

2 Florogenesis

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1. Introduction

Flowering is one of the most fascinating and yet complicated processes in nature, involving a variety of strategies and physiological processes to guarantee the development of the generative organs for optimal production of seeds and to ensure continuation of the species. Flowering of various taxa within the genus *Allium* is extremely diverse with regard to morphology, developmental biology, genetic control and response to the environment. Until now, florogenesis has only been studied in a few species of the large *Allium* genus, mainly those of current economic importance.

We shall review the transition of *Allium* plants from the vegetative to the generative phase, the development of the *Allium* inflorescence from initiation to anthesis and its regulation by internal and external factors. We shall also discuss the factors involved in the differentiation of floral parts and inflorescence structure, with special attention to differences between biomorphological groups. Pollination and seed development in edible *Alliums* have been reviewed comparatively recently (Rabinowitch, 1985, 1990a, b; Currah, 1990; Brewster, 1994) and will only be mentioned when appropriate.

2. Morphological Structure and Differences among Biomorphological Groups

The complex process of flowering varies among members of the genus *Allium*. The various biomorphological groups respond differently to inductive conditions and develop from initiation to bloom in different ways. They also vary significantly in the morphological organization of the storage organs and in life cycle.

Wild *Allium* species have been divided into three main biomorphological groups (Pastor and Valdes, 1985; Hanelt *et al.*, 1992; Kamenetsky, 1992, 1996a; Fritsch and Friesen, Chapter 1, and Kamenetsky and Fritsch, Chapter 19, this volume).

2.1 The rhizomatous group

This group includes members of the subgenera *Rhizirideum* and *Amerallium*, which, in the wild, are confined mainly to mesoxerophytic habitats: meadows, forests and high mountain zones (Hanelt *et al.*, 1992). The fleshy rhizomes are built up through successive concrescence of the basal plates over several generations and function primarily as underground storage organs. Bulbs of these species are composed of leaf sheaths of different thickness. Wild rhizomatous species grow continuously all year round with no apparent dormant stage, and low winter temperatures only slow this down (Cheremushkina, 1985, 1992; Pistrick, 1992). The juvenile period lasts 1–2 years. In post-juvenile plants, flowering occurs late in the spring or in the summer. Differentiation of the inflorescence occurs at the base of the youngest leaf, and the number of flowering cycles ranges from one to three per season in different species (Kruse, 1992; Fig. 2.1).

2.2 The bulbous group

This group includes members of the subgenera *Allium* and *Melanocrommyum* and some members of the subgenus *Amerallium*. Wild plants of these taxa inhabit mainly steppes, semi-desert and desert areas. The storage organs are completely or partially subterranean and consist of a compressed

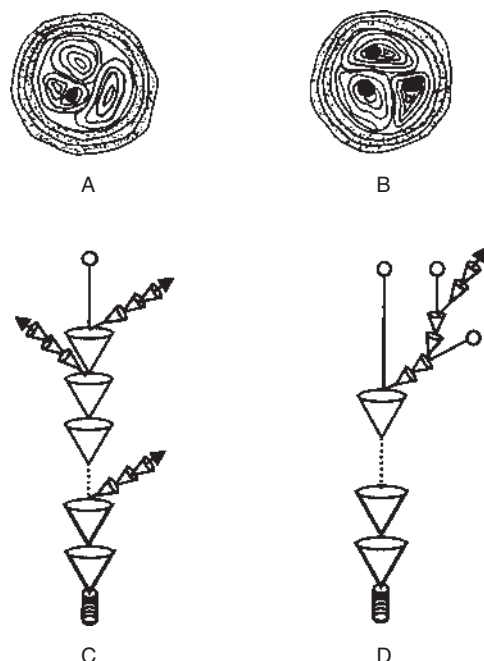


Fig. 2.1. Diagrammatic representation of morphological structure of rhizomatous *Allium* species. A, C. Cross-section and diagram of *A. victorialis*, showing a single terminal generative shoot and several vegetative shoots. B, D. Cross-section and diagram of *A. tuberosum*, showing several flowering cycles during one season. ▽, Foliage leaf; ♀, inflorescence; ▢, rhizome; ▲, vegetative growing point or shoot apex.

and flattened stem – the basal plate – together with the fleshy, succulent leaf-bases and/or specialized true scales, which assume the storage functions (De Mason, 1990; Kamenetsky, 1996a). In the summer, the bulbs enter a rest period, and sprouting recommences either in the autumn or in the spring (Pistrick, 1992). The juvenile period lasts 2–5 years and post-juvenile plants flower in the spring. Differentiation of the inflorescence occurs at the base of the youngest leaf during summer/autumn of the previous year (Kamenetsky, 1997; Fig. 2.2).

2.3 Edible *Allium* species

These are probably best considered as a separate group. For several millennia, these

plant species have been selected by humans for specific morphological and physiological traits (Hanelt, 1990). Today, the domesticated onion, *A. cepa* of the subgenus *Rhizirideum*, behaves very much like a true bulbous plant. Its bulb consists of specialized leaf sheaths ('false scales') and modified bladeless leaves ('true scales'), which swell to form a bulb, the storage organ (Brewster, 1990, 1994; De Mason, 1990). In contrast, leek, a selection from the bulbous *A. ampeloprasum*, forms a long false stem, consisting of leaf sheaths and within them, folded immature leaf blades (the storage organ) (van der Meer and Hanelt, 1990; De Clercq and Van Bockstaele, Chapter 18, this volume).

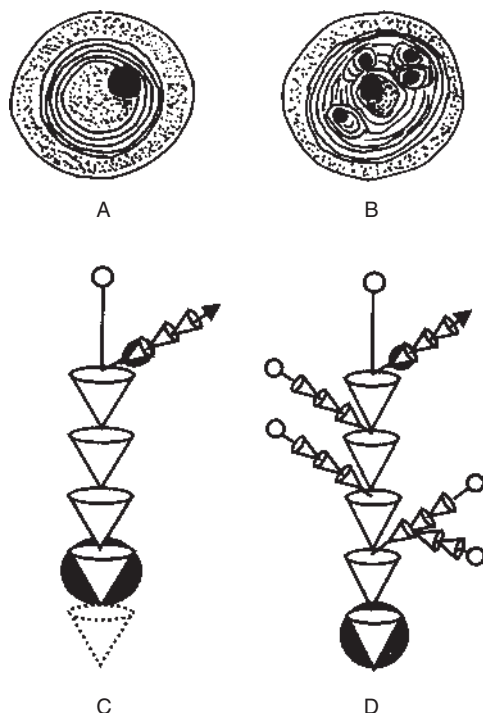


Fig. 2.2. Diagrammatic representation of morphological structure of bulbous species. A, C. Cross-section and diagram of *A. nigrum*, showing development of a single terminal inflorescence and one renewal bud. B, D. Cross-section and diagram of *A. moly*, showing the main flowering shoot and several lateral shoots and secondary inflorescences. ▽, Foliage leaf; ♀, inflorescence; ●, storage leaf (scale); ▲, vegetative growing point or shoot apex.

Taxonomically, many economically important species belong to the subgenus *Rhizirideum*, e.g. *A. cepa* (onion, shallot), *A. fistulosum* (Japanese bunching onion) and *A. schoenoprasum* (chives), while *A. sativum* (garlic) and *A. ampeloprasum* (leek, elephant garlic, kurrat and pearl onion) belong to the subgenus *Allium* (Hanelt, 1990; Fritsch and Friesen, Chapter 1, this volume). The two groups differ markedly in both morphological organization and life cycle. Moreover, significant physiological differences occur even within one botanical species (e.g. *A. cepa*) (Rabinowitch, 1990a; Krontal *et al.*, 1998).

3. Transition from the Vegetative to the Generative Stage

In many geophytes, florogenesis can be divided into five consecutive steps, comprising induction, initiation, differentiation (organogenesis), maturation and growth of floral parts and anthesis (Le Nard and De Hertogh, 1993).

The induction and initiation of flowering are greatly affected both by the genetic make-up of the individual plant and by environmental factors; their interactions affect a series of molecular and biochemical processes, leading to the transition from vegetative to reproductive development (Halevy, 1990; Bernier *et al.*, 1993).

3.1 Genetic effects

There is a significant genetic variation in the response of *Allium* genotypes to the environment. Differences in the length of the juvenile phase (physiological age), the responses to photoperiod and to the optimum, minimum and maximum temperatures for floral induction have been recorded within the gene pools of bulb onion (Rabinowitch, 1985, 1990a), shallot (Messiaen *et al.*, 1993; Krontal *et al.*, 1998; Rabinowitch and Kamenetsky, Chapter 17, this volume), Japanese bunching onion (Tindall, 1983) and leek (van der Meer and Hanelt, 1990; De Clercq and Van Bockstaele, Chapter 18, this volume). Garlic clones differ significantly in

their ability to form a floral stem and inflorescence (Takagi, 1990; Section 3.4.6 below; Etoh and Simon, Chapter 5, this volume). Some garlic clones develop normal flower primordia and long scapes and go on to bloom, but topsets (bulbils), widely varying in numbers, develop in the inflorescence concurrently with flowers. Plants of other clones initiate a flower scape but the inflorescence degenerates prematurely. A third group comprises non-bolting clones.

3.2 Physiological age

When propagated from seeds, all *Allium* plants need to reach a certain physiological age (or critical mass) before being capable of florogenesis and blooming. The length of the juvenile phase ranges from a few months, e.g. bulb onion (Rabinowitch, 1990a), chives *A. schoenoprasum* (Poulsen, 1990), Japanese bunching onion (Inden and Asahira, 1990), leek (van der Meer and Hanelt, 1990; De Clercq and Van Bockstaele, Chapter 18, this volume) and shallot (Messiaen *et al.*, 1993; Krontal *et al.*, 1998; Rabinowitch and Kamenetsky, Chapter 17, this volume), to 5–6 years, e.g. *A. giganteum* and *A. karataviense* (De Hertogh and Zimmer, 1993). The length of the juvenile phase depends on the genetic make-up of the plant and the growth environment, e.g. bulb onion (Heath and Mathur, 1944; Ito, 1956; Shishido and Saito, 1976; Brewster, 1985; Rabinowitch, 1990a) and Japanese bunching onion (Inden and Asahira, 1990). Both factors control the amount of accumulated reserves necessary for successful blooming. It has been suggested, however, that the ability to flower depends not only on the amount of available reserves but also on the size of the apical meristem (Halevy, 1990; Le Nard and De Hertogh, 1993).

With a few exceptions, in seedlings of bulb onion (Rabinowitch, 1990a) and of Japanese bunching onion (Inden and Asahira, 1990), the transition to the reproductive stage normally occurs in the first or second growing season after the formation of 10–14 leaves (including leaf buds). Under

inductive conditions, floral initiation in shallot (Krontal *et al.*, 1998) and in leek (van der Meer and Hanelt, 1990; De Clercq and Van Bockstaele, Chapter 18, this volume) is already possible after formation of the first six and seven true leaves (including leaf primordia), respectively.

In nature, seedlings of the rhizomatous *A. senescens* branch after emergence to form a primary clump. Growth and branching continue for 3–5 years before the vegetative plant reaches the required physiological age (or critical mass) for blooming; then all shoots become reproductive simultaneously (Cheremushkina, 1985).

In ornamental bulbous *Allium* species, the ability to flower depends on the amount of reserves (the critical mass of the bulb). The minimum bulb circumference needed for flowering varies between 3 and 5 cm for *A. caeruleum*, *A. neapolitanum* and *A. unifolium*, between 12 and 14 cm for *A. aflatumense* (= *A. hollandicum*), *A. cristophii* and *A. karataviense* and between 20 and 22 cm for *A. giganteum* (De Hertogh and Zimmer, 1993). In general, seedlings of ornamental species with small bulbs flower in the second year of development (e.g. *A. neapolitanum*, *A. caeruleum*; R.M. Fritsch, Gatersleben, 1999, personal communication), whereas those of plants with large bulbs (e.g. members of the subgenus *Melanocrommyum*) require 3–5 years of growth before they reach the blooming phase (De Hertogh and Zimmer, 1993; Kamenetsky, 1994). In *A. aschersonianum* (subgenus *Melanocrommyum*) the transition of the apical meristem to the reproductive stage occurred in bulbs as young as 2 years. However, these plants were too small to support a normal bloom and therefore the young reproductive bud aborted inside the bulb (Kamenetsky *et al.*, 2000).

3.3 Morphological changes during floral initiation

Juvenile *Allium* plants exhibit a monopodial growth habit, and only become sympodial after the formation of the first generative meristem. Thereafter, *Allium* plants produce

renewal bulbs and flower every year. During the vegetative stage, the apical meristem is flat and leaf primordia initiate from the periphery towards the centre (Fig. 2.3A, B). On the transition of the apical meristem from vegetative to generative, the meristem swells to form a dome shape, a spathe is formed in the apex and leaf initiation ceases. The spathe arises as a nearly uniform ring, elongates quickly and envelops the reproductive meristem (Fig. 2.3C, D).

3.4 Environmental control of flower induction and initiation

Cold exposure is required for floral induction in the major cultivated *Allium* crops, including bulb onion (Rabinowitch, 1985, 1990a), chives (Poulsen, 1990), shallot (Krontal *et al.*, 2000), garlic (Takagi, 1990; Section 3.4.6 below) and Japanese bunching onion (Inden and Asahira, 1990). In addition, some *Allium* crops require a long photoperiod for inflorescence initiation and further differentiation; they include Chinese chives (*A. tuberosum*) (Saito, 1990), leek (van der Meer and Hanelt, 1990; De Clercq and Van Bockstaele, Chapter 18, this volume) and rakkyo (*A. chinense*) (Toyama and Wakamiya, 1990).

The ornamental species of the subgenus *Melanocrommyum* show a different physiology, as the transition from the vegetative to the reproductive phase occurs at the end of the growth period or during the 'rest' period without cold induction.

3.4.1 Bulb onion

In the bulb onion, floral initiation in the post-juvenile plant requires cold induction. This thermophase occurs in plants with a minimum leaf and leaf primordia number estimated variously as 7–10 (Brewster, 1985, 1994), 11–12 (Heath and Mathur, 1944; Ito, 1956) or 12–14 (Heath and Mathur, 1944; P.B. Mathur, unpublished). For many onion cultivars, optimum temperatures in the thermophase range between 8 and 12°C, and response is markedly slower at temperatures below 6 and above 17°C (Brewster,

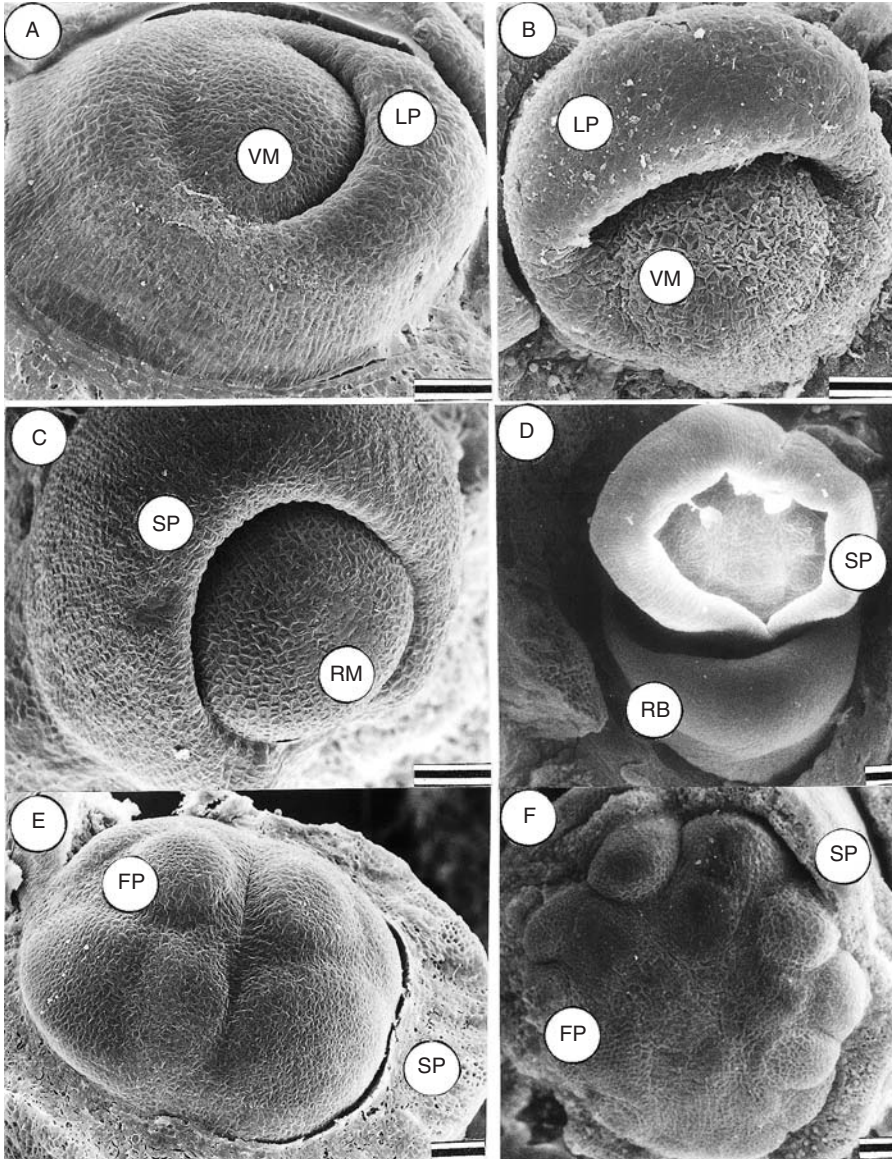


Fig. 2.3. Scanning electron photomicrographs of *Allium* spp. vegetative apex and initial stages of floral development. Bar = 0.1 mm. A. Initiation of leaf primordia (LP) in the vegetative apical meristem (VM) of *A. aschersonianum*. Older leaf primordia removed. B. Further development of leaf primordium (LP) in the vegetative apical meristem (VM) of *A. aschersonianum*. Older leaf primordia removed. C. Floral initiation in *A. aschersonianum*. Spathe (SP) surrounds the swollen reproductive meristem (RM). D. Spathe (SP) of *A. nigrum* envelops the reproductive meristem. Renewal bulb (RB) is initiated in the axis of the last leaf (removed), near the base of the floral stalk. E. Differentiation of four centres of development in a reproductive meristem of shallot, with spathe (SP) removed. First flower primordia (FP) are visible. F. Initiation of the first flower primordia (FP) in the periphery of the reproductive meristem of *A. nigrum*. Spathe removed.

1985). However, the West African onion cv. 'Bawku' is optimally induced to flower between 15 and 21°C (Sinnadurai, 1970a, b) and some landraces from northern Russia have an optimum of 3–4°C (for reviews, see Rabinowitch, 1985, 1990a). Relatively little is yet known of the responses of tropical onions and shallots in this respect (for more details, see Currah and Proctor, 1990; Currah, Chapter 16, this volume).

Post-juvenile onion plants respond to cold induction both at rest and during active growth in the field, and their sensitivity to cold induction increases with age, i.e. older plants require less cold induction (Gregory, 1936; Thompson and Smith, 1938; Heath and Mathur, 1944). In growing seedlings, the critical dry weight of shoot (basal plate plus leaves) for inflorescence induction ranges from 60 to 450 mg (Brewster, 1985). The minimum critical dry weight required by dry bulbs to initiate flowering during storage is much higher than that in growing plants and, in both cases, the threshold is determined by the genetics of the plant (Brewster, 1994).

High temperatures of 28–30°C throughout storage not only inhibited inflorescence initiation in onion, but also exerted a marked after-effect during the subsequent growing season, expressed as delayed flowering (Heath and Mathur, 1944; Aoba, 1960), or led to greatly reduced flowering (Jones, 1927; Jones and Emsweller, 1936; Heath, 1943a, 1945; van Beekom, 1953; Lachman and Michelson, 1960; van Kampen, 1970).

3.4.2 Shallot

In shallot (*A. cepa* Aggregatum group) seedlings of tropical origin, floral initiation becomes evident after formation of the sixth true leaf (Krontal *et al.*, 1998). Unlike the bulb onion, in which, after floral initiation, the lateral meristems form dormant adventitious buds, shallot leaf formation continues at the axillary meristems, simultaneously with floral development at the main apex. As in bulb onion, low temperatures induce flowering of shallots, with the optimum between 5 and 10°C, either in storage or during growth, whereas high or intermediate growing or storage temperatures delay or prevent inflorescence development (Krontal *et al.*, 2000; Rabinowitch and Kamenetsky, Chapter 17, this volume). Some shallot genotypes, however, are very resistant to flowering, possibly due to a long history of selection against this trait, as suggested with garlic.

3.4.3 Japanese bunching onion

Like the bulb onion, Japanese bunching onion varies according to the cultivar in both juvenile age and cold requirement (Table 2.1; Watanabe, 1955; Yakura and Okimizu, 1969; Lin and Chang, 1980; Inden and Asahira, 1990; Yamasaki *et al.*, 2000a). Genotypic differences exist in the interaction between low temperature and photoperiod: two mid-season flowering cultivars exhibited a similar response to temperature in flower initiation and bolting, but

Table 2.1. Effect of genotype, physiological age, day length and temperature on floral induction in Japanese bunching onion.

Cultivar	Origin	Physiological age		Induction requirements	
		Leaf number	Pseudostem diameter (mm)	Temperature (°C)	Duration (days)
Kaga ^{1,2}	Japan	11–12	5–7	<13	30
Gao Jiao ³	China	–	3	5	30
Pei Chang ⁴	Taiwan	–	4.5	5	5
			4.5	20	10

¹Yakura and Okimizu (1969).

²Watanabe (1955).

³Lin and Chang (1980).

⁴Inden and Asahira (1990).

they differed markedly in their photoperiodic response. The primary requirement in cv. 'Kincho' was low temperature, while in 'Asagi-kujo' it was a short day (Yamasaki *et al.*, 2000a).

3.4.4 Wild members of the section *Cepa* (subgenus *Rhizirideum*)

In their natural habitats, *A. altaicum*, *A. oschaninii* and *A. pskemense* have a short summer 'rest' period. Sprouting begins in the autumn, but the low winter temperatures retard or completely inhibit leaf development and elongation (Pistrick, 1992). Only plants with more than 10 or 11 leaves (including leaf primordia) progress to the reproductive stage, which occurs in the autumn, when temperatures decrease and day length becomes short (Cheremushkina, 1985).

3.4.5 Wild rhizomatous species

Little is known about florogenesis in this group of plants. Under natural conditions, the renewal bulbs of nine Siberian species formed in the leaf axils of the parent plants, which remained vegetative during the first and second growing seasons. In the third season, and following the development of 7–10 (*A. senescens*) or 16–20 (*A. nutans*) leaves, the renewal bulbs became reproductive (Cheremushkina, 1985). Initiation of flowering occurs either in the spring, when it is followed by instant scape elongation and bloom (*A. nutans*, *A. senescens*, *A. galanthum*), or in the autumn, before the harsh winter (*A. obliquum*) (Cheremushkina, 1985).

In Israel, where winters are mild, rhizomatous species such as *A. trachyscordum*, *A. petraeum*, *A. platyspathum* and *A. nutans* from Siberia and Kazakhstan bloom in the spring and summer, between May and July, without any additional cold treatment (Kamenetsky, 1996b).

3.4.6 Garlic

All current commercial clones of *A. sativum* (subgenus *Allium*) are completely sterile (Etoh and Simon, Chapter 5, this volume).

Possible reasons for this include competition for nutrients between generative and vegetative buds (topsets) within the developing inflorescence (Koul and Gohil, 1970), premature degeneration of the tapetum (Novak, 1972), or infection with degenerative-like diseases (Konvicka, 1973, 1984). Etoh (1985) suggested that garlic is in transition from a sexual to an asexual reproductive state and that farmers have accelerated the process through numerous generations of selection.

Garlic clones vary in their ability to bolt and have been classified accordingly (Gvaladze, 1961; Takagi, 1990; Etoh and Simon, Chapter 5, this volume), as follows:

1. Complete bolting – plants produce a long thick flower stalk, with many topsets and a variable number of flowers.
2. Incomplete bolting – plants produce a thin short flower stalk, with a few large topsets; usually no flowers are formed.
3. Non-bolting – plants do not normally form a flower stalk; instead, only cloves are produced inside the pseudostem (Takagi, 1990).

When grown under the appropriate environmental conditions, plants of the first two groups, but not those of the third group, produce inflorescences and floral buds. Genotypes from the temperate zone require stronger cold induction for inflorescence formation than those from subtropical and tropical regions. The inductive temperatures vary significantly with cultivar and range between –2 and 10°C (Takagi, 1990; R. Kamenetsky, personal observations). Long storage at low temperatures resulted in the blooming of plants with smaller numbers of leaves and in earlier flowering than in bulbs stored for a shorter period. However, a very long cold treatment (2°C for 5 months) reduced blooming of garlic cv. 'Yamagata' (Takagi, 1990).

Transition of the apical meristem from the vegetative to the reproductive state occurs only in growing plants with a minimum of six to eight leaves and leaf primordia, but not during cold or ambient storage (Kamenetsky and Rabinowitch, 2001), and low field temperatures promote inflorescence induction

(Takagi, 1990). However, after storage at low temperatures, garlic plants from the complete-bolting group (Israeli Gene Bank, Rehovot, plant introduction no. 2091) were able to initiate flowers at relatively high growth temperatures (23/15°C, day/night, respectively) (Kamenetsky and Rabinowitch, 2001).

3.4.7 Ornamental species (subgenus *Allium*)

In this group, inflorescence initiation occurs only in growing plants, following the formation of seven to nine green leaves. Growth temperatures of 17–20°C and long days are essential for floral initiation and scape elongation, whereas high field temperatures and short days are not inductive and plants remain vegetative (Berghoef and Zevenbergen, 1992; Kamenetsky, 1996b).

3.4.8 Ornamental species (subgenus *Amerallium* = former section *Molium*)

Plants originating in Mediterranean climates (Mediterranean basin, California) remain vegetative during a summer 'rest', when soil temperatures are high. A visible transition of the apex to the reproductive state occurs only in the autumn, when temperatures decrease. Thus, an optimum temperature range of 9–17°C has been recorded for floral initiation in members of the subgenus *Amerallium*, including *A. unifolium* (Kodaira *et al.*, 1996), *A. neapolitanum* and *A. roseum* (Maeda *et al.*, 1994; van Leeuwen and van der Weijden, 1994).

3.4.9 Ornamental species (subgenus *Melanocrommyum*)

Plants from the Irano-Turanian region (Central Asia, Iran, Afghanistan) (e.g. *A. aflatunense* = *A. hollandicum*, *A. altissimum*, *A. karataviense*) initiate leaf primordia in the renewal bulb during the flowering of the mother plant. Following the differentiation of five to seven leaf primordia, the apical meristems of *A. altissimum* and *A. karataviense* become latent. No detectable changes occur for 6–10 weeks, and then floral initiation

becomes visible at the apex within the bulb (Kamenetsky, 1997; Kamenetsky and Japárova, 1997).

In *A. aflatunense* (= *A. hollandicum*) the transition from the vegetative to the reproductive phase occurs at the end of the growth period, immediately after the cessation of leaf initiation. The differentiation of the floral meristem has been observed in plants grown at all temperatures from 4 to 26°C (Zemah *et al.*, 2001).

In *A. aschersonianum*, *A. nigrum* and *A. rothii* of the Israeli flora, flowering of the mother plant in February–March is followed by the high-temperature induction of a 12–15-week latent period of the apical meristem within the bulb. During July–October, five to seven leaf primordia form and the meristem becomes reproductive without cold induction. When the plants are stored at 20–25°C, the summer rest becomes considerably shorter and floral initiation occurs in August. In such cases, plants can be forced into flower 2–3 months earlier than under ambient Israeli summer conditions (Kamenetsky, 1994, 1997; Kamenetsky *et al.*, 2000).

To the best of our knowledge, there are no data on the photoperiod effect on floral induction in wild species of the subgenus *Melanocrommyum*.

4. Floral Differentiation (Organogenesis) and Inflorescence Structure

The *Allium* inflorescence appears to be simple. In reality, however, it is very complex. For many years, botanists referred to it as a monopodial umbel. However, as early as 1837, Louis and Auguste Bravais described the inflorescence of *A. moly* (subgenus *Amerallium*) as having two sequential layers of sympodial flower clusters (cited by Mann, 1959). Later, Weber (1929) reported that the inflorescence of *A. odorum* (= *A. ramosum*) consists of a terminal flower, which bears two bracts on its pedicel, each with an axillary flower. This dichasial branching continues, and thus each flower gives rise to two lateral flowers.

4.1 Bulb onion

Jones and Emsweller (1936) made an analysis of the structure and development of the onion inflorescence and of the individual flower. Over the broad surface of the stem tip, which is situated within the developing spathe, numerous membranous bracts develop, which cover the cluster of young flowers in their first stages. De Mason (1990) notes that the generative meristem of onion subdivides into multiple centres, each of which gives rise to a group of flowers, a cyme (= bostryx). The flower buds in each cyme are arranged in a spiral order. Thus, the bulb-onion inflorescence, often with 400–600 flowers, comprises many flower clusters, each consisting of several flowers.

4.2 Shallot

Krontal *et al.* (1998) reported that differentiation of shallot flowers begins with subdivision of the apical meristem into four centres (Fig. 2.3E). The floral initials occur in one of these centres only after the scape reaches 5–7 mm in length above the basal plate. In each of the four centres of differentiation, floral primordia develop unevenly in a helical order. Each centre of development is covered by thin membranous bracts and contains six or seven developing flower clusters (Fig. 2.4A). Initiation and differentiation of additional new primordia continue simultaneously with the sequential differentiation, growth and development of older flowers. Thus, the shallot inflorescence consists of clusters, each containing five to ten flower buds arranged in a spiral order: it can therefore be described as an umbel-like flower arrangement, the branches (flower clusters) of which arise from a common meristem (Rabinowitch and Kamenetsky, Chapter 17, this volume).

4.3 Garlic

Morphological events in the flower development of garlic are of special interest because of its inherited sterility (Konvicka, 1984; Etoh *et al.*, 1988; Etoh and Simon, Chapter

5, this volume). Floral development has been described in Japan for the bolting-garlic cv. 'Shanghai-wase' (Etoh, 1985) and in Israel for accession no. 2091, introduced from Russia (Kamenetsky and Rabinowitch, 2001). The differentiation of floral initials begins only after the scape has reached 5–7 mm in length and the apex diameter exceeds 0.5 mm. Later, the apical meristem subdivides into several swellings, each of which gives rise to a number of individual flower primordia (Fig. 2.4B). When the floral stalk reaches 15 cm in length, the pedicels elongate and the inflorescence becomes spherical (Fig. 2.4C).

Long leaf-like bracts develop both at the periphery and in the centre of the inflorescence, thus separating the developing umbel into distinct floral clusters (Fig. 2.4D). Further inflorescence growth and development include both initiation and differentiation of new flower primordia, and sequential differentiation, growth and development of older flowers. At this time, new undifferentiated domes, 0.15 mm in diameter, form at the base of the inflorescence. These swellings quickly differentiate into vegetative buds and grow to form small inflorescence bulbils: the topsets (Fig. 2.4E, F).

Topset differentiation begins in the periphery of the apical surface; their number, size and rate of development are determined by the genotype and show great variability. After differentiating, the topsets develop quickly, a process followed by degeneration and abortion of many of the developing flowers. Similar observations by Etoh (1985) led to the conclusion that garlic is in a transitional state from sexual to asexual reproduction.

When the spathe breaks open, differentiated flower buds of garlic become visible to the naked eye, but the fast-growing topsets stifle them and the flower buds quickly degenerate. Therefore, in some garlic clones, continuous removal of the developing topsets can result in normal flowering, pollination and seed production (Koul and Gohil, 1970; Konvicka, 1984; Etoh *et al.*, 1988; Pooler and Simon, 1994; Jenderek and Hannan, 2001; Etoh and Simon, Chapter 5, this volume).

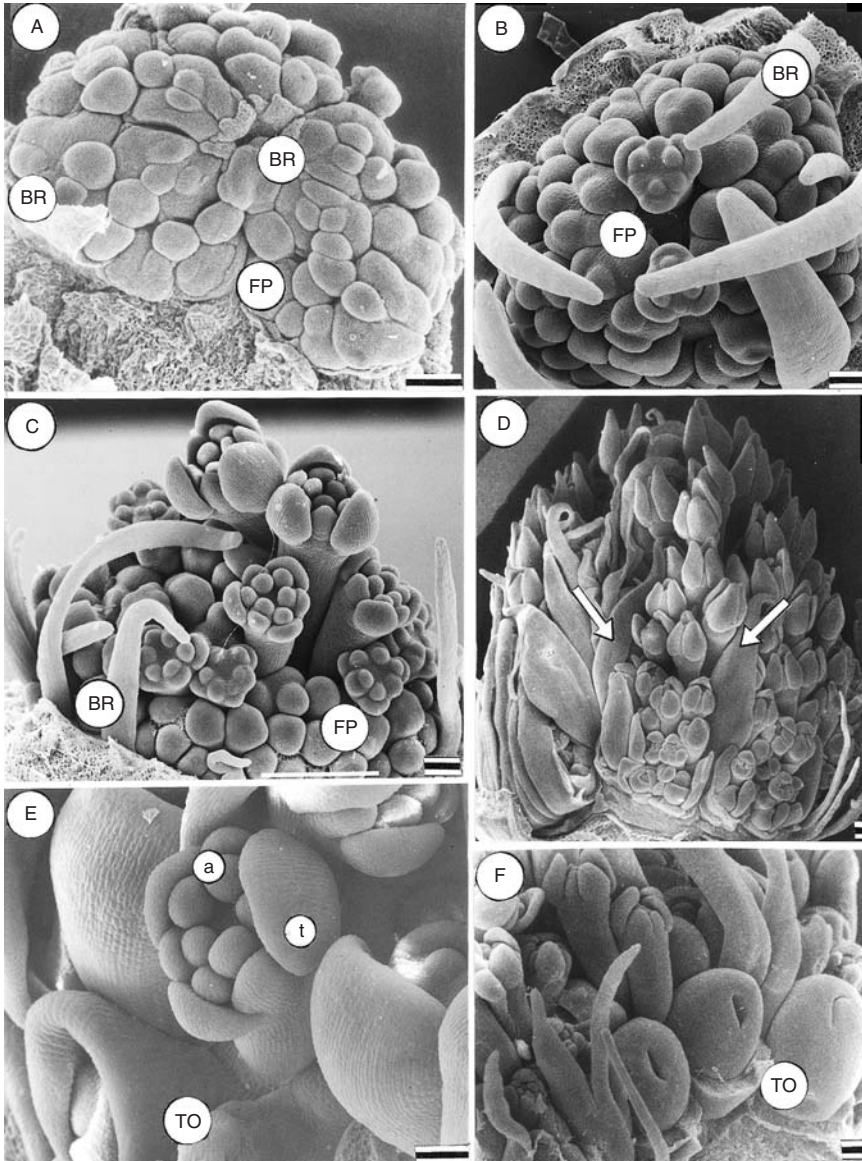


Fig. 2.4. Scanning electron photomicrographs of *Allium* spp. floral development. Bar = 0.1 mm. A. Flower primordia (FP) are visible in shallot inflorescence. Four centres of differentiation are separated by the bracts (BR). Spathe and peripheral and central bracts removed. B. Early stages of garlic floral development. Floral differentiation is visible in older flower primordia (FP), while younger flowers still appear as meristematic domes. Leaflike bracts (BR) form at the periphery of the inflorescence. Spathe removed. C. The inflorescence of garlic becomes hemispherical in shape and consists of numerous floral primordia (FP). Differentiation of floral primordia is uneven: floral parts occur in the oldest floral primordia, while younger ones still appear as undifferentiated meristematic domes. Spathe removed. D. Floral pedicels and leaf-like bracts elongate. In individual garlic flower clusters (arrows), which are separated by leaf-like bracts, floral primordia develop unevenly in a helical order. New flower primordia continue to appear at the base of the inflorescence. E. Magnification of the basal part of garlic inflorescence. Newly developed meristems appear and rapidly differentiate to form small inflorescence bulbs: topsets (TO). In the individual flowers, tepals (t) and anthers (a) are visible. F. Topsets (TO) in garlic inflorescence.

4.4 Japanese bunching onion

After flower initiation, the early stage of flower development is day-neutral and, after floret formation stage, a long-day photoperiod promotes flower development and elongation of the seed-stalk (Yamasaki *et al.*, 2000b). In Israel, cultivated *A. fistulosum* plants bloom in the spring and early summer, just before entering summer dormancy (H.D. Rabinowitch, personal observation), thus ending the production season. In Japan, this crop is of high economic value. Work is in progress by Yamasaki and colleagues to exploit the genetic variability within existing cultivars for day-length response (e.g. stronger requirement for a short day (SD) in cv. 'Asagi-kujo' compared with cv. 'Kincho' (Yamasaki *et al.*, 2000b)) in order to control or delay flowering so as to extend the harvest season, which is normally curtailed when the plants start to flower in Japan.

Recently greenhouse culture and plug-seedling transplanting of Japanese bunching onion have increased in Japan, where a new method of bolting control using long-day treatment is easily applicable.

4.5 Ornamental species (subgenus *Amerallium* = former section *Molium*)

A detailed description of the developing inflorescences of six Mediterranean species (Mann, 1959) indicated that the single spathe consists of four bracts, each of which bears in its axil a flower cluster (a helicoid cyme or bostryx) of three to seven flowers. Several smaller cymes differentiate later in the centre of the inflorescence; they contain smaller numbers of flowers. The first peripheral cyme is formed opposite the uppermost foliage leaf; the others follow in alternating positions. The four peripheral cymes flower first and the central ones flower last. Within each cyme, the flowers open in a strict sequence from oldest to youngest (Fig. 2.5).

4.6 Ornamental species (subgenus *Melanocrommyum*)

Flower differentiation of the Central Asian species *A. aflatumense* (= *A. hollandicum*), *A.*

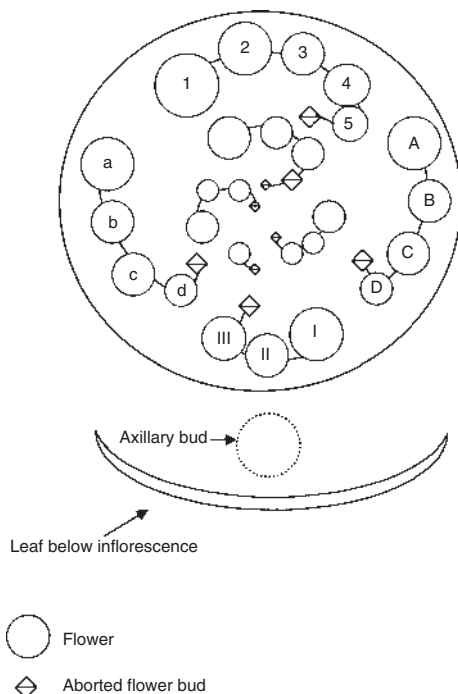


Fig. 2.5. Cross-section of the inflorescence of *A. neapolitanum*, showing its flower arrangement. The first four helicoid cymes (bostryces) are located around the periphery of the inflorescence and are designated by different signs, in the following order: 1,2,3,...; I,II,III,...; A,B,C,...; a,b,c,... The first cyme develops opposite the uppermost foliage leaf (last leaf) and axillary bud. (From Mann, 1959, with permission.)

altissimum and *A. karataviense*, as well as the species from the Mediterranean area *A. nigrum*, *A. rothii* and *A. tel-avivense*, begins during the rest period of the bulb (Kamenetsky, 1994, 1997; Kamenetsky and Japarova, 1997). Despite the significant variation in their life cycle and pace of floral development, they all have a similar inflorescence structure within a spathe, which is shaped at first as a nearly uniform ring.

Following the cessation of leaf formation and the initiation of a spathe, the apical meristem grows markedly in size, and several peripheral swellings differentiate to produce a row of flower primordia (Fig. 2.3F). Within each peripheral swelling, the flat meristematic surface protrudes to become round and smooth; it later divides

into many centres, each of which gives rise to a flower cluster (Fig. 2.6A, B). As flower primordia continue their development, the circular spathe grows upward to envelop the developing inflorescence.

Flower number per umbel and per flower cluster vary with species, plant age and size, and probably with growth conditions (Table 2.2). Differentiation and development of flowers within each cluster proceed in a spiral order to form a complex monochasium, the cyme (or bostryx). New flower primordia continue to form within each cyme while older flowers already have differentiated floral parts (Fig. 2.6C, D). The youngest primordium in each cyme sometimes aborts.

The sequence of differentiation affects the inflorescence structure and is maintained throughout from flower anthesis to seed maturation (Kamenetsky, 1997). The strict developmental sequence from the oldest to the youngest flower was observed within each flower cluster (Fig. 2.6E, F). As flowers open, the pedicels reach similar lengths, so that, in a fully developed inflorescence, cymes can no longer be recognized.

Based on the sequence of inflorescence differentiation, we hereby propose the following classifications of *Allium* inflorescence structures:

1. The apical meristem divides initially into several (usually four) centres, separated by leaf-like bracts. Each centre gives rise to a number of flower clusters (cymes). Floral differentiation and organogenesis occur simultaneously with both scape elongation and vegetative growth and development. This type of florogenetic process has been

reported for onion (Jones and Emsweller, 1936; De Mason, 1990), garlic (Etoh, 1985; Kamenetsky and Rabinowitch, 2001) and shallot (Krontal *et al.*, 1998).

2. The inflorescence is composed of monopodially arranged clusters, of which the first one is formed opposite to the uppermost foliage leaf and others follow in alternating positions. Within each cyme, the flowers differentiate and open in a strict sequence from oldest to youngest. Floral differentiation and organogenesis occur both during storage and during active growth and development (Mann, 1959). This type of florogenetic process has been reported for species from the subgenus *Amerallium*, e.g. *A. neapolitanum* and *A. roseum*.

3. All flower clusters (cymes) arise from a common meristem. Differentiation of clusters commences in the periphery of the apical meristem and continues towards its centre. Within each cluster, flowers are formed in a helical order. Floral differentiation and organogenesis take place during the summer rest period (Kamenetsky, 1994, 1997; Zemah *et al.*, 2001). This type of florogenetic process has been reported for the subgenus *Melanocrommyum*, e.g. *A. aflatumense* (= *A. hollandicum*), *A. altissimum*, *A. karataviense*, *A. nigrum* and *A. rothii*.

5. Differentiation of the Individual Flower

All *Alliums* produce flowers with six perianth lobes, six stamens and a tricarpeillary pistil, situated in the centre of the flower. Ovaries of differentiated *Allium* flowers include the

Table 2.2. Number of flowers within umbels of *Allium* spp. of subgenus *Melanocrommyum* (adapted from Kamenetsky, 1997).

Species and stage of development	Number of flowers		
	Umbel	Peripheral cymes	Central cymes
<i>A. karataviense</i> , old*	450–600	12–15	6–10
<i>A. nigrum</i> , old	140–160	6–7	3–5
<i>A. nigrum</i> , young	60–75	4–5	2–3

*Young and old = the plants have undergone the first flowering cycles or experienced a number of cycles, respectively.

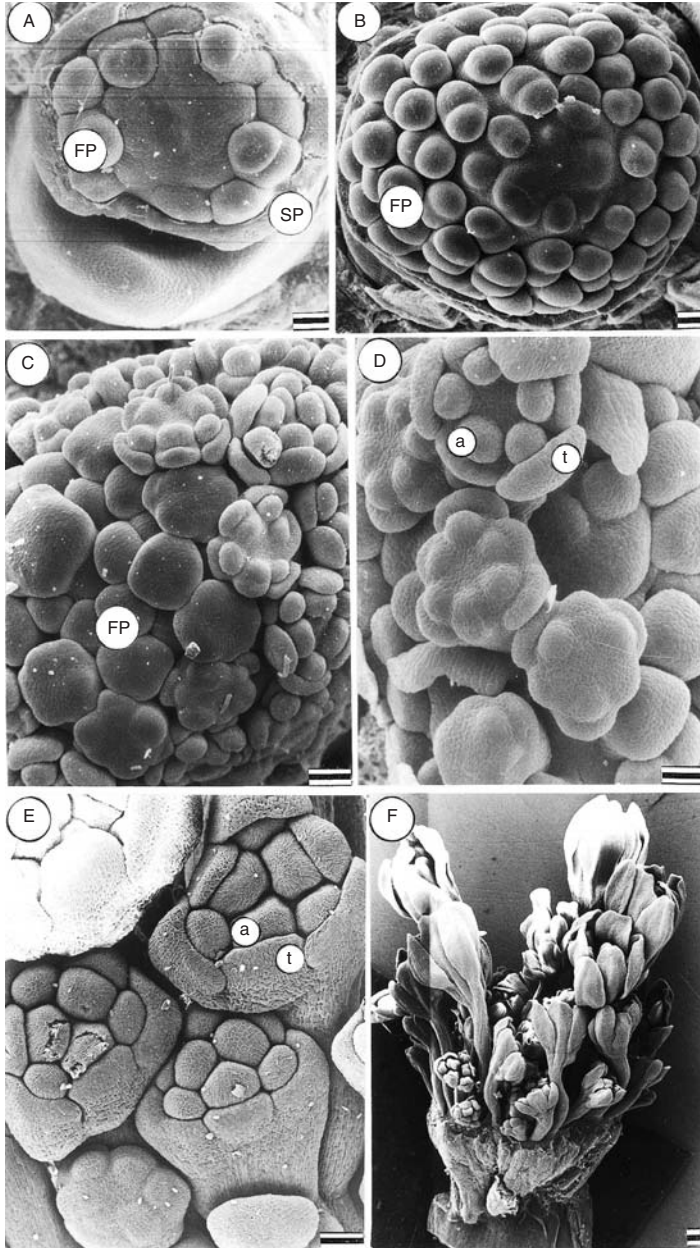


Fig. 2.6. Scanning electron photomicrographs of *Allium* floral development. Bar = 0.1 mm. A. Flower differentiation in *A. nigrum*. Individual peripheral flower primordia (FP) are visible. Spathe (SP) removed. The development of the renewal bulb is visible. B. Progress in flower differentiation in *A. nigrum*. Within the peripheral floral primordia (FP) differentiation occurs centripetally and the flat meristematic surface subdivides into several central cymes. Spathe removed. C. Differentiation of flower parts in older (first-formed) flower primordia of *A. aflatunense*. Younger primordia are not yet differentiated. D. Magnification of individual cluster in the inflorescence of *A. aflatunense*. Floral primordia develop unevenly in a helical order. In older flowers, tepals (t) and anthers (a) are visible. E. Flower differentiation in individual inflorescence cluster of *A. karataviense*. Young flower buds are undifferentiated. F. Fully developed inflorescence of *A. karataviense* at the end of September.

nectaries, which consist of secretory cells situated on the outer ovary walls (Fritsch, 1992). Shapes and positions of the nectaries and their canals differ between taxonomic groups of the genus. At anthesis, nectar secretion begins through a spurlike prolonged part of the ovary or special canal. The nectar accumulates in the gap between the ovary and the bases of the filaments and tepals.

In the bulb onion, anthers shed their pollen at anthesis or 1–2 days later. The delicate style of the protandrous flower reaches full length and becomes receptive (develops a sticky surface to retain pollen) 2–3 days after anthesis, when the flower's own pollen has already been shed (Jones and Rosa, 1928; Jones and Emsweller, 1933; Moll, 1954; Chang and Struckmeyer, 1976; Currah and Ockendon, 1978; Ali *et al.*, 1984; Currah, 1990; De Mason, 1990). Colour of the tepals varies with species, from white or yellow to pink, red, purple and blue (Brewster, 1994; Kamenetsky and Fritsch, Chapter 19, this volume). The number of flowers per umbel varies within and between species and is greatly affected by environment, age and the position within the plant – e.g. a primary inflorescence consists of more flowers than a secondary umbel. In the bulb onion, there are commonly 200–600 flowers per umbel (Currah and Ockendon, 1978; Ali *et al.*, 1984), and similar numbers were reported for leek and Japanese bunching onion. Shallot inflorescences are smaller, while chives, Chinese chives and rakkyo produce between a few and 30–40 flowers per umbel (De Mason, 1990; Brewster, 1994). The ornamental value of the most popular species is based on their multiflowered inflorescences, which include 400–500 flowers (e.g. *A. aflatunense*, *A. giganteum*, *A. karataviense*). However, some ornamental alliums have only a few large flowers per umbel (e.g. *A. insubricum*, *A. moly*, *A. oreophilum*) (Kamenetsky and Fritsch, Chapter 19, this volume).

5.1 Bulb onion

In *A. cepa*, the outer three tepals arise first, each simultaneously with its respective

stamen in its axil. These outer tepals and their associated stamens occur in a clockwise succession, whereas the inner tepals also arise together with their subtended stamens, but in an anticlockwise direction. The carpels develop as three protruding areas within the inner stamens and meet at the heart of the flower to form the trilocular ovary (Jones and Emsweller, 1936; Esau, 1965; De Mason, 1990). Each flower has three nectaries located between the broad bases of the filaments of the inner stamens and the lower ovarian walls. The nectaries open to the surface through a pore (De Mason, 1990).

5.2 Shallot

The floral morphology in shallot is very similar to that of bulb onion, but no clear direction of primordia differentiation in individual shallot flowers has been observed (Krontal *et al.*, 1998; Rabinowitch and Kamenetsky, Chapter 17, this volume).

5.3 Garlic

As in onion and shallot, during the differentiation of flower primordia, each perianth lobe and the subtended stamen arise simultaneously from a single primordium (Kamenetsky and Rabinowitch, 2001).

5.4 Ornamental species (subgenus *Melanocrommyum*)

The outer perianth lobes and stamens of *A. aflatunense* (= *A. hollandicum*), *A. altissimum*, *A. aschersonianum*, *A. karataviense* and *A. nigrum* usually arise first, followed by the differentiation of the inner whorl (Fig. 2.7A–D). The carpels initiate last, when the outer perianth lobes overarch the stamens (Fig. 2.7E, F; Kamenetsky, 1994, 1997; Kamenetsky and Japárova, 1997). When the stigma becomes receptive, the tepals spread widely to expose the accumulated nectar to potential pollinators. Nectar attractiveness depends on its aroma as well as on its fluorescence in the ultraviolet (UV) range,

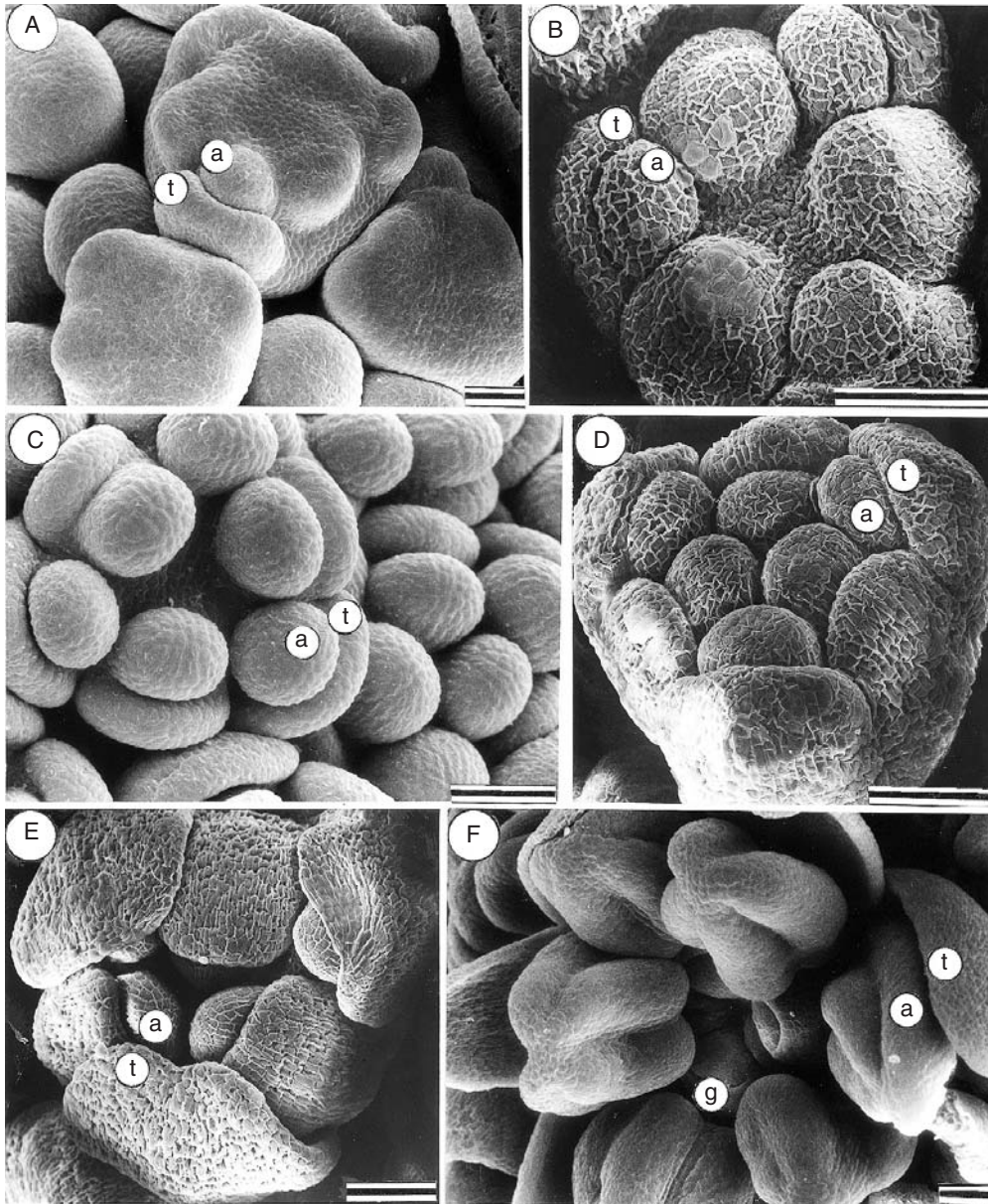


Fig. 2.7. Scanning electron photomicrographs of differentiation of individual flowers in *Allium* spp. Bar = 0.1 mm. A. Initial stages in differentiation of individual flower of *A. aflatunense*. Tepals and their respective anthers form from common primordia. One outer tepal (t) and its respective anther (a) form first, then two adjacent inner tepals with stamens are differentiated. B. Differentiation of individual flower of *A. altissimum*. Outer whorl of three tepals (t) and their related anthers (a) are visible. Three undifferentiated common primordia are formed in the inner whorl. C. Differentiation of flower parts of *A. karataviense*. Tepals (t) and anthers (a) of outer and inner whorls form simultaneously. D. Advanced development of individual flower of *A. karataviense*. Tepals (t) and anthers (a) increase in size. E. Further development of individual flower of *A. karataviense*. Tepals (t) elongate and overarch the anthers (a). F. Final stage in flower differentiation of *A. karataviense*. Gynaecium segments (g) form in the centre of the flower, and the anthers (a) reach their characteristic form.

which is visible to insects (Waller and Martin, 1978), but a high potassium level in the nectar may discourage honey-bees from visiting onion flowers (Waller *et al.*, 1972).

6. Floral Malformations and Topset Formation

Aberrations in floral initiation and differentiation may lead to modifications in inflorescence formation. In many *Allium* species, floral malformations occur as a direct consequence of adverse conditions during floral initiation and differentiation, but sometimes, as in garlic, the major factor is genetic.

Abnormal floral development may negatively affect seed production or, in the case of ornamental species, reduce the decorative value of the plant.

6.1 Bulb onion

High temperatures during storage of bulbs with inflorescence initials or in the field may cause reversion from the floral to the vegetative phase. The more advanced the reproductive bud, the longer the treatment required to cause such a reversion (Heath and Mathur, 1944; Sinnadurai, 1970a). When exposed to high temperatures, flower primordia in bulbs that had been stored at 21–27°C shrunk, withered and turned brown (Woodbury, 1950). After the emergence of the scape, injury to the spathe of the developing inflorescence promotes the development of topsets (Rabinowitch, 1990a), probably because of a significant change in the endogenous hormonal balance. Cytokinin applications can be used to promote higher rates of bulbil formation in umbels from which the flower buds have been trimmed (Thomas, 1972).

Male sterility has been known in the bulb onion since 1925 (Jones and Clarke, 1943; Berninger, 1965). Male sterility in 'Italian Red 13–53' was conditioned by the interaction of a particular form of cytoplasm (S cytoplasm) with a homozygous recessive form (*ms*) of the single nuclear restorer (*Ms*) locus. In plants carrying S cytoplasm, fertil-

ity is restored by a dominant nuclear allele (*Ms*) at this restorer locus. Additional cytoplasmic and genetic mechanisms were described later (Berninger, 1965; Schweisguth, 1973). The latter, however, were hardly used in hybrid seed production (Dowker, 1990; Rabinowitch, 1990a; Havey, 1995, 2000; Havey, Chapter 3, and Eady, Chapter 6, this volume).

6.2 Shallot

Malformed flowers and topsets have been observed in tropical shallots grown from seeds under high temperatures of 26/18°C, day/night, respectively (Rabinowitch and Kamenetsky, Chapter 17, this volume). Storage of bulbs at 30°C caused a delay in the emergence of scapes as compared with plants from low and intermediate storage temperatures, but did not induce floral malformations (Krontal *et al.*, 2000). Male sterility is common in shallots grown in Israel and elsewhere (H.D. Rabinowitch, personal observation). Male-sterile shallots are readily fertilized by pollen from shallot and/or bulb onion to form viable seeds. The inherited characteristics of shallot enable male-sterile plants to be easily maintained and multiplied by vegetative propagation. To the best of our knowledge, no information is available on the heredity of male sterility in shallot; however, we can speculate that it will be much the same as that of bulb onion.

6.3 Garlic

Gustafsson (1946/47, cited by Etoh, 1985) assigned garlic and some other *Allium* species (*A. caeruleum*, *A. carinatum*, *A. proliferum*, *A. scorodoprasum*, *A. vineale*) to the group of viviparous plants, in which topsets (bubils) develop instead of flowers or intermingle with flowers in the inflorescence. Topsets differentiate in between the flower initials, at the base of the inflorescence (Fig. 2.4E, F; Kamenetsky and Rabinowitch, 2001). As a result of the strong competition with the developing topsets, the garlic flowers wither and die.

Flowers in the Japanese garlic cv. 'Shanghai-wase' exhibited floral malformations and abnormal development of the embryo sacs, possibly because of an unfavourable environment during floral differentiation (Etoh, 1985), but perhaps more probably due to the numerous generations of selection by humans for larger bulbs and cloves and against flowering.

6.4 Chives, Japanese bunching onion and leek

For a detailed review on these crops, see Havey, Chapter 3, this volume. In chives, male sterility is conditioned by genic male sterility (GMS), which is controlled by a single nuclear gene *wi*, with recessive inheritance (Engelke and Tatlioglu, 2000a). An alternative cytoplasmic male sterility (CMS) depends on the interaction between the cytoplasm (S) and a single nuclear fertility-restoration locus (X) (Tatlioglu, 1982). There is a high degree of variability of the mitochondrial genome in chives (Engelke and Tatlioglu, 2000b) and consequently two CMS systems were described (Engelke and Tatlioglu, 2000c). Fertility of some male-sterile plants, however, can be regained under favourable environmental conditions. Hence, exposure to a constant temperature of 24°C resulted in production of viable pollen (Tatlioglu, 1985). This temperature sensitivity is controlled by a single dominant allele (*T*) (Tatlioglu, 1987). A third gene, *a*, restores fertility in combination with tetracycline treatment (Tatlioglu and Wricke, 1988).

In Japanese bunching onion, male sterility is controlled by the interaction of a cytoplasmic factor (S) with two nuclear genes: *ms₁* and *ms₂* (Moue and Uehara, 1985).

In leek, a genic male-sterility system has been described (Schweisguth, 1970; De Clercq and Van Bockstaele, Chapter 18, this volume) and naturally occurring male-sterile plants reproduced clonally now provide the basis for hybrid leek production (Smith, 1994; Smith and Crowther, 1995). The appearance of male-sterile leek flowers is described by De Clercq and Van Bockstaele (Chapter 18, this volume), who also illus-

trate how removing or wounding young flower buds can induce topset formation in the leek umbel (see Fig. 18.3a, b).

6.5 Ornamental species (subgenus *Melanocrommyum*)

These plants develop topsets in response to adverse storage conditions. High temperatures at the time of differentiation promoted floral malformations in *A. aflatunense* (= *A. hollandicum*) (Fig. 2.8A–D; Colour Plate 1A–C) (H. Zemah, Israel, 2000, personal communication).

Preplanting exposure of *A. aschersonianum*, from the Mediterranean semi-desert, to relatively low temperatures of 9–13°C during floral initiation and differentiation, affected apical meristem division and led to the formation of two or three short scapes with small and partly malformed flowers (Z. Gilad, Israel, 2000, personal communication). However, exposure of the bulbs of *A. aschersonianum* to 48–50°C for 4–6 h in September–October, during within-bulb flower differentiation, resulted in a small number of flowers in the inflorescence, with the simultaneous formation of topsets and/or lateral bulbs (Kamenetsky *et al.*, 2000; E. Hovav, Israel, 2000, personal communication).

7. Maturation and Growth of Floral Parts and Floral Stalk Elongation

Interactions between storage and growth temperatures play the most important role in normal scape elongation and flowering of *Allium* species, although light conditions can markedly affect this process.

As with leaf-blade structure, there is a great variation in the morphological structure of the inflorescence axis (also named the floral stem, scape or stalk) among *Allium* species (Jones and Mann, 1963; Vvedensky, 1968). In all cases, the stalk represents a single internode, elongating out of the innermost ensheathing leaf base. In the bulb onion, the scape is hollow and its anatomy reveals more similarity to that of onion leaves than to that of the vegetative stem.

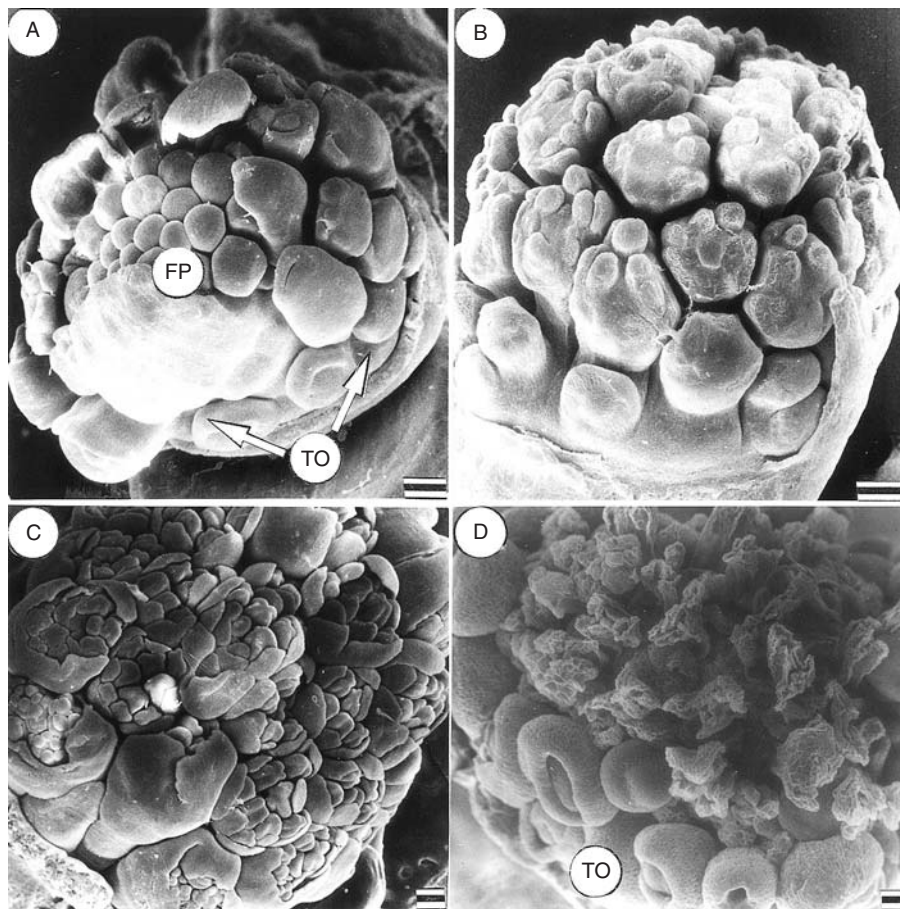


Fig. 2.8. Scanning electron photomicrographs of floral malformations in *A. aflatunense*. Bar = 0.1 mm. A. Leaf-like bracts are formed in the centre of the reproductive meristem. Topsets (TO) are formed in the periphery of the inflorescence. FP, flower primordia. B. Irregular development of individual flowers leads to flower abortion. C. Development of numerous anthers and tepals. D. Topset (TO) formation in the periphery of the inflorescence.

The epidermis is heavily cutinized and contains stomata, and the mesophyll has palisade cells on the outside and spongy cells on the inside (De Mason, 1990). In most of the *Melanocrommyum* species used as ornamentals, as well as in garlic, leek and chives, the scape is round and solid (Jones and Mann, 1963; De Mason, 1990; Fritsch, 1993). Others (e.g. *A. neapolitanum*, *A. triquetrum*) produce solid triangular scapes, whereas *A. fistulosum*, *A. proliferum* and species from the section *Cepa* produce cylindrical fistulose scapes (Jones and Mann, 1963; R. Kamenetsky, personal observa-

tions). The distribution of several anatomical characters of floral scapes broadly corresponds to taxonomic relationships within the genus *Allium* (Fritsch, 1993).

7.1 Bulb onion and shallot

Cool temperatures of around 17°C (Thompson and Smith, 1938; Holdsworth and Heath, 1950) or 10–16°C in the greenhouse enhanced scape elongation in onion (Woodbury, 1950) and shallot (Krontal *et al.*, 2000), while high temperatures of 25–30°C

suppressed the emergence of inflorescences already initiated (Heath, 1943a, b; Heath and Mathur, 1944; Holdsworth and Heath, 1950; Rabinowitch, 1985, 1990a; Krontal *et al.*, 2000).

In tropical shallots grown at high temperatures (29/21°C, day/night), normal bloom was evident only in plants from bulbs stored at 5°C, while those from bulbs stored at 10, 20 and 30°C had shrivelled scapes. When grown at 17/9°C, the first to bloom were plants from bulbs stored at 10°C, followed by those stored at 5, 20 and 30°C (Krontal *et al.*, 2000; Rabinowitch and Kamenetsky, Chapter 17, this volume).

7.2 Garlic

Storage at low temperatures (from -2 to 9°C) and growth at mild temperatures (from 17 to 23°C during the day and from 9 to 15°C at night) promote early scape emergence and elongation. In bolting types, day length in the field plays a dominant role in the promotion of scape elongation (Takagi, 1990; Kamenetsky and Rabinowitch, 2001).

7.3 Ornamental species (subgenus *Allium*)

During growth and development, *A. ampeloprasum* (a domesticated long-scape cut flower, selected from plants growing wild in Israel) and *A. sphaerocephalon* require intermediate temperatures (17–20°C) and long days for normal scape elongation and flowering (Berghoef and Zevenbergen, 1992; De Hertogh and Zimmer, 1993; Maeda *et al.*, 1994). Under high growth temperatures and short days, the plants remain vegetative and do not bloom (*A. sphaerocephalon*) (Berghoef and Zevenbergen, 1992). Storage temperatures affect floral initiation and flowering percentage but do not influence scape emergence and bloom. Autumn storage at 2, 5 or 9°C reduced the percentage of flowering plants and resulted in inferior flower quality (*A. caeruleum*) (van Leeuwen and van der Weijden, 1994).

7.4 Ornamental species (subgenus *Amerallium*)

Storage temperatures of 9–17°C, followed by mild temperatures of 10–20°C during growth, enhance stem elongation. Storage at lower temperatures (2–5°C) or growth at temperatures higher than 20°C accelerated flowering but also resulted in a low percentage of flowering plants and short scapes (Maeda *et al.*, 1994; van Leeuwen and van der Weijden, 1994; Kodaira *et al.*, 1996).

7.5 Ornamental species (subgenus *Melanocrommyum*)

As in other geophytes from the Irano-Turanian region (e.g. tulip), *Allium* species require a long cold exposure for stem elongation, normal flowering and initiation of the renewal bud(s). Moderate growth temperatures (17–23°C during the day and 9–15°C at night) also promote scape elongation (Dossier, 1980; Zimmer and Renken, 1984; De Hertogh and Zimmer, 1993; Zemah *et al.*, 1999, 2001). However, day length has no effect on scape elongation in *A. aflatunense* (= *A. hollandicum*) (Zemah *et al.*, 2001).

A few exceptions are the *Melanocrommyum* species from the Mediterranean basin, such as *A. rothii*, *A. aschersonianum* and *A. nigrum*, which flower without post-differentiation cold treatment, possibly due to adaptation to local climatic conditions.

8. Concluding Remarks

In most plants, flowering plays an essential role in the perpetuation of the species, including the majority of the *Allium* spp. This is particularly evident in ornamentals, where flowers are the final product, but it is also true in edible crops. Understanding of the flowering processes, including the developmental biology, physiology and genetics of the reproductive organs, improves our knowledge of one of the most important processes in nature. The added value from studies of this topic results from

increased efficiency in forcing, blooming and shelf-life of ornamental species, in induction of flowering for breeding and seed production and/or the prevention of undesired bolting in all crops. However, regardless of numerous works on the flowering of geophytes (for reviews, see Hartsema, 1961; Halevy, 1985, 1990; Rabinowitch, 1985, 1990a; Rees, 1992; Le Nard and De Hertogh, 1993), we know little of the basic chain of processes which, if successful, ends in normal flowering.

For ornamentals and edible species, florogenesis studies focus on two major objectives: (i) timing of flowering; and (ii) prevention of flowering. When put into practice, manipulation of earliness and lateness allows for year-round production, while the prevention of flowering (including flower bud/scape abortion) facilitates vegetative propagation and bulb production, which may be essential for clonal production.

A gene coding for flowering in *Arabidopsis* has recently been identified (Samech *et al.*, 2000). This discovery may stimulate similar studies in other plant species and in alliums. However, little is known about the endogenous changes during flower induction and initiation, including hormonal balance and hormone functions, from dormancy release to anthesis, as well as gene and protein expression (genomics and proteomics). Molecular markers for the various developmental phases are urgently needed (Le Nard and De Hertogh, 2000).

The role of physiological age and that of the size of critical mass in relation to flowering are of paramount importance for the ornamental industry and for seed production. The wide range of critical sizes found in *Allium* species (Brewster, 1994; Kamenetsky *et al.*, 2000) indicates that, while energy balance may provide one explanation for the plant's state of readiness for floral induction, it may not be the only one. Better understanding of the role of juvenile phase/plant age in flowering should eventually enable us to shorten breeding cycles and reduce production costs.

Apomixis has been demonstrated in *A. odorum* (= *A. ramosum*) (Modilewski, 1930; Hakanson and Levan, 1957) and in *A.*

tuberosum (Kojima and Kawaguchi, 1989; Kojima *et al.*, 1991; Bohanec, Chapter 7, this volume). The trait is of high value for clonal propagation of new selections, especially of ornamentals with low rates of vegetative propagation, as well as for maintaining male-sterile lines. On the other hand, it greatly interferes with genetic studies and breeding. Hence, intimate knowledge of the apomixis mechanism and the means of switching it on and off will have a great importance in the future. Likewise, the production of topsets is common in alliaceous crops, such as garlic and great-headed garlic (Jones and Mann, 1963), and occurs infrequently in other alliums, such as bulb onion and leek. Better understanding of the control mechanism leading to the conversion of the umbel from generative to vegetative and vice versa could serve similar ends, though the generative process is to be preferred, due to the biotic cleansing that is associated with the production of true seed.

Male sterility is important for hybrid seed production and for extended vase-life of ornamentals. Identification of male-sterile genotypes in many other alliums could be of high importance to both industries (seed production and floriculture). The understanding of genetic make-up or the introgression of simply controlled mechanisms encoding for male sterility could improve our capabilities in breeding, production and product handling. Hence, cytoplasmic male sterility, if introduced in ornamentals, could facilitate the production of hybrids with sterile flowers and long flower life.

In *Allium* spp., the genetics of most important flowering traits is unknown. With regard to flowering, male sterility (*Ms*, *T*) (for details see Havey, Chapter 3, this volume) and *dw* are the only known genes in bulb onion (Rabinowitch *et al.*, 1984; Horobin, 1986; Friedlander, 1988). There is no information on genetic regulation of umbel size, flower colour, length of bloom and odour, just to name a few traits, in any *Allium* spp., nor do we have any knowledge of the genetic control of the five stages of flower development or of the genetic \times environment interactions.

Undoubtedly, of the biological sciences, genetics is emerging as the leading discipline in the 21st century. It is expected that, with the new molecular (Havey, Chapter 3, and Kik, Chapter 4, this volume) and physiological (Kik, Chapter 4, and Bohanec, Chapter 7,

this volume) tools, breakthroughs in the genetics of *Allium* spp. will enable the crossing of species barriers, the managing of economically important traits and the improvement of our capabilities in controlling blooming in alliums and other plant species.

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