PHENOMENON OF FLORAL REVERSION IN BOLTING GARLIC (*Allium sativum* L.)

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ABSTRACT

In this study, we present investigations of morphological changes in the inflorescence of bolting *Allium sativum* L., which forms umbel-like inflorescences with small, inconspicuous flowers, bulbils, and leaf-like membranous bracts. Particular attention was focused on the architecture of a single flower, and the full sequence of developmental events and the differentiation of flower elements and inflorescence were traced. During the several-year long investigations of the garlic species, we observed that all inflorescence elements emerged chaotically, taking a completely random place in the inflorescence receptacle and it was impossible to identify the sequence of formation of the individual inflorescence elements. The absence of regular phyllotaxis and the specific sequence of formation of inflorescence elements are characteristic for inflorescence reversion. Since domesticated garlic has lost the capacity for sexual reproduction, it has probably evolved alternative reproduction modes in its developmental strategy, which is reflected by the formation of numerous bulbils (vegetative buds, topsets) in the inflorescence. This is one of the forms of reproductive strategy of the species, which through domestication progresses from sexual to asexual reproduction.

Key words: garlic, inflorescence, bulbils, reproductive primordial, vegetative primordial, vegetative reproduction

INTRODUCTION

A highly important stage in the ontogeny of flowering plants is the formation of the flower, which is associated with transition of the identity of the shoot apical meristem (SAM) from the vegetative to the reproductive stage. The anatomical structure of the vegetative apical meristem is characterised by histological zonation [Battey and Lyndon 1990, Benlloch et al. 2007]. Cells constituting this meristem have an embryonic character and their primary function is to form stem tissues and auxiliary primordia. When readiness to flower has been achieved by the plant, the morphogenetic pattern of the shoot apical meristem is changed. At this stage, through multiple mitotic divisions in the juvenile vegetative meristem, somatic cells proliferate and gradually differentiate [Meyerowitz and Pruitt 1985, Meyerowitz 1994]. Upon transition to the reproductive phase, the SAM becomes an inflorescence meristem (IM) and the new lateral primordia produced after that point develop as floral meristems (FM) [Benlloch et al. 2007]. This is accompanied by fundamental hormonal and metabolic changes in the SAM leading to important structural (anatomical and morphological) and functional changes within the meristem [Parcy 2004, Irish

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2010]. Other changes include alterations in leaf phyllotaxis, shortening of internodes, and formation of flowers instead of leaf primordia as well as suppression of axillary buds [Battey and Lyndon 1984, 1990, Eckardt 2005]. These processes are controlled by a set of meristem identity genes (i.e. *TFL1*, *LFY*, *AP1*), whose activity induces formation of the flower. Next, the meristem identity genes activate further genes (ABCE class of genes) involved in the so-called floral changes in organ identity [Coen and Meyerowitz 1991, Li and Johnston 1999, Pidkowich et al. 1999, Hempel et al. 2000, Pelaz et al. 2000].

In some cases, transition of the generative into vegetative meristem, i.e. reversion, takes place during plant ontogeny. This phenomenon can be observed in single flowers or the entire inflorescence [Tooke et al. 2005]. The return to the earlier vegetative stage changes the identity of initiated primordia, which results in formation of leaf primordia instead of floral organ primordia. Since the newly formed vegetative elements develop through modification of generative structures, they often exhibit completely different morphology from that of typical vegetative elements. Several factors may cause reversion; it can be induced by drastic changes in environmental factors [Battey and Lyndon 1990, Tooke et al. 2005] or viral infections [Latvala et al. 1997]. It can also be induced *in vitro* [Zayed et al. 2016]. It has recently been found that a majority of species that do not exhibit reversion in the natural environment react weakly to exogenous factors that can usually induce reversion, since the process of flower formation in such species is relatively stable [Okamuro et al. 1996].

The formation of the characteristic umbel-like inflorescence of the *Allium sativum* (garlic) cultivars analysed in this study is independent of climatic variables, in contrast to several plant species in which reversion resulted from modification of external conditions [Washburn and Thomas 2000]. The inflorescence is composed of few flowers and numerous vegetative elements. Vegetative structures in the garlic inflorescence are believed to have appeared spontaneously and, as a secondary trait, they have been conserved by humans through vegetative reproduction [Pooler and Simon 1993, 1994]. In terms of inflorescence formation, garlic genotypes that can be observed at present are categorized as completely bolting (plants producing a long, thick flower stalk with flowers and bulbils), incompletely bolting (plants producing a thin, short flower stalk, and bearing only a few large bulbils), and non-bolting (plants not normally forming a flower stalk) [Takagi 1990, Kamenetsky and Rabinowitch 2001, Etoh and Simon 2002, Kamenetsky et al. 2004a, b]. Bolting genotypes form umbel-like inflorescences with flowers and modified vegetative structures like bulbils (topsets) and leaf-like membranous bracts [Kamenetsky and Rabinowitch 2001, Kamenetsky et al. 2004a, b, Shemesh Mayer et al. 2013]. Floral development has been described in some plants from the genus Allium: *A. moly* and *A. odorum* [Mann 1959]; *A. rothii*, *A. altissimum*, and *A. karataviense* [Kamenetsky 1994, 1997], *A. cepa* [Krontal et al. 1998], and *A. sativum* [Kamenetsky and Rabinowitch 2001]. However, studies of the *A. sativum* inflorescence were focused on analysis of its morphology and description of only the initial and final stages of single flower development [Kamenetsky and Rabinowitch 2001] or described only the whole inflorescence [Rotem et al. 2007]. In this study, we present investigations of morphological changes in the inflorescence of three *A. sativum* cultivars. Particular attention was paid to the architecture of a single flower, and the full sequence of developmental events and the differentiation of flower elements and the inflorescence were traced. These analyses indicate that the vegetative inflorescence elements are likely to have resulted from reversion. It is noteworthy that generative elements present in the current cultivars of *A. sativum* flowers do not form functional gametes, which results in total sterility of this species [Shemesh Mayer et al. 2013, Tchórzewska et al. 2015, 2017]. It can be hypothesised that the loss of sexual reproduction capability in garlic has led to the emergence of alternative reproduction pathways in the developmental strategy of this species. The observations presented in this paper indicate that reversion can be a propagation and species survival strategy. The investigation of the development of vegetative elements of the inflorescence and differentiation of generative flower elements in garlic will expand the knowledge of the progression of this species from sexual to asexual reproduction.
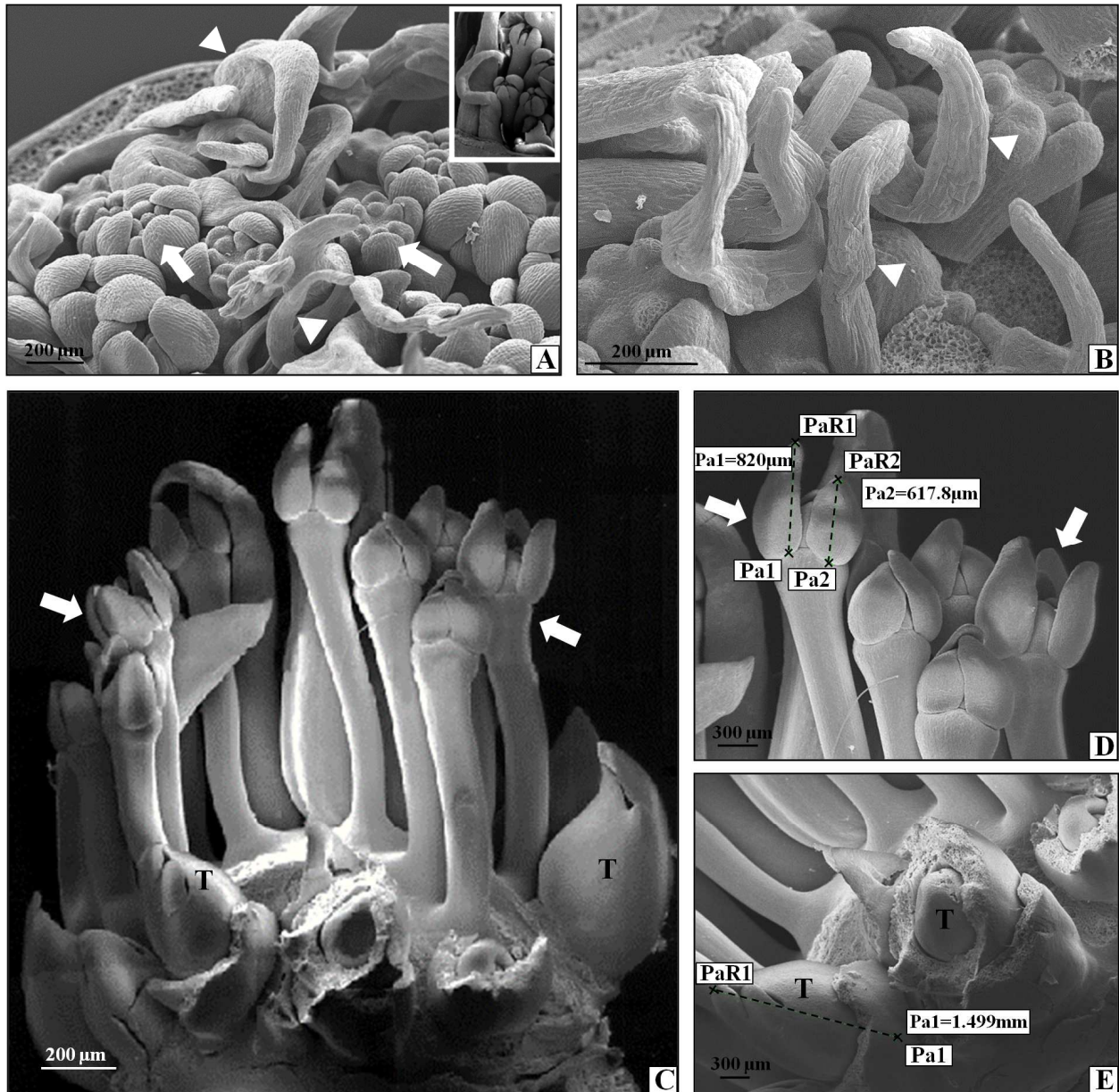
MATERIALS AND METHODS

Plant material. The *A. sativum* cultivars L13, Arkus and Harnas, analysed in this study were cultivated in the Botanical Garden of University of Maria Curie-Skłodowska (Lublin, 51°16'N, 22°30'E). The plants were grown on a universal, slightly acidic pH 5.5–6.5 soil, under a normal photoperiod depending on the season. No herbicide, fungicide, or any chemical inputs were incorporated, and manual weeding methods were used in each case before and throughout the investigated plant cultivation periods. The observations were carried out for 12 years. Approximately 50 plants per year were analysed. To trace the development of a spathe-free inflorescence at an early stage of its development (8-mm inflorescence), the spathe was mechanically removed from 30 randomly selected plants. After the treatment, all inflorescence elements developed with full exposure to sunlight. Macroscopic images were taken with a Nikon D300 camera equipped with an AF MICRO NIKKOR 60-mm objective.

Scanning electron microscopy. The investigations of the morphology of the *A. sativum* inflorescence were based on an analysis of spathe-covered inflorescences in the following size ranges: up to 3 mm, between 3 and 5 mm, over 5 mm, and mature inflorescences with ruptured spathe. For scanning electron microscope (SEM) observations, freshly collected samples were fixed overnight in 2.5% glutaraldehyde in 0.2 M sodium phosphate buffer (pH 7.4), washed in distilled water, and dehydrated in increasing concentrations of ethanol (Hayat, 1981). The dehydrated samples were then dried in a Critical Point Dryer (Denton Vacuum, Moorestown, NJ, USA) using liquid CO_2. The dried samples were mounted on aluminium stubs and sputter-coated with gold (Hummer 6.2 Sputter Coater, Anatech USA, Union City, CA, USA). The samples were analysed under a scanning microscope (LEO1430VP) with accelerating voltage of 15 kV equipped with a Bruker Ouantax 200XFlash EDX Spectrometer System attached to a Zeiss EVO 50 Variable Pressure SEM at 15kV, using INCA-Mapping software (Billerica, MA, USA). The measurements of the sizes of developing structures were carried out from SEM images of 20 randomly selected objects. The results were averaged.

RESULTS

In the *Allium sativum* plants analysed in this study, we observed development of an inflorescence shoot, with an apical meristem exhibiting altered identity from vegetative to generative after formation of 6–7 leaves. The first observations included the morphology of the inflorescence and the sequence of the development of generative organs in inflorescence buds up to 3 mm long. After the removal of the spathe from developing inflorescences, two types of primordia were visible in such buds: reproductive (RM) and vegetative (VM) (fig. 1A). Flowers (F) developed from the reproductive primordia, whereas vegetative elements, i.e. bulbils (T) and filamentous modified leaf-like membranous bracts (B), originated from the vegetative primordia (fig. 1B). The youngest floral primordia observed in the inflorescence (fig. 1C, star) had a characteristic shape of an inverted pyramid on an equilateral triangular base with approximately 280 µm long sides. Three expanded protuberances were visible on the perimeter of these primordia, which gave rise to the first whorl (I), i.e. the establishment of perianth elements (fig. 1C). The next stage in floral ontogeny was formation of the second whorl of small protuberances (II), i.e. the establishment of the second whorl of perianth elements and the first whorl of stamens. Opposite the primordia of the outer perianth, primordia of the third whorl (III) formed, which gave rise to the second whorl of stamens. All elements in a single flower formed regular whorled arrangements of protuberances in the reproductive primordium. The individual floral elements differentiated in the acropetal direction, i.e. the three marginal primordia were older and larger than the primordia in the second and third whorls (fig. 1C). Further development consisted of elongation of the RM primordia and expansion of the protuberances. Moreover, a furrow dividing the small lateral protuberances of each primordium was becoming more visible (fig. 1D, arrowhead). The furrow divided the primordium into two parts: an outer part, which later gave rise to perianth primordia and an inner part, from which columnar primordia of stamens were formed (fig. 1D). During the further development of

Fig. 1. *Allium sativum* – morphology of inflorescences up to 3 mm long (SEM). A – inflorescence after removal of the spathe (S), visible flower primordia (RM) and vegetative primordia (VM). B–F – elements of the inflorescence: B – flowers (F), bulbils (T), bracteoles (B); C – the youngest floral primordium (star), the first whorl of floral elements (I), an older floral primordium with visible second (II) and third (III) whorls of floral elements; D – differentiating primordia in a single flower, furrow dividing the primordium of the second whorl (arrowhead), undifferentiated central domain (star); E – flower with three oldest adaxially curved outer primordia (stars); F – young vegetative primordium with furrow dividing it asymmetrically (arrowhead)

Fig. 2. *Allium sativum* – morphology of inflorescences: A–B – with a length from 3 to 5 mm; C–E – over 5 mm (SEM).
A – floral bud sets (arrows), vegetative elements (arrowheads); B – elongated leaf-like membranous bracts (arrowheads);
C – fragment of an inflorescence with spathe removed and marginal leaf-like membranous bracts removed, developing
flowers (arrows), bulbils (T); D – differentiating floral buds (arrows); E – bulbils (T)

Fig. 3. *Allium sativum*: A–C – elements of a single flower (SEM) from approximately 30 × 30 mm inflorescences; D–F – inflorescences. A – young stamens with two filament appendages (arrows); B – a single flower with the perianth (star), anthers (arrowhead), elongated filament appendages (arrow), non-elongated filament appendages (white arrow), and pistil (cross); C – filament appendages (arrow) growing over the perianth (P); D – inflorescence size 15 × 15 mm without the spathe, bulbils (T); E – mature inflorescence size 30 × 30 mm with a ruptured spathe (S), bulbils (T); F – 2 inflorescences after early removal of spathe during inflorescence development, visible elongated bulbils (T)

the flower, the three oldest outer primordia greatly expanded, which resulted in bending towards the central axis of the forming flower. Thus, a cover for the inner, younger primordia was formed (fig. 1E stars). At this stage (ca. 156-µm long), the vegetative primordia present in the inflorescence had one clearly visible furrow, which divided the entire primordium dome into two asymmetrical parts (fig. 1F). As a result of the subsequent stage of the development of these two unequal in size parts, the bigger part give rise to bulbils and the smaller one – the spathe.

Analysis of young 3–5 mm long inflorescences, after removal of the spathe, showed young developing flower buds and many vegetative elements. All structures were strongly compressed (fig. 2A, small picture). The generative primordia in such an inflorescence developed asynchronously. Besides the young, weakly differentiated floral primordia, there were some with easily identifiable floral elements (fig. 2A, arrows). In contrast, the vegetative elements of the inflorescence, i.e. the leaf-like membranous bracts, developed considerably faster than the floral elements (fig. 2A, arrowheads). These were long, conical, curved, leaf-like forms developing from developed bracts. Due to their rapid growth, the vegetative elements predominated over the floral parts of an inflorescence of this size and occupied a large part (approximately 70%) of the inflorescence base (fig. 2B). In older, over 5 mm long inflorescences, young flowers, bulbils, and leaf-like membranous bracts emerged from the inflorescence base. In such an inflorescence, the bulbils usually occupied the marginal parts of the inflorescence. The length of floral pedicels was highly varied and ranged from 211 µm to 444 µm (fig. 2C). In turn, in the 8 mm long inflorescences, the length of single floral buds only plus pedicel usually ranged from 1280 µm to 2770 µm, with the length of the floral bud ranging from 570 to 820 µm (fig. 2D). It should be emphasised that the scaly bulbils in older inflorescences reached a larger size and a height from 1240 µm to 1500 µm (fig. 2E).

Subsequent observations involved flowers with mature stamens and carpels. The young stamens in such flowers had two small appendages at the filament base (fig. 3A, arrows). The appendages of the stamens of the first whorl quickly elongated and extended over other floral elements (fig. 3B, arrow). In contrast, the filament appendages present in the second-whorl stamens did not elongate (fig. 3B, white arrow). *A. sativum* flowers consisted of 6 parts of the perianth arranged in two whorls, which was undifferentiated into sepals and corolla petals (asterisk), six anthers arranged in two whorls (fig. 3 B, arrowhead), and one inferior pistil with a trilocular ovary (fig. 3B, cross). Mature flowers exhibited long, modified filament appendages (originating from the first whorl), which grew above the closed perianth; floral formula: $P_{3+3}A_{3+3}G_{\underline{3}}$ (fig. 3C, arrow). Notably, there was no anthesis phase in the *A. sativum* flowers analysed in this study. The differentiation of the individual elements in a single *A. sativum* flower was acropetal. However, it was impossible to identify clearly whether the formation of flower buds was basipetal or acropetal. After removal of the spathe from the 1.5 cm-long inflorescences, bulbils predominated in the inflorescence (fig. 3D). While growing, these structures may limit the space for the growth of flowers and leaf-like membranous bracts; because of that, older inflorescences bear only a small number of these elements (fig. 3E). Since the spathe covering the inflorescence limits the free growth of inflorescence elements, the spathe was mechanically removed at an early stage of inflorescence development (8 mm long inflorescences). Associated with this treatment, there were always changes in the development of the elements of the inflorescence, which developed with full sunlight exposure. Intensive growth of bulbils equipped with green distal structures was observed in these inflorescences.

DISCUSSION

The most important determinant of elongation of the *A. sativum* shoot and transition of the juvenile vegetative into reproductive form is the effect of low temperature (4°C) on the meristem at an early stage of its development, i.e. in the underground

bulb [Rotem et al. 2007]. Additionally, the formation of the generative meristem in this species is determined by such factors as development of a stem with a proper length, a specific number of leaves (6–7) with an adequate assimilation surface area, photoperiod (4200 h of the light phase), and underground bulb biomass. Importantly, these factors do not influence inflorescence architecture, e.g. the formation of bulbils in the garlic inflorescence takes place at both reduced and elevated temperature [Deepu et al. 2005].

The umbel-like inflorescence, typical for all ecotypes of bolting garlic studied in this paper, always comprises vegetative and reproductive elements. During the multiyear investigations of garlic species, we always observed small, inconspicuous flowers, bulbils, and leaf-like membranous bracts in the inflorescence. In a spathe-covered inflorescence, all these elements were compacted and compressed, competing with each other for the place in the inflorescence and we have shown that the competition was won by the vegetative elements, which at maturity dominated the smaller flower buds. Our observations are supported by earlier reports indicating that dominance of vegetative elements may contribute to the progressive degeneration of the small flowers and consequently to *A. sativum* sterility [Koul and Gohil 1970, Kamenetsky and Rabinowitch 2001]. As indicated by literature data and our multiyear investigations of the biology of *A. sativum* flowering, all garlic ecotypes have an umbel-like inflorescence composed of vegetative and reproductive elements in different proportions. The different ecotypes have inflorescences with a slightly different composition: either those composed of many flowers, few peripheral leaf-like membranous bracts, and few small bulbils or flowerless inflorescences with many bulbils and leaf-like membranous bracts. The absence of flowers in the latter type is related to the fact that, after being formed, bulbils develop quickly and, in most cases, their development leads to degradation and abortion of the developed flowers [Kamenetsky and Rabinowitch 2001]. Additionally, Etoh [1985] reported marked variations among *A. sativum* clones with respect to the flowering ability and ratio of flowers to bulbils in the umbel. The author suggested that domesticated garlic is undergoing a process of transition from sexual to asexual reproduction. In terms of the organisation of the inflorescence, species from the genus Allium are characterised by high morphological diversity [Ohri et al. 1996]. Although the umbel is the main inflorescence type in the genus Allium, this organ in different Allium ecotypes may vary. For instance, in fertile shallot (*A. cepa* L., *aggregatum* group), the inflorescence was described as an umbel-like flower arrangement with branches growing from a common meristem [Krontal et al. 1998]. The inflorescence in *A. moly* (subgenus *Amerallium*) and *A. odorum* (subgenus *Rhizirideum*) formed branching of the floral meristem [Mann 1959], whereas the apical meristem in *A. rothii*, *A. altissimum*, and *A. karataviense* (subgenus Melanocrommyum) differentiated into several peripheral swellings, thus producing flower clusters [Kamenetsky 1994, 1997]. However, according to a recent inflorescence developmental model called the transient model [Prusinkiewicz et al. 2017], inflorescence architectures cannot evolve freely but are restricted to evolutionary wormholes, influenced by climate fluctuations and life history, generally regarded as multidimensional fitness space. Thus, it can be inferred that despite the high morphological variety in the genus Allium, there is a strict developmental pathway, which leads to fertile flowers. However, in the course of evolution, the inflorescence developmental pathway in *A. sativum* was interrupted, which resulted in transformation of the umbel inflorescence into an umbel-like inflorescence with few sterile flowers. These changes led to development of branches in the inflorescence. This process was depended on the activity of bract axillary buds and resulted in development of bulbils in *A. sativum* as an alternative propagation mode. Since the *A. sativum* ancestor cultivated in Europe has not been identified yet, i.e. some researchers indicate *A. longicuspis* Regel [Hanelt 1990, Mass and Klass 1995] and others *A. tuncelianum* Kollamn [Mathew 1996], the inflorescence evolution in garlic seems to be unresolved.

In this paper, we postulate that the presence of the vegetative structures in the *A. sativum* inflorescence can be regarded as a reversion phenomenon, i.e. transition of the generative meristem into the vegetative

type. The analysis of the phyllotaxis in the *A. sativum* inflorescence showed that the whorl-alternate arrangement was completely disrupted in the umbel-like garlic inflorescence. As described by Kamentsky and Rabinowitch [2001], already at the earliest stages of meristem differentiation, all inflorescence elements emerged chaotically, taking a completely random place in the inflorescence receptacle and floral primordia developed unevenly in helical order. This phenomenon was also observed in some species from the genus Allium of the subgenus *Melanocrommyum* [Kamenetsky 1997] and shallot (Krontal et al. 1998). It has been found that differentiation of bulbils and leaf-like membranous bracts begins after floral differentiation on the peripheral part of the apical surface. Additionally, it is impossible to identify the sequence of formation of the individual inflorescence elements [Kamenetsky and Rabinowitch 2001, Kamenetsky 2007]. Since the absence of regular phyllotaxis and the specific sequence of formation of inflorescence elements is characteristic for the phenomenon of inflorescence reversion [Battey and Lyndon 1990], we propose that the *A. sativum* inflorescence should be regarded as an example of reversion. Although the inflorescence structure in bolting garlic has been described in the literature [Kamenetsky and Rabinowitch 2001, Kamenetsky 2007, Rotem et al. 2007, Shemesh Mayer et al. 2013], it has never been related to the process of floral reversion, and the sequences of a single flower development have never been analysed. It should be emphasised that the present morphogenetic study is the first attempt to classify the structures of the *A. sativum* inflorescence. The postulated phenomenon of reversion in garlic is observed only in the inflorescence, but not in single flowers. The only modification observed in the morphological structure of the *A. sativum* flower included the vegetative structures growing over a closed perianth. These structures were formed through modification of two appendages located at the filament base of three stamens from the outer flower whorl. It may be hypothesised that these transformations of the filament elements during the morphogenetic development are associated with corolla petals, which are absent in the perianth of garlic and some other *Allium* species. This conclusion is supported by the fact that the elongated filament appendages are present only in the stamens of the first whorl. The classification of new structures emerging through reversion requires an interpretation that differs from the classic one. Classic morphology uses well-defined concepts such as the root, stem, or leaf and takes into account the degree of similarity to these structures. The ontological description of organ morphology uses such terms as "is_a", "part_of", and "develops_from". In the morphological description of the structures formed in garlic via reversion, alternative so-called fuzzy morphology using terms such as "both" and "like" should be applied. The structural categories in this type of classification are open due to the existence of intermediate forms that combine typical concepts in a dynamic morphological continuum [Sattler 1988, Lehmann and Sattler 1993, Sattler 1996, Rutishauser 1997]. Therefore, in the description of phenotypic traits with blurred boundaries, the logics of similarity and continuity should be employed [Rutishauser 1995, Sattler and Rutishauser 1997, Rutishauser and Isler 2001]. The morphological and anatomical structures of the vegetative elements in *A. sativum* do not fit into the ontological architecture of angiosperms. Hence, with the use of fuzzy morphology, we can propose that the leaf-like membranous bracts arise from bracteoles and the bulbils develop from vegetative inflorescence primordia after reversion of generative primordia.

In the umbel-like *A. sativum* inflorescence, in which many vegetative elements co-occur with reproductive parts, there is competition for nutrients provided by true leaves. In the garlic inflorescence, sterile elements formed in the reversion process are capable of photosynthesis, which was evident upon the early removal of the spathe surrounding the inflorescence. The presence of the green structures suggests that the additional assimilation surface contributes to higher photosynthetic efficiency and produced assimilates can be delivered directly to the vegetative elements of the inflorescence. This in turn allows the growth and dominance of the bulbils in the inflorescence. This conclusion is supported by the fact that carbohydrates, i.e. the main products of photosynthesis, are important factors in the induction of flowering and floral morphogenesis. Analyses of isolated

Pharbitis nil apical meristems showed clearly the importance of glucose, fructose, and sucrose availability in the process of development of the individual floral whorls in this plant [Durdan et al. 2000]. Therefore, nutrient availability may significantly contribute to the dominance of vegetative elements in the garlic inflorescence. The present observations indicate that the presence of bulbils in the *A. sativum* inflorescence compensates for the incapability of sexual reproduction of the species. Unable to reproduce sexually, garlic reproduces in a vegetative mode through not only underground bulbs but also inflorescence bulbils. The experiment conducted in the present study involving removal of the inflorescence spathe demonstrated that the absence of a cover and spatial limitation in the inflorescence did not promote development of flowers, but facilitated considerable expansion of vegetative elements.

CONCLUSION

The results presented in this paper allowed formulation of a thesis that reversion in *A. sativum* resulted in development of vegetative structures increasing the reproductive potential of garlic, which "retreated" from sexual reproduction. In the holistic approach to "life strategy", the most important goal of species is the possibility to spread [Howe and Smallwood 1982, Stearns 1989, Molau 1993, Salguero-Gómez 2017]. Hence, the inability of *A. sativum* to reproduce sexually directs the garlic to vegetative propagation, involving all underground and aboveground organs and increasing its reproductive success.

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