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Edited by
IAN WARRINGTON

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edited by
Ian Warrington

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Contents

Contributors	ix
Dedication: Guglielmo Costa	xiii
<i>A. Ross Ferguson</i>	
1. Recent Advances in Sexual Propagation and Breeding of Garlic	1
<i>Einat Shemesh-Mayer and Rina Kamenetsky Goldstein</i>	
I. Introduction	2
II. Horticultural Diversity and Genetic Resources	3
III. Life Cycle and the Flowering Process	6
IV. Fertility Barriers	16
V. Unlocking Variability by Sexual Reproduction	24
VI. Concluding Remarks	29
Literature Cited	29
2. Control of Fruit Tree Vigor Induced by Dwarfing Rootstocks	39
<i>Boris Basile and Theodore M. DeJong</i>	
I. Introduction	40
II. Biological Complexity of Grafted Fruit Trees and Rootstock–Scion Interactions	42
III. Physiology of the Dwarfism Induced by Rootstocks in Fruit Trees	52
IV. Conclusions	81
Literature Cited	83
3. Turmeric: Botany and Production Practices	99
<i>D. Prasath, K. Kandiannan, N.K. Leela, S. Aarthi, B. Sasikumar, and K. Nirmal Babu</i>	
I. Introduction	102
II. Botany	104

III. Biochemistry	110
IV. Plant Genetic Resources and Breeding	116
V. Biotechnology	122
VI. Horticultural Management	133
VII. Postharvest Processing	154
VIII. Future Prospects	156
Literature Cited	157
4. Fruit Thinning: Advances and Trends	185
<i>Guglielmo Costa, Alessandro Botton, and Giannina Vizzotto</i>	
I. Introduction	186
II. Thinning	191
III. Abscission Physiology	206
IV. Future Perspectives	212
Literature Cited	217
5. Eastern Hemlock (<i>Tsuga canadensis</i> (L.) Carrière): Perspectives from its Northwestern Range Limit	227
<i>Emily K. Ellingson, Stan C. Hokanson, and James M. Bradeen</i>	
I. Introduction and History	228
II. Ecology	232
III. Horticulture	239
IV. Conservation	243
V. Conclusion	246
Literature Cited	247
6. Apple Crop Load Management with Special Focus on Early Thinning Strategies: A US Perspective	255
<i>Thomas M. Kon and James R. Schupp</i>	
I. Introduction	256
II. Pruning to Reduce Crop Load	259
III. Blossom Thinners	263

IV. Integrated Crop Load Management Strategies	285
V. Conclusion	286
Acknowledgments	288
Literature Cited	289
7. Grow Us Our Daily Bread: A Review of Breadfruit Cultivation in Traditional and Contemporary Systems	299
<i>Noa Kekuewa Lincoln, Diane Ragone, Nyree J.C. Zerega, Laura B. Roberts-Nkrumah, Mark Merlin, and A. Maxwell P. Jones</i>	
I. Introduction	301
II. Botanical Classification	303
III. Origins	306
IV. Pacific Distribution	309
V. Archeological Evidence of Breadfruit	310
VI. Traditional Cultivation	311
VII. Traditional Uses	317
VIII. Historical Movement	320
IX. Climate, Range, and Ecology	323
X. Physiology	325
XI. Morphology	326
XII. Reproductive Biology	328
XIII. Growth and Development	330
XIV. Agronomy	336
XV. Diseases	351
XVI. Pests	360
XVII. Conclusions and Future Research Needs	363
Literature Cited	366
8. Kiwifruit Biology: The Commercial Implications of Fruit Maturation	385
<i>Jeremy N. Burdon</i>	
I. Introduction	386
II. Kiwifruit in Global Trade	387
III. Harvest Indices	389

IV. Fruit Development	391
V. Physical and Compositional Changes During Maturation	394
VI. What are we Missing About Fruit Maturation?	403
VII. Postharvest Performance	405
VIII. Commercial Implications of Understanding Maturation	410
IX. Concluding Comments	413
Acknowledgments	415
Literature Cited	415
Subject Index	423
Cumulative Subject Index	427
Cumulative Contributor Index	465

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Guglielmo Costa

Dedication: Guglielmo Costa

This volume of *Horticultural Reviews* is dedicated to Professor Guglielmo Costa in recognition of his contributions to horticulture and horticultural research both in Italy and throughout the world.

Professor Costa was born in Bologna, Italy. Most of his professional life was undertaken at Alma Mater Studiorum, University of Bologna. His wife, Roberta, also comes from Bologna, where they raised their three children. He has now retired to remain there. Professor Costa is therefore a true citizen of Bologna, and he is immensely proud of his home city. However, he is not parochial and has professional contacts and friends throughout the world, where he is universally known as Mimmo.

Professor Costa graduated (Laurea) in Agriculture (Crop Science) from the University of Bologna in 1969 with marks of 110/110 cum laude, an outstanding result equivalent to 1st Class Honors. In 1971, he was appointed Assistant Professor in Fruit Science, University of Bologna; was promoted to Associate Professor in 1983; and then became Full Professor (Professore Ordinario) of Fruit Science at the University of Udine, Italy, in 1986. At Udine, he soon became a charismatic team leader and served as Head of Department and Director of the Experimental Agricultural Farm. He transferred back to the University of Bologna as Full Professor of Fruit Science in 1997 and retired, 18 years later, at the end of 2015. At Bologna, he did much to maintain and enhance that university's reputation as an Italian center of excellence in horticultural research and teaching. He was also active in promoting international cooperation in education. The most outstanding example of this involvement is the International Masterate in Horticulture (IMaHS – International Master Course in Horticultural Science), an Erasmus Mundus European Union project now involving eight universities in five European countries. Getting cooperation and agreement between so many institutions of differing academic traditions and practices must have been a real challenge.

Professor Costa may have what, at first sight, appear to be extraordinarily diverse research interests with a prodigious output of scientific papers: more than 90 in peer-reviewed international journals, several hundred technical publications, and a large number of conference presentations and related proceedings. His publications include about 90 papers in at least 40 different volumes of *Acta Horticulturae* – a record most unlikely to be matched by any other member of the International Society for Horticultural Science (ISHS). While doing this, he maintained a heavy teaching load involving both undergraduate and post-graduate teaching. He was thesis supervisor of 61 graduate students and 18 PhD students.

In his research, there have been two common underlying themes: practical pomology and a determination to be of real assistance to fruit growers and the fruit-growing industries of the Emilia-Romagna Region and Italy as a whole. He has therefore developed strong connections with all parts of the fruit industry, including nurseries, growers, pack-houses, and companies supplying the requirements of the industry such as chemicals or equipment. He certainly believes in the importance of listening to good growers: this, he considers, can lead to solutions previously not even imagined. He has tried to address fundamental pomological questions with the goal of increasing production and management efficiency. This has required cooperation with many other workers, both students and established scientists within his own departments at Bologna and Udine, elsewhere in Italy, and internationally. He has been able to create strong and very active research groups, by motivating colleagues and young scientists to share work, experience, and knowledge. To this day, he has retained a lively, enquiring mind; he has never stopped being curious. He stimulated his coworkers to look “outside the window” by participating in international meetings, and by joining international and national research projects. He encouraged his students to work in other laboratories or in other countries. He himself spent several extended periods of leave at the Pomology Department, University of California, Davis, USA.

Professor Costa began his research career with investigations on agronomic, genetic, and chemical methods to control vegetative growth in apples, peaches, and pears. He was particularly interested in the use of plant growth regulators as growth retardants, thinning agents, and promoters of fruit set and shape, or to control fireblight in apples and pears. It is this use of plant growth regulators in fruit crop management that is probably the area of research for which he is best known in Italy as well as overseas. He was different to many of his contemporaries in that he would approach a problem directly but also would think

laterally, trying to understand the processes underlying the tree's responses to the treatments that were being applied. He has long been involved with the European Fruit Research Institutes Network (EUFRIN) Working Group on Fruit Thinning and has led the group since 1994. In that role, he has placed great emphasis on the importance of good links with chemical companies involved in the production of chemical thinning compounds. He was also interested in the efficacy of growth regulators and growth substances acting as ethylene inhibitors and, therefore, affecting the maturation and ripening of fruit while still on the plant. This work with growth regulators led to a study of the involvement of phenolics in resistance to diseases such as fireblight.

Another major interest has been in the nondestructive assessment and prediction of fruit quality, particularly by use of near-infrared spectroscopy (NIRS) and E-nose. NIRS has been used for the determination of internal quality parameters of major fruit species such as apples, peaches, pears, and kiwifruit, as well as for the determination of innovative harvesting indices for grouping homogeneous classes of fruits on the basis of their stage of ripening. The result of the research in this field was the development of devices, such as the DA-meter, patented by the University of Bologna and now widely used in the industry. The quantities of antioxidants in different fruit species and cultivars have also been measured.

I first met Professor Costa in 1987 at the 1st International Symposium on Kiwifruit in Padova. He initially became involved in kiwifruit science and management soon after kiwifruit cultivation started in Italy, and he is now widely considered as one of the fathers of the development of kiwifruit as a commercial crop in that country. He was active in promoting its diffusion via dozens of talks to growers and by attending kiwifruit seminars, symposia, and technical workshops throughout the whole country, always with technical contributions on the significance for growers of innovative research. In collaboration with others, he studied such aspects as vegetative propagation, planting and training systems, bud dormancy, fertilization, irrigation, pollination, nondestructive methods of maturity forecasting, postharvest physiology and storage, and breeding, as shown by the recent selection of a yellow-fleshed, early-maturing, kiwifruit cultivar, 'AC1536', marketed as Dori™. Over the past few years, he became active in studying the devastating new disease, bacterial canker of kiwifruit (Psa), caused by *Pseudomonas syringae* pv. *actinidiae*.

Professor Costa has been a strong proponent of cooperation worldwide in horticultural research. He has been extraordinarily active in promoting, attending, or organizing seminars and workshops, national

and international meetings, and symposia, many of which have resulted in publications in *Acta Horticulturae*. He has edited or coedited several volumes of *Acta Horticulturae* and has served a term as Chair of the ISHS Pome and Stone Fruit Section. He has also undertaken the very demanding role of organizing national and international meetings. In successive years, 2009 and 2010, he accepted the daunting task of organizing two separate ISHS symposia, seeking financial support, coordinating all activities at the symposia, and editing or coediting the consequent volumes of *Acta Horticulturae*. Each symposium – the 11th International Symposium on Plant Bioregulators in Fruit Production, held in Bologna in 2009, and the 7th International Kiwifruit Symposium, in Faenza in 2010 – required an enormous amount of work. To organize two such ISHS symposia in successive years requires an extraordinary commitment. Recently, he was elected a Fellow of the ISHS, recognition by his peers of his dedication to horticulture and horticultural research throughout the world and of his commitment to the activities of ISHS.

I have known Mimmo for nearly 30 years. I have always enjoyed meeting him, particularly, of course, in his hometown of Bologna. I have appreciated his warm friendship and his generous hospitality, and I have always been impressed by his apparently inexhaustible energy and his seeming ability to multitask successfully. I am honored to write this dedication.

A. ROSS FERGUSON

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Recent Advances in Sexual Propagation and Breeding of Garlic

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ABSTRACT

The restoration of flowering ability, sexual hybridization, and seed production in garlic (*Allium sativum* L.) has resulted in an increase in genetic variability available to agriculture and has opened new avenues for the breeding of this important crop. In this review, the current status of flower development, fertility, hybridization, sexual propagation, and seed production in garlic is discussed. We summarize the main stages in the life cycle of garlic from true seeds to flowering and bulb formation, and recent advances in our understanding of floro- and gametogenesis. Flowering and fertility of garlic are tightly regulated by environmental conditions, and therefore the seed production cycles in various climatic zones are complex and challenging. Recent establishment of modern molecular tools and the creation of large transcriptome catalogs provide a better understanding of the molecular and genetic mechanisms of flowering and fertility processes, and accelerate the breeding process by using molecular markers for desirable traits.

KEYWORDS: *Allium sativum*, environmental regulation, fertility, genetic regulation, hybridization, male sterility, seed production

I. INTRODUCTION

II. HORTICULTURAL DIVERSITY AND GENETIC RESOURCES

III. LIFE CYCLE AND THE FLOWERING PROCESS

A. Seed and Seedling Development

B. Annual Life Cycle and Florogenesis

C. Environmental and Genetic Control of Flowering

IV. FERTILITY BARRIERS

A. Morphology and Anatomy of the Individual Flower

1. The Male Gametophyte
2. The Female Gametophyte

B. Environmental and Genetic Control of Male Sterility

V. UNLOCKING VARIABILITY BY SEXUAL REPRODUCTION

A. Morphological Variability in Seedling Populations

B. Environmental Regulation of Seedling Development

C. Molecular Markers in Variable Garlic Populations

VI. CONCLUDING REMARKS

LITERATURE CITED

I. INTRODUCTION

Garlic (*Allium sativum* L.) is one of the most popular vegetable crops, being cultivated in different continents for flavor, nutrition, and medicinal purposes. The wild ancestor of cultivated garlic probably originated in Central Asia, and was gathered by seminomadic tribes about 10 000 years ago. Later, traders introduced plants to the Mediterranean Basin, India, and China, and from there garlic spread across various regions of the world (Engeland 1991; Etoh and Simon 2002). Widespread geographical distribution of cultivated garlic resulted in its adaptation to different climatic conditions and in the development of many local types and varieties with specific morphological and physiological traits.

Taxonomically, *A. sativum* belongs to the section *Allium* of the genus *Allium*. Among 114 species in this section, about 25 are closely related to the cultivated plant, such as *A. tuncelianum* (Kollman) Özhatay, Mathew, Şiraneci from Turkey and *A. moschatum* L. from the Caucasus (Mathew 1996). *A. sativum* is not found in native populations, but most garlic relatives grow wild in regions characterized by relatively cold winters and hot and dry summers, have garlic-like taste and smell, and are used by local populations as food and nutraceuticals.

Similar to many wild *Allium* species, the ancestors of garlic from Central Asia probably produced flowers, seeds, and relatively small bulbs. However, since the development and growth of flowering scapes consume energy at the expense of storage organs, it is likely that human selection for early maturation of large garlic bulbs deprived the developing scapes of nutritional supplies. Cultivated garlic has lost its flowering potential and fertility, and today commercial production is based exclusively on vegetative propagation (Etoh 1985; Etoh and Simon 2002). Consequently, garlic breeding has been limited to selection from established genetic variation, and breeding was attempted only via mutation and *in vitro* techniques (Takagi 1990). In recent years, flowering ability

was restored in several garlic genotypes, and an increase in garlic variability was achieved via sexual hybridization and seed production (Etoh 1983b; Etoh et al. 1988; Pooler and Simon 1994; Inaba et al. 1995; Jenderek 1998, 2004; Jenderek and Hannan 2000; Jenderek and Zewdie 2005; Kamenetsky et al. 2005; Kamenetsky 2007).

Fertility restoration and seed production have opened a new stage of genetic research into garlic. Similar to many other perennial monocots, *Allium* species possess a large genome size (7–32 Gb) (Ricroch et al. 2005). Despite its domestication, garlic has maintained its ploidy level ($2n=2x=16$), and the diploid garlic nuclear genome is estimated at 15.9 Gbp, 32 times larger than the genome of rice (Arumuganathan and Earle 1991; Fritsch and Friesen 2002; Kik 2002). Therefore, full sequencing of the garlic genome is still a challenging task, but transcriptome assembly using next-generation sequencing (NGS) might be efficiently employed for the generation of functional genomic data. At the same time, an enormous amount of genetic and molecular data, collected in model plants over recent decades, can be translated to commercial crops by using various experimental tools such as candidate genes, library screening, expressed sequenced tags (ESTs), and genomic, transcriptomic, proteomic, and metabolomic databases (Leeggangers et al. 2013).

New genetic variability obtained by sexual hybridization, in combination with research results, has provided solid ground for a new phase in garlic breeding (Pooler and Simon, 1994; Jenderek and Hannan 2004; Kamenetsky et al. 2004a, 2015; Jenderek and Zewdie 2005; Shemesh et al. 2008; Shemesh-Mayer et al. 2015a). Generation of garlic S1 families provided the first source of variability for genetic studies for breeding purposes (Hong and Etoh 1996; Jenderek 2004; Jenderek and Zewdie 2005). In Israel, a breeding program was established 10 years ago and is currently focused on sexual hybridization and selection of superior garlic plants, the introduction of new useful traits that are uncommon in commercial clones, and the development of new cultivars for different climatic zones. In this review, the current status of sexual propagation, hybridization, and seed production in garlic is discussed.

II. HORTICULTURAL DIVERSITY AND GENETIC RESOURCES

During a long cultivation history, garlic plants were grown in diverse climatic and biogeographic regions. They exhibit wide variations in bulb size, shape and color, number and size of cloves, peeling ability, maturity date, flavor and pungency, bolting capacity, and numbers and sizes of topsets and flowers in the inflorescence (Figure 1.1) (McCollum

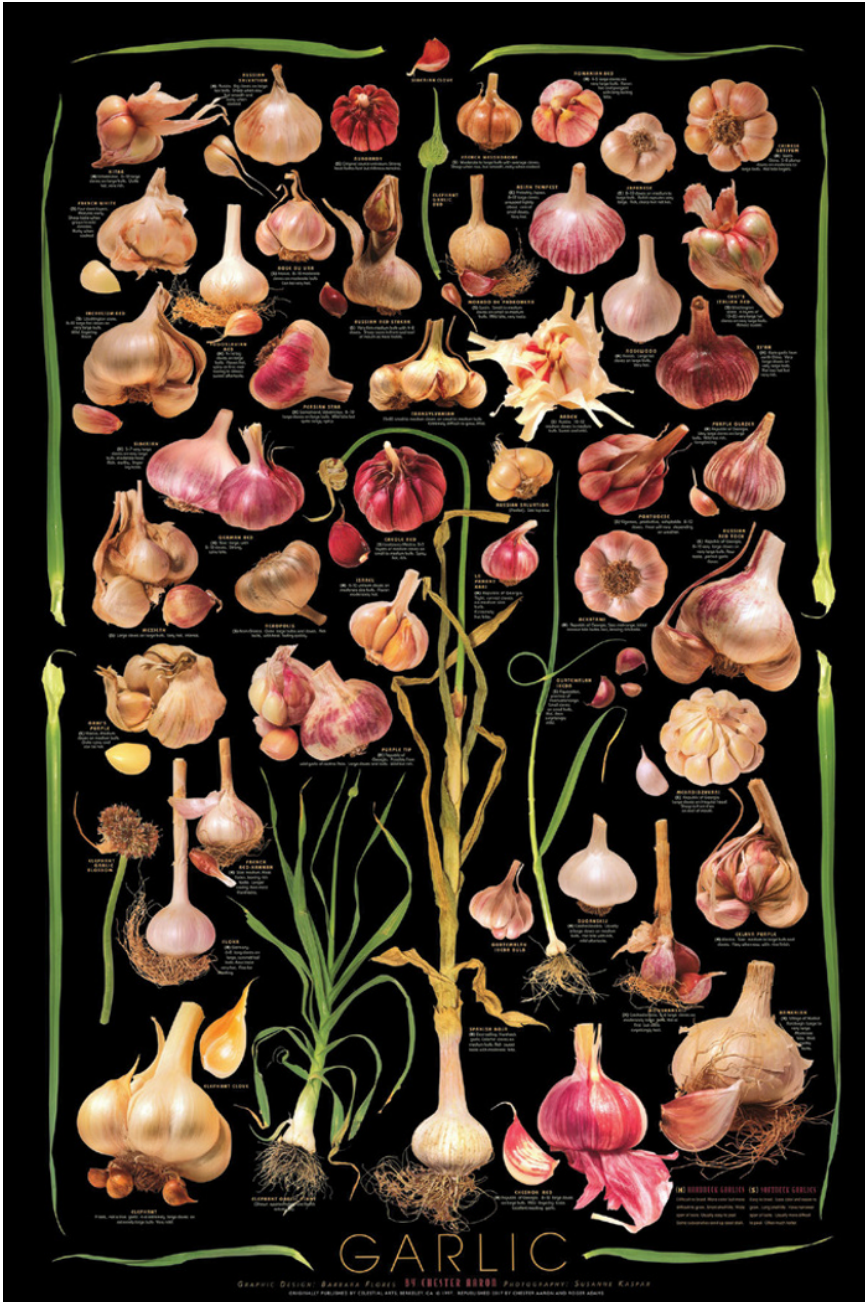


Figure 1.1 Morphological variation in garlic cultivars, propagated vegetatively in various climatic areas (*Source: C. Aaron and R. Adams, poster, 2017, with permission.*)

1976; Astley et al. 1982; Astley 1990; Hong and Etoh 1996; Lallemand et al. 1997; IPGRI, ECP/GR, AVRDC 2001; Kamenetsky et al. 2005; Meredith 2008). A strong interaction between genotype and environment has led to a variety of phenotypic expressions (Lallemand et al. 1997; Portela 2001; Kamenetsky et al. 2004b; Meredith 2008).

Depending on the ability to develop a flower stem, garlic producers distinguish between softneck and hardneck varieties (Engeland 1991; Meredith 2008). However, from a physiological point of view, the terminology *bolters* and *nonbolters* is more accurate. Depending on the traits of scape elongation and inflorescence development, garlic varieties were classified by Takagi (1990) as: (i) *nonbolters*, which normally do not form a flower stalk or produce cloves inside an incomplete scape; (ii) *incomplete bolters*, which produce a thin, short flower stalk, bear only a few large topsets, and usually form no flowers; and (iii) *complete bolters*, which produce a long, thick flower stalk, with many topsets and flowers. It was observed that these traits might be altered by different environmental conditions, but the mechanisms of their regulation are still unknown.

Based on morphological and physiological phenotype, worldwide garlic cultivars were classified into several horticultural groups, reflecting the broad diversity of the crop. The group named Purple Stripe, which includes bolting hardneck cultivars, is considered to be genetically closest to the origin of garlic. The other groups include the Artichoke, Asiatic, Creole, Glazed Purple Stripe, Marbled Purple Stripe, Middle Eastern, Porcelain, Rocambole, Silverskin, and Turban types (Meredith 2008). These groups vary in bolting ability and bulb structure. Moreover, plant performance is affected by environment, and therefore phenotypes of the same variety change dramatically under different climatic conditions. Amplified fragment-length polymorphism (AFLP) analysis of 211 genotypes indicated duplications of 41–64% of the garlic accessions in the National Plant Germplasm System (NPGS) and commercial collections in the USA (Volk et al. 2004). Therefore, accurate discrimination between different cultivars and groups requires further application of modern molecular tools (Meredith 2008; Volk and Stern 2009; Kamenetsky et al. 2015).

Central Asia, the center of origin for many *Allium* species, is a valuable source of garlic diversity (Hanelt 1990; Simon 2005). In the early 1980s, Japanese expeditions to Central Asia collected a number of garlic accessions in Uzbekistan, Tajikistan, Kirgizstan, and Kazakhstan (Etoh et al. 1988). Later, fertile garlic plants were also found in Armenia, Georgia, and Xinjiang. The garlic plants collected in these regions were grown at Kagoshima, Japan, and, following topset excision, some clones developed fertile flowers and viable seeds with germination up to 40%

(Etoh 1983b, 1986; Etoh et al. 1988, 1991). Pooler and Simon (1994) improved floral production and seed set, but seed germination still remained low and ranged between 10 and 12%. Screening of several garlic collections identified larger variability of highly fertile clones, producing over 400 seeds per umbel, with seed germination of 67–93% (Etoh 1986, 1997; Inaba et al. 1995; Hong and Etoh 1996; Jenderek 1998; Jenderek and Hannan 2000, 2004). In 1995–2001, international collecting missions to Central Asia gathered over 300 garlic landraces and plants from natural populations (Baitulin et al. 2000; Kamenetsky et al. 2004b). The collected material was evaluated in Israel, and 30 accessions showed high ability for flowering and seed production, with germination rates around 90%, and normal seedling development (Kamenetsky et al. 2005). These collections laid the groundwork for large scientific projects and the initiation of garlic hybridization and breeding programs in Israel and other locations.

III. LIFE CYCLE AND THE FLOWERING PROCESS

A. Seed and Seedling Development

The seed shape, color, and seedling morphology of garlic are typical of the subgenus *Allium* (De Mason 1990; Druselmann 1992; Kruse 1992; Shemesh et al. 2008). The weight of 1000 fresh garlic seeds reaches 1.5–2g, approximately half the weight of bulb onion and leek seeds. The germination process can take several weeks to several months (Etoh and Simon 2002; Shemesh et al. 2008). Scarification, stratification, and chilling promote germination, while phytohormone treatments have only little effect (Etoh and Simon 2002). The germination rate ranged between 20–40% (Etoh 1983b; Etoh et al. 1988; Shemesh et al. 2008) and 90% of viable seeds (Kamenetsky et al. 2004b). The germination of garlic seeds begins with the appearance of a loop-shaped cotyledon, followed by the initiation of new leaves, and elongation and production of a cylindrical stem-like structure termed the “false” stem (Shemesh et al. 2008). Limitations to seedling development include weak performance, abnormal morphology, low survivability, and dying at the stage of 2–3 leaves (Etoh 1983b; Pooler and Simon 1994).

B. Annual Life Cycle and Florogenesis

The mature bulb of an adult garlic plant is a cluster of lateral cloves, which arise in the axils of foliage leaves (Mann 1952; De Mason 1990; Messiaen et al. 1993). At the end of the growth period, the aboveground

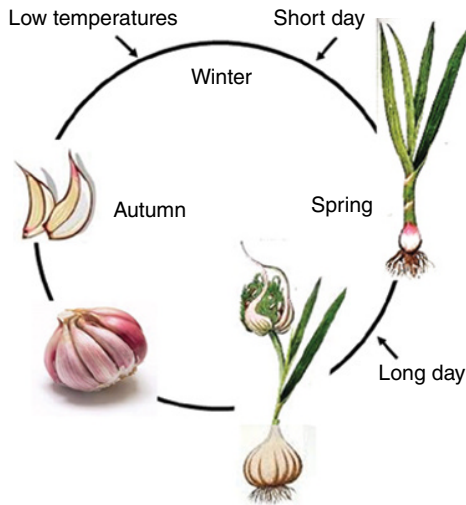


Figure 1.2 Schematic presentation of the annual cycle of vegetatively propagated bolting garlic. Low temperatures support spring elongation of foliage leaves and the flower stem. A long photoperiod enhances bolting and bulb development.

organs dry up, and following bulb maturation, the cloves enter a summer dormancy period (Figure 1.2).

After dormancy release and planting in the fall, adventitious roots arise from the base of the clove, and leaf primordia in the apical bud become active, producing characteristic flat leaves. Under suitable environmental conditions, some varieties bolt and develop inflorescences with flower buds and small bulblets (i.e. topsets) (Mann and Lewis 1956; Takagi 1990; Brewster 1994; Simon et al. 2003; Kamenetsky 2007).

In bolting and flowering garlic genotypes, florogenesis consists of four main phases: meristem transition from the vegetative to reproductive stage, scape elongation, inflorescence differentiation, and completion of floral development to anthesis (Etoh 1985; Kamenetsky et al. 2004b) (Figure 1.3). The transition of the apical meristem from a vegetative to a reproductive state occurs during the active growth stage (Kamenetsky and Rabinowitch 2001). An initial elongation of the flower stalk precedes spathe (prophyll) formation and the swelling of the reproductive meristem. This meristem subdivides to form several clusters, each of which gives rise to a number of individual flower primordia (Figure 1.3b and 1.3c). Similar to other *Allium* species, floral primordia within each cluster (cyme) develop unevenly in a helical order (Qu et al. 1994; Kamenetsky and Rabinowitch 2001; Rotem et al.

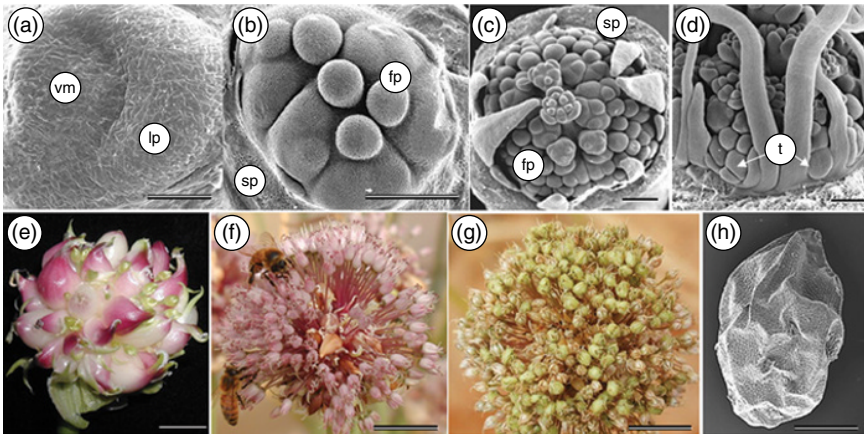


Figure 1.3 Stages of reproductive development in flowering garlic (adapted from Rotem et al. 2007). (a) Vegetative meristem (vm) produces leaf primordia (lp), six weeks after planting. Scanning electron microscopy (SEM) image. Bar=0.5 mm. (b) Inflorescence meristem, nine weeks after planting. Differentiation of first flower primordia (fp) is visible. Spathe (sp) removed. SEM image. Bar=0.5 mm. (c) Inflorescence meristem produces flower primordia (fp), 12 weeks after planting. Spathe (sp) removed. SEM image. Bar=1 mm. (d) Differentiation of topsets (arrows) following flower differentiation. Bar=1 mm. (e) Topset formation in the inflorescence. Flowers are squeezed and eventually aborted. Bar=2 cm. (f) Fully differentiated inflorescence after spathe opening. Bar=2 cm. (g) Seed setting in garlic hybrid with full capacity of seed production. Bar=2 cm. (h) Garlic seed. SEM image. Bar=0.5 mm.

2007). In most garlic genotypes, elongation of the floral pedicels is accompanied by quick differentiation of new meristematic vegetative domes, developing into small inflorescence bulbils (topsets) (Figure 1.3d) (Etoh 1985; Qu et al. 1994; Kamenetsky and Rabinowitch 2001; Rotem et al. 2007). The topsets are interspersed with young flowers and physically squeeze the developing floral buds, thus causing their degeneration (Figure 1.3e). Therefore, in some garlic clones, perpetual removal of the developing topsets resulted in the development of a number of normal flowers, some of which produced viable pollen and seeds (Konvicka 1984; Etoh et al. 1988; Pooler and Simon 1994; Jenderek 1998; Jenderek and Hannan 2000; Kamenetsky and Rabinowitch 2002; Simon and Jenderek 2004).

In flowering genotypes, a fully developed inflorescence consists of about 100 acropetal cymes, each made up of five to six flower buds and/or open flowers (Figure 1.3f). Further seed development and ripening (Figure 1.3g) are associated with the location of the flower within the cyme and with the location of the cyme in the inflorescence. In different

genotypes, the development of an individual flower from color break to senescence takes 15–25 days, while seed maturation occurs about one month after fertilization (Qu et al. 1994; Shemesh-Mayer et al. 2013).

C. Environmental and Genetic Control of Flowering

As in many other *Alliums* (Kamenetsky and Rabinowitch 2002, 2006), the environment plays a major role in garlic development. In bolting garlic clones, florogenesis is differentially regulated by photoperiod and temperature. Therefore, information on the interactions between genotype and environment might enable fertility restoration as well as effective seed production in different genotypes (Kamenetsky et al. 2004a; Mathew et al. 2011).

Low temperature (vernalization) is the main factor affecting flowering in garlic. In general, vernalization is the induction of a flowering process by exposure to the prolonged cold of winter, or by an artificial cold treatment. Many plant species require vernalization in order to acquire the ability to flower. In the major cultivated *Allium* crops, including bulb onion, shallot (*A. cepa* L.) (Rabinowitch 1985, 1990; Krontal et al. 2000), chives (*A. schoenoprasum* L.) (Poulsen 1990), and Japanese bunching onion (*A. fistulosum* L.) (Inden and Asahira 1990), vernalization is required for floral induction. Similarly, in bolting garlic, cold storage of cloves prior to planting promotes the transition of the apical meristem from the vegetative to the reproductive stage with subsequent leaf and scape elongation and spathe breaking (Takagi 1990; Kamenetsky et al. 2004a; Rotem et al. 2007; Wu et al. 2015, 2016). Bolting garlic genotypes vary in cold requirements and in the number of days from planting to meristem transition and to elongation of flower stalks (Mathew et al. 2011). However, in the semibolting Israeli cultivar ‘Shani’, adapted to warm Mediterranean conditions, low storage temperatures inhibited meristem transition to flowering and promoted fast bulbing after planting, indicating the considerable genotype variation in plant response to environmental factors (Rohkin-Shalom et al. 2015).

Following meristem transition, flower differentiation and further development of the inflorescence are affected by growth temperatures (Shemesh-Mayer et al. 2015a) (Figure 1.4). Study of the development of a fertile genotype under controlled conditions indicated that plant exposure to a sequence of moderate (22/16 °C day/night) and then warm (28/22 °C day/night) temperatures enhanced the differentiation of many intact flowers and viable anthers, while continuous exposure to moderate or relatively low temperatures during the entire growth period

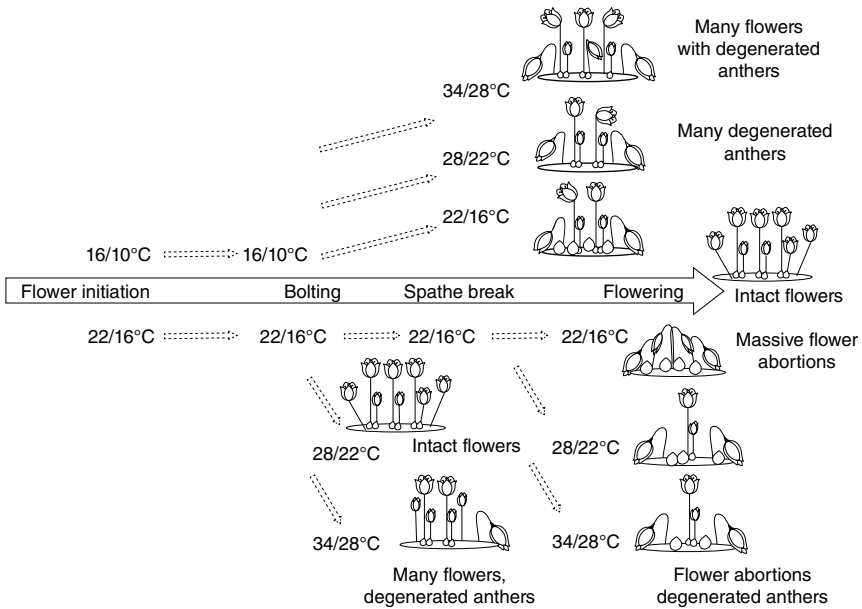


Figure 1.4 Effect of temperature regime on development of the reproductive organs in garlic. Plants were exposed to different growing temperatures at the stage of bolting or at the stage of spathe breaking. Alterations in temperature regime resulted in a varied response with respect to the inflorescence structure and number of viable flowers. Combinations of the controlled day/night temperatures are: low (16/10°C), intermediate (22/16°C), warm (28/22°C), and hot (34/28°C). (Source: Adapted from Shemesh-Mayer et al. 2015a.)

resulted in the development of topsets in the inflorescence, massive flower degeneration, anther abortion, and reduced pollen production. Dense and viable inflorescences were promoted by outdoor growth conditions during winter and spring in Israel. It was proposed that since natural habitats at the center of the origin of garlic, in Central Asia, are characterized by a gradual warming during the growing season (Hanelt 1990; World Weather Online 2014), such conditions are optimal for floral and pollen development (Shemesh-Mayer et al. 2015a). However, bolted plants exposed to a sudden increase in temperature responded by a reduction in time to spathe opening and anthesis. Similar to other plant species (Erwin 2006), high-temperature stress considerably shortened the period assigned for microsporogenesis, fertilization, and seed set in garlic (Shemesh-Mayer et al. 2015a; Figure 1.4).

Another important environmental factor is photoperiod. Photoperiodic signals are translated in plants into internal signals and to changes in the

hormone profile. A long photoperiod (LP) often enhances endogenous gibberellin levels, with subsequent transition to florigenesis (King et al. 2006). *Allium* crops, including Chinese chives (*A. tuberosum* L.) (Saito 1990), leek (*A. ampeloprasum* L.) (Van der Meer and Hanelt 1990; De Clercq and Van Bockstaele 2002), and rakkyo (*A. chinense* G. Don) (Toyama and Wakamiya 1990), require LPs for inflorescence initiation and differentiation. In garlic, an LP promotes the elongation of the scape, but an extended LP also promotes topset development in the inflorescence (Kamenetsky et al. 2004a).

Garlic genotypes of different biomorphological groups are differentially affected by environment in regard to florigenesis and bulbing, suggesting that competition for resources by the bulb, topsets, and flowers varies among genotypes (Mathew et al. 2011; Figure 1.5). A combination of low storage and growth temperatures with LPs can promote elongation of the flower stalk, while warm temperature combined with LPs led to the degeneration of the developing inflorescence and early bulbing. A short photoperiod (SP), interrupted with a one week LP, enhanced scape elongation and flower differentiation, supporting the concept of environmental manipulation as a tool for fertility restoration (Kamenetsky et al. 2004a; Mathew et al. 2011).

To understand the genetic mechanisms of garlic development, two main strategies of knowledge transfer from model to nonmodel plants might be employed: (i) creating large-scale transcriptome profiling and correlating the phenotype to the expression pattern and to specific genes, and (ii) searching for conserved candidate genes of known molecular pathways and their functions in the nonmodel crops (Leeggangers et al. 2013). Both strategies have been used in garlic. An initial search for the specific genes involved in the control of flowering in garlic resulted in the identification of *gaLFY* – a homolog to the key genes in flower development: *LFY* from *Arabidopsis* and *FLO* from *Antirrhinum majus* L. (Coen et al. 1990; Weigel et al. 1992; Rotem et al. 2007). In *Arabidopsis*, *LFY* is expressed during the development of floral meristems and activates a group of floral-organ identity genes within the flower (Krizek and Fletcher 2005; Moyroud et al. 2010). Similarly, an expression of *LFY/FLO* homologs during flower initiation and differentiation has been shown in many different plant species (Mouradov et al. 1998; Shu et al. 2000; Shitsukawa et al. 2006). In some plants, such as *Eucalyptus* (Southerton et al. 1998), apple (Wada et al. 2002), and maize (Bomblies et al. 2003), the presence of two differentially expressed *LFY* homologs was reported. In garlic, *gaLFY* was identified as a single-copy gene with the two transcripts generated by alternative splicing (Rotem et al. 2007).

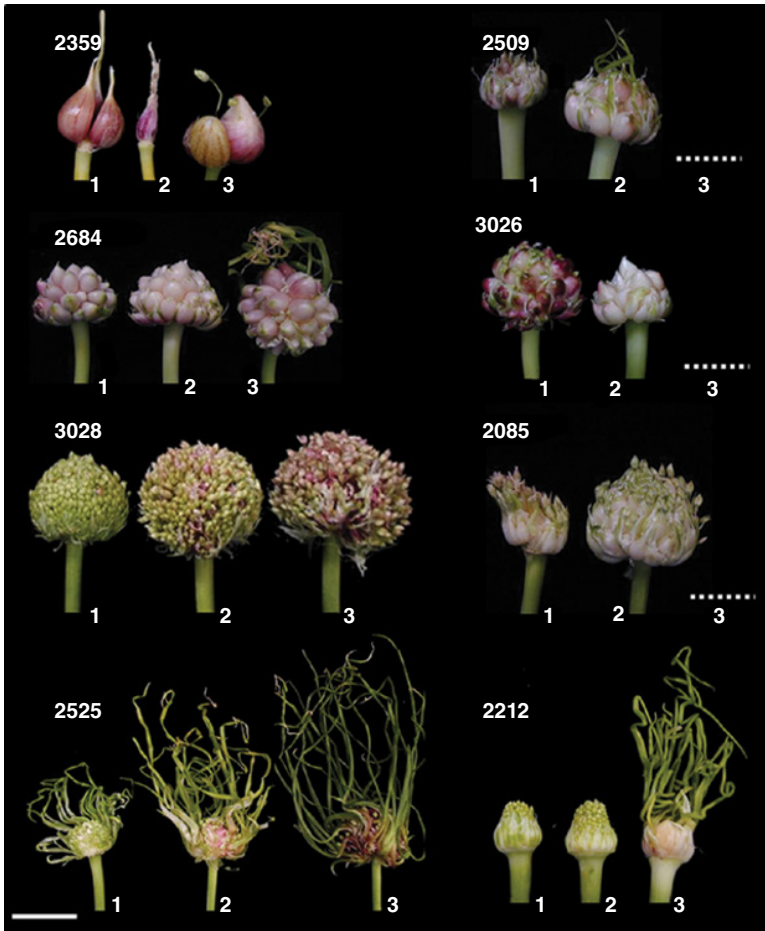


Figure 1.5 Effect of photoperiod on inflorescence development in eight bolting genotypes. Three photoperiod treatments were applied: (1) a natural photoperiod in Israel, (2) interruption by a long photoperiod of 16 hours for 10 days, and (3) interruption by a long photoperiod of 16 hours for 30 days. Note the complete absence of an inflorescence in accessions #2509, #3026, and #2085 under the long photoperiod applied for 30 days. (Source: Mathew et al. 2011, with permission.)

The accumulation of *gaLFY* is associated with reproductive organs; it increases during florigenesis and gametogenesis in garlic, while it is downregulated in vegetative meristems and in topsets (Rotem et al. 2011). The transcripts of the gene are differentially expressed during inflorescence development and florigenesis, suggesting the involvement of *gaLFY* in different stages of sexual reproduction, similar to the