Scientia Horticulturae 242 (2018) 69–75

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Temporal and spatial effect of low pre-planting temperatures on plant architecture and flowering in bolting garlic

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ARTICLE INFO

Keywords:
Allium sativum
Vernalization
Plant reproduction
Bulbing
Seed production

ABSTRACT

Garlic flowering and bulbing are prone to photo-thermal regulation during its annual cycle. As in many other geophytes, these pathways are parallel but competitive, and can be manipulated by the environment. Both flowering and bulbing are of paramount physiological value, and of great horticultural interest. We argue that, in bolting garlic, differential regulation of only one of the two pathways by pre-planting vernalization is unfeasible, and that garlic's response to cold shows an optimal curve. Within limits, long vernalization treatments have resulted in rapid development of 'Reproductive and Bulbing Phenotype', with fast leaf elongation, early transition of the apical meristem to the reproductive state, development of axillary buds, flowering and bulbing. Low temperatures trigger primary signaling components, thus modulating organogenesis even under a relatively short photoperiod. We therefore propose that under a suboptimal photoperiod, favorable temperatures could substitute the plant's requirements for photoperiod and signal for the meristem transition, flowering and bulbing. The optimum response of the studied genotype was obtained after vernalization of four weeks at 4 °C. No transition of the apical meristem was evident in plants exposed to only short or no vernalization, namely the apex remained vegetative. These plants continuously produced foliage leaves, thus forming a “Leafy Phenotype”, which did not branch, bulb or flower. Comprehension of the plant’s response to environment is expected to facilitate physiological manipulations on the production of either bulbs or true seeds in garlic.

1. Introduction

Originating in Central Asia (Fritsch and Friesen, 2002) garlic (*Allium sativum* L.) is one of the earliest domesticated horticultural crops (Zohary et al., 2012) and is now consumed world- wide for its flavor and nutraceutical properties (Block, 2010; Kamenetsky, 2007). Global annual garlic production in 2015 and 2016 amounted to ~26–27 M tons cultivated on ~1.5 million ha in a variety of climates (FAOSTAT, 2018).

All modern garlic cultivars are sterile due to long-term human selection for both the largest bulbs and minimum bolting. Hence, classical breeding became impossible, and improvements resulted solely from random mutations and selections (Etoh and Simon, 2002). Recently fertility and seed production were restored in a number of garlic genotypes. The consequent seedlings’ populations exhibit a very high genetic diversity in both vegetative and reproductive traits, and a considerable differential response to environmental cues (Pooler and Simon, 1994; Jenderek and Hannan, 2004; Jenderek and Zewdie, 2005; Kamenetsky et al., 2004, 2015; Shemesh et al., 2008; Shemesh-Mayer et al., 2015). Sexual hybridization has generated genetic variability and has provided a solid basis for garlic classical breeding. However, to date, vegetative propagation is still the only means of commercial propagation, and the cloves' quality and pre-planting storage conditions have a major impact on plant development and bulb quality.

In the vegetative annual cycle, clove dormancy breaks down at a rate determined by the genotype and storage environment, and development of garlic begins with sprouting, root development, and leaf elongation (Takagi, 1990; Kamenetsky, 2007; Wu et al., 2015, 2016; Lopez-Bellido et al., 2016). New leaves sequentially develop until leaf initiation ceases and/or a transition of the apical meristem from

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https://doi.org/10.1016/j.scienta.2018.07.025
Received 9 April 2018; Received in revised form 17 July 2018; Accepted 20 July 2018
0304-4238/

vegetative to reproductive state occurs. This is followed by differentiation and development of lateral buds. When photo-thermal cues indicate seasonal changes (e.g., temperature and photoperiod increase), the rate of active aboveground vegetative growth slows down. Concomitantly, the axillary buds become a strong sink for assimilates from the foliage leaves, and a clustered bulb made of cloves is formed (Takagi, 1990; Lopez-Bellido et al., 2016). Bulbing ends and dormancy begins when storage of most of the assimilates in the cloves is complete (Kamenetsky et al., 2004; Mathew et al., 2010). However, when growth conditions are suboptimal, new lateral buds sprout green leaves and do not enter dormancy. In horticultural practice, this phenomenon is termed “brooming” and results in the formation of multi-cloved bulbs of low quality.

In geophytes, temperature and photoperiod are the two main environmental cues for plant growth and for control of transition either to bulbing or from the vegetative phase to flowering (Le Nard and De Hertogh, 1993; Khodorova and Boitel-Conti, 2013). However, the mechanisms for regulation of bolting, flowering and seed production by photo-thermal effects are still unclear. Garlic bulb production often requires propagules' vernalization before planting in commercial fields in both, warm and cold climates. An excessive dose of cold treatment, however, promotes early sprouting, enhances vegetative growth and consequently, the early development of only a few axillary buds thus resulting in small bulbs and low yields (Bandara et al., 2000; Guevara-Figueroa et al., 2015; Rohkin-Shalom et al., 2015; Wu et al., 2015). At the same time, bolting, scape elongation and floral development require both cold induction (vernalization) and a long photoperiod (LP) (Takagi, 1990; Kamenetsky et al., 2004; Mathew et al., 2010; Wu et al., 2015, 2016). Pooler and Simon (1993) reported from Wisconsin that generally, cold storage of propagation cloves resulted in only a few flowering plants, while others reported on the importance of vernalization in garlic flowering (Kamenetsky et al., 2004; Rotem et al., 2007; Shemesh et al., 2008; Wu et al., 2015, 2016). Similarly, onions raised from vernalized (0–5 °C) bulbs had a shorter vegetative phase and produced smaller bulbs than the control (Khokhar, 2017), but the same cold treatment promoted early flowering and seed production (Khokhar, 2014).

Parallel development of both bulbs and flowers is common in garlic and in many bulbous plants (Mathew et al., 2010; Okubo et al., 2012). These processes become two strong competitive sinks on the limited available resources when the assimilating foliage leaves are weakening and senescing. Lee et al. (2013) reported that the genetic control of both processes in onion is at least partially regulated by the same nucleic factors. The fate of these two parallel, yet alternative and competitive developmental pathways, is associated with significant changes in the hormonal balance between the two important processes (Etoh and Simon, 2002), and the dominating route can be manipulated by even small changes in the environment (Kamenetsky et al., 2004). This flexible response poses a great challenge to both breeders and growers of geophytes for flowers, seeds or bulbs, everywhere. No single recipe is available, and each genotype requires specific attention to the local effective environment, such as day length, temperature, and stress posing factors, that benefit either flower or bulb production.

In order to improve our understanding of the competitive processes that finally determine whether the garlic plant will either bulb, or flower, or produce both storage and reproductive organs, we studied the physiological response to pre-planting conditions on the active growth and bulbing of flowering garlic genotype.

2. Materials and methods

2.1. Plant material

The bolting and flowering garlic clone #96 was raised in 2008 from a single seed produced by uncontrolled pollination, and then clonally propagated at the Agricultural Research Organization (ARO), The Volcani Center, Bet Dagan, Israel. The experiments were carried out in 2015–2016 at the Experimental Farm, the Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot, Israel, 31.9 °N.

Table 1
Pre-planting temperature treatments of garlic #96 bulbs. Intact bulbs were placed for 0–12 weeks in dark, temperature controled chambers at 4 or 9 °C, RH 65–70%. Chilling units (CU) were calculated according to Utah model.

Storage period, weeks	Storage at 4 °C, code	Chilling units	Storage at 9 °C, code	Chilling units
0 (control)	0W	0	0W	0
2	2 W4 °C	336	2 W9 °C	168
4	4W4 °C	672		
6	6W4 °C	1008	6W9 °C	504
8 (control)	8W4 °C	1344		
10	10W4 °C	1680	10W9 °C	840
12	12 W4 °C	2016		

2.2. Storage treatments and growth conditions

In summer 2015, freshly harvested bulbs were cured and stored under ambient conditions (22–35 °C), in a roofed shed. In August-October, healthy intact bulbs were transferred for pre-planting vernalization at 4 or 9 °C for 0–12 weeks in temperature and humidity-controlled dark chambers (Table 1). Non-vernalized control bulbs were shelved under ambient conditions (20–30 °C), in the same roofed-shed, until planting. Bulbs stored at 4 °C for 8 weeks were considered vernalized controls (Kamenetsky et al., 2004). All treatments ended on November 11, 2015, and uniform sized cloves from healthy intact bulbs were planted in the soil in a 30% shaded screenhouse. The cloves were planted in three replications in randomized block design, 30 cloves per replication. Planting density was 50 cloves per m^2. Air temperature and photoperiod records for the entire growth period are presented in Fig. 1, and the number of chilling units/treatment (CU) was calculated according to a weighted Chilling Hour Model, a well referred method for counting cold exposure in crops (The Utah Model, 2018).

Fertigation with “Shefer” liquid fertilizer (N:P:K = 59:35:94 g L^{-1}, Dshanim, Israel) and standard agriculture practice was applied throughout. For each treatment, fertigation was discontinued independently in May-June 2016, when the aboveground parts dried up, and bulbs were harvested selectively, upon maturation.

During the growing season, phenological and morphological measurements were taken at 0, 15, 34, 54, 81 and 138 days after planting (DAP). Phenology and morphological traits were analyzed for 20 plants per replication (60 plants/treatment). Inflorescence measures were analyzed for 8–10 inflorescences/treatment, and three plants/treatment

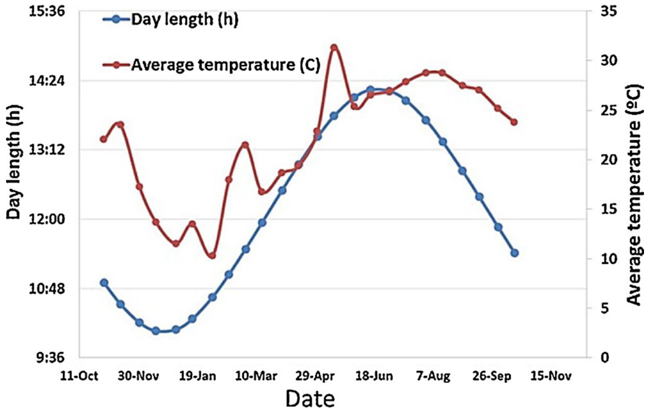

Fig. 1. Daylength and average air temperatures (based on eight measurements per day) from November 2015 to October 2016 in Rehovot, Israel.