (r=0.84, p<0.001) as well as *A. oleraceum* (r=0.59, p<0.001). No one of *A. oleraceum* plants isolated from insects produced seeds, wile some *A. vineale* covered plants matured up from 1 to 3 seeds (0.4 on average). Although some of uncovered *A. vineale* plants produced from 1 to 23 seeds (4.8 on average), no statistically significant differences were found between covered and uncovered plants neither in seed number nor in the ratio of seed productivity.

Table 2. Correlation coefficients between different characters in *Allium oleraceum*. SN – seeds number, bulb mass is given of all underground bulbs (renewal and daughter)

Character	BN	BM	MM	FN	SN
Stem height	0.53*	0.64*	0.45*	0.32*	0.12
Stem diameter	0.54*	0.57*	0.22*	0.42*	0.11
Leaf length	0.39*	0.47*	0.30*	0.30*	0.08
Leaf width	0.52*	0.56*	0.27*	0.36*	0.05
Leaves number	0.35*	0.36*	0.12	0.07	-0.01
Bulb diameter	0.45*	0.55*	0.27*	0.44*	0.19
Bulb length	0.39*	0.37*	-0.01	0.51*	0.25*
Bulb mass	0.40*	0.57*	0.36*	0.49*	0.22*
Bulbils number (BN)	–	0.79*	0.02	0.24*	-0.06
Bulbils mass (BM)	–	–	0.51*	0.28*	0.09
Mean bulbil mass (MM)	–	–	–	-0.01	0.16
Flowers number (FN)	–	–	–	–	0.43*

*– effects are significant, p<0.05

All *Allium* species possess ability of vegetative propagation which occurs with the participation of specialized shoots – bulbs. *Allium* bulbs are not only multiplication but also renewal structures. Every year in an axil of the uppermost leaf a new renewal bulb is formed. It replaces an old and dried up one. Sometimes additional so called daughter bulbs are formed in axils of lower leaves. The daughter bulbs of *A. oleraceum* were found sporadically on mature plants only, whereas *A. scorodoprasum* and *A. vineale* daughter bulbs are formed not only on flowering but also sometimes on juvenile plants. Mature plants of *A. scorodoprasum* produced up to 9, *A. vineale* up to 10 daughter bulbs, whereas *A. oleraceum* – not more than 1 daughter bulb. The daughter bulb of *A. oleraceum* is connected with the main renewal bulb via long axis which elevates it up to the soil surface. *A. scorodoprasum* and *A. vineale* produced daughter bulbs covered by sheathing bases of the foliage leaves side by side to renewal bulb. The daughter bulbs of *A. vineale* differed in shell hardness, size and position. The bulbs enclosed in hard shell were formed next to central renewal bulb, while bigger bulbs covered with soft shell were formed more outwards.

The second type of vegetative propagules is aerial bulbils formed in the central part of an umbel. Number of bulbils in the inflorescence of

Table 3. Correlation coefficients between different characters in *Allium vineale*. SN – seeds number, DBN – daughter bulb number, DBM – daughter bulb mass, bulb mass is given of all underground bulbs (renewal and daughter)

Character	BN	BM	MM	FN	SN	DBN	DBM
Stem height	0.67*	0.66*	0.16	-0.04	0.05	036	0.67*
Stem diameter	0.63*	0.69*	0.21	-0.03	0.09	0.27	0.61*
Leaf length	0.61*	0.50*	0.10	0.08	0.10	0.34	0.72*
Leaf width	0.63*	0.74*	0.32*	0.16	0.15	0.36	0.36
Leaves number	0.19	0.17	0.01	0.03	0.18	0.18	0.01
Bulb diameter	0.52*	0.64*	0.26*	-0.01	-0.03	0.65*	0.52*
Bulb length	0.50*	0.61*	0.23	-0.21	-0.13	0.25	0.36
Bulb mass	0.40*	0.62*	0.30*	-0.09	-0.06	0.60*	0.69*
Bulbils number (BN)	1.00	0.81*	0.01	0.08	0.09	0.29	0.65*
Bulbils mass (BM)	0.81*	1.00	0.41*	-0.01	0.00	0.07	0.04
Mean bulbil mass (MM)	0.01	0.41*	1.00	-0.06	-0.09	-0.25	-0.60*
Flowers number (FN)	0.08	-0.01	-0.06	1.00	0.70*	-0.07	-0.09

*– effects are significant, $p<0.05$

the species studied usually exceeds the number of flowers. One *A. oleraceum* individual produces from 3 to 161 bulbils. A very similar number of bulbils was observed in the studied *A. vineale* plants – the number of bulbils in the inflorescences varied from 5 to 163, while one plant of *A. scorodoprasum* produced much more bulbils – from 5 to 237. The mean mass of aerial bulbils per plant varied from 0.7 to 2.9 g in *A. oleraceum*, from 1.2 to 3.3 in *A. scorodoprasum* and from 0.5 to 1.7 in *A. vineale* (Table 1). Mean mass of one aerial bulbil was very similar and was the only feature in which no differences between species were observed. However, some distinct differences were found within species in this character (Table 1). The statistically significant correlation was found between underground bulbs (the renewal and daughter ones) and aerial bulbils in all studied species: *A. oleraceum* – $r=0.57$, *A. vineale* – $r=0.61$ and *A. scorodoprasum* – $r=0.52$; $p<0.001$. The underground bulbs are heavier than aerial bulbils by 2.2 times in *A. oleraceum*, 2.1 – in *A. vineale* and 1.4 – in *A. scorodoprasum*.

The large differences were found among *A. scorodoprasum* accessions in number of flowers and mean mass of aerial bulbils (Table 1). Moreover, a statistically significant negative correlation ($r=-0.43$, $p<0.05$) was observed between these characters (Table 4). Plants of two accessions producing bigger bulbils (3.0–3.3 mg on average) and fewer flowers (4.9–5.1 on average) formed one group and the other two accessions producing smaller bulbils (19.3–25.3 mg on average) and more flowers (18.4–20.6 on average) formed a second group of plants (Fig. 2).

DISCUSSIONS

The number of flowers per plant was the feature in which the interspecific and infraspecific differences were the highest in all three studied species. Plants with bulbils and without flowers are common in all species studied. Such variant of *A. vineale* is referred to as *A. vineale* var. *compactum* (Stearn, 1980). The variant of *A. vineale* with only flowers but without bulbils (distinguished as var. *capsuliferum* Koch.) likewise such plants of *A. scorodoprasum* was not found in Lithuania. Moreover, *A. oleraceum* plants without bulbils are not found in all area of its distribution, while such plants of *A. vineale* occur in the USA and Sweden (Ronsheim 1997, Ceplitis & Bengtsson 2004). The range of variation of flowers number in *A. vineale* plants studied in Great Britain (Richens 1947) and the Czech Republic (Duchoslav 2000) are analogous to the results of the current study (0–33 flowers), whereas in Scandinavian countries this feature varies in a much larger range – from 0 to 230–350 (Hæggström & śström 2003; Ceplitis & Bengtsson 2004).

The results of our study revealed that *A. vineale* plants with bulbils and without flowers are more frequent than such plants of *A. oleraceum* or *A. scorodoprasum*. But if flowers occured, the allocation to seed production was more efficient – the ratio of seed productivity in *A. vineale* plants was higher than that in *A. oleraceum*, let alone *A. scorodoprasum*. However, according to A. Ceplitis & B. O. Bengtsson (2004), the natural selection operates to reduce the allocation to sexual reproduction in *A. vineale.* Moreover, C.-A. Hæggström & H. śström (2003) found out that in Finnish herbaria *A. vineale* voucher specimens with more than 30 flowers were more common during the 19th and early 20th centuries: such plants form 37 % of all specimens collected before 1940 and only 5 % of specimens collected after 1940.

Table 4. Correlation coefficients between different characters in *Allium scorodoprasum*. FN – number of flowers, bulb mass is given of all underground bulbs (renewal and daughter)

Character	BN	BM	MM	FN
Stem height	0.42*	0.56*	0.32*	0.16
Stem diameter	0.61*	0.38*	-0.01	0.50*
Leaf length	0.25*	0.36*	0.30*	-0.03
Leaf width	0.44*	0.51*	0.21*	0.27*
Leaves number	0.40*	0.32*	0.01	0.44*
Bulb diameter	0.02	0.40*	0.39*	-0.05
Bulb length	0.28*	0.30*	0.18	0.18
Bulb mass	0.19	0.62*	0.41*	-0.11
Bulbils number (BN)	1.00	0.54*	-0.28*	0.47*
Bulbils mass (BM)	0.54*	1.00	0.55*	-0.04
Mean bulbil mass (MM)	-0.28*	0.55*	1.00	-0.43*

*– effects are significant, $p<0.05$

The high infraspecific differences between accessions in flower number demonstrate the genetic implications on this character but statistically significant correlation between flowers number and plant size (especially bulb size and mass) in *A. oleraceum* shows the influence of environment and resource availability for this character. There is no distinct trade-off in resource allocation to vegetative and generative reproduction in *A. oleraceum*: both modes of reproduction are correlated together and with almost all characters studied. Nonetheless, it seems that preference is given to vegetative propagation in case when resources are scarce: smaller mature plants did not form flowers more often. However, such strategy is not manifested in *A. vineale* or *A. scorodoprasum.*

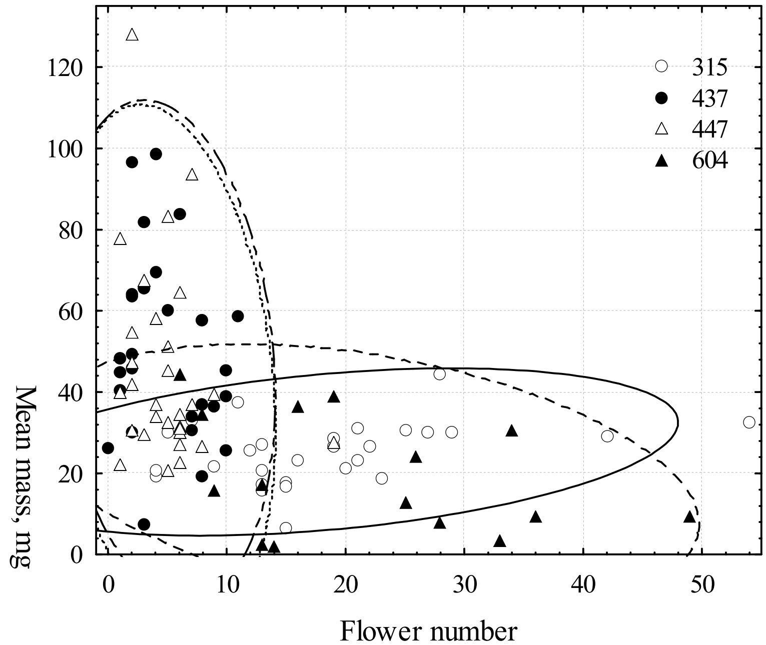

Fig. 2. Correlations between mean mass of an aerial bulbil and flower number per plant in four *Allium scorodoprasum* accessions (No. 315, 437, 447 and 604). Ellipses show a 95 % confidence area

The flowers number shows only potential of generative reproduction. Despite the fact that real seed productivity is strongly correlated with flowers number as demonstrate the results of the study; it depends not only on the number of ovules but also on many biotic and abiotic factors: meteorological conditions, nutrients allocation, abundance of pollinators and herbivores (Levina 1981). Insect pollinators are indispensable for seed formation in *A. oleraceum* while in *A. vineale* self-pollination or apomixis presumably appears side by side to cross-pollination. The seed productivity of *A. oleraceum* is very sparse not only *ex situ* but *in situ* as well in its area of distribution. From 0.1 to 4.5 seeds per plant were found in populations of *A. oleraceum* in Lithuania (Karpavičienė 2002), 0–6.7 in the Netherlands (Bremer 1999) and 0–1.7 in the Czech Republic (Duchoslav 2000).

According to V. A. Cheryomushkina (2004) the mean ratio of seed productivity does not exceed 50 % in majority of *Allium* species independent of their ecological nature. Actually, this ratio has large interspecific variation: in populations of *A. ursinum* it reaches 16–37 % (Karpavičienė, 2003), in the field accessions of *A. angulosum* – 37.4–46.4 and *A. lusitanicum* 69.1–88.4 (Karpavičienė, unpublished data) and are much higher than in all three species studied. All species abovementioned do not form bulbils in their inflorescences. According to E. I Ustinova (1944) bulbils in the inflorescences of *A. oleraceum* as well as *A. scorodoprasum* prevent seed formation. Thus, removal of bulbils in various stages of development improves seed formation in *A. oleraceum* (seeds were formed in 16.5–32.0 % of flowers) and even in *A. scorodoprasum* (seeds were formed in 8.1–13.1 % of flowers). As a result of the strong competition with the developing bulbils, the flowers of the studied *A. scorodoprasum* plants withered to death before anthesis like in an allied species *A. sativum* (Etoh 1985, Kamenetsky & Rabinowitch, 2002). However, the occurrence of diploids and triploids in populations of *A. scorodoprasum*

(Karpavičienė 2007 a) could be explained only by the occurrence of natural seed reproduction.

Despite the fact that seed production was absent in studied *A. scorodoprasum* plants two reproductive strategies were established in this species, with one group of plants producing bigger bulbils and fewer flowers and a second group producing smaller bulbils and more flowers. These reproductive strategies may be based on ploidy level because according to A. Murķn and V. Ferįkovį (1988) the number of flowers of *A. scorodoprasum* was much higher in diploid plants than in triploid ones.

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