Field Crops Research 115 (2010) 234–242

Contents lists available at ScienceDirect

Field Crops Research

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

Review

Physiology of flowering and grain filling in faba bean

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ARTICLE INFO

Article history:
Received 21 August 2008
Received in revised form 4 June 2009
Accepted 6 June 2009

Keywords:
Vernalization
Photoperiod
Thermal time
Transfer cells
Seed filling
Sucrose/H^+ antiport
Embryo
Endosperm
Seed coat
Vicia faba

ABSTRACT

The development of flowers and then that of seeds are key processes in the formation of yield in faba bean (*Vicia faba* L.), as in other grain legumes. Winter faba bean generally has a quantitative vernalization requirement, allowing flowering to occur at a lower node than in unvernalized plants. Some germplasm is day-neutral, other germplasm is long-day with a critical daylength between 9.5 and 12 h. Progress toward flowering follows a conventional thermal-time model, with 830–1000 °C-d above 0 °C required for the onset of flowering and an optimum temperature of 22–23 °C. Flowers may abscise from the crop because of lack of pollination, because proximal flowers on the same raceme are fertilized, because of vegetative–reproductive competition for assimilate, or because of stresses such as drought.

The large seed size of faba bean has enabled this species to be a model for studies of the molecular physiology of seed development. Seed filling in the retained pods proceeds through well defined pre-storage and storage phases. During the pre-storage phase, cell expansion occurs mostly in the endosperm and seed coat while the embryo is in a cell division phase. Extracellular invertase from the inner cell layers of the seed coat acts on sucrose unloaded from the phloem, ensuring that the rapidly dividing embryo cells are bathed in hexose-rich fluid. With further development of the embryo, endosperm sugar levels become depleted and the embryo relies more directly on nutrients released by the seed coat. In the transition to the storage phase, the cotyledon cells expand, synthesize storage proteins and starch, and undergo endopolyploidization. Thin-walled parenchyma cells in the seed coats differentiate into transfer cells and the enhanced area of plasma membrane results in increased nutrient flow to the rapidly growing embryo. Release of sucrose and potassium into the seed apoplasm is energy-coupled through a plasma membrane H^+-ATPase and a sucrose/H^+-antiport. Subsequent radial transfer of nutrients to the storage parenchyma cells of the cotyledons follows a symplastic pathway through numerous plasmodesmata. Cotyledon cell expansion stops when the mechanical restraints of the seed coat and space within the pod cavity are met. It is now possible to identify genes for manipulation that may make seed setting and final seed size less susceptible to environmental stresses.

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0378-4290/$ – see front matter
doi:10.1016/j.fcr.2009.06.005

1. Introduction

Faba bean (*Vicia faba* L.) is conventionally grown as a grain legume, not as a forage crop. The induction of flowering, retention of flowers and development of seeds are all therefore critical processes in yield formation. Spring, winter and Mediterranean types of faba bean have different phenologies and the relative importance of vernalization, photoperiod and thermal time in the induction and maintenance of flowering differs among these three classes. Appropriate time of flowering is an essential part of adaptation to the local environment, in order that flowering starts after risk of frost and ends soon enough to allow a timely harvest to mature before either frost or drought, depending on the climate. While progress has been made in understanding the photothermal requirements for flowering in faba bean, more basic understanding at the levels of molecular physiology and gene action is lacking in this species.

Following fertilization of the flowers, processes determining potential seed size (Davies, 1977) and final seed number per pod (Duthion and Pigeaire, 1991) dominate a pre-storage phase of seed development during which most expansion growth occurs in the endosperm and seed coat while cell division largely contributes to embryo growth (Borisjuk et al., 1995). The latter growth activity is nourished by nutrients mobilized from the endosperm but is very sensitive to alterations in leaf photosynthesis, reductions in which can lead to decreases in seed size or the selective abortion of seeds within a pod (Adisarwanto and Knight, 1997; Toker, 2004).

Once the embryo enlarges through cotyledon growth to occupy the space delimited by the seed coat, the transition to the storage phase of seed development is initiated. This transition is marked within cotyledons by a shift from cell division to cell expansion, coupled with induction of metabolic machinery for storage product biosynthesis (Borisjuk et al., 1995). In faba bean and many other grain legumes, the principal storage products are storage proteins and starch (Hill-Cottingham, 1983). At the onset of the storage phase, the endosperm is depleted and embryo nutrition relies on imported nutrients directly released from the maternal seed coats. Seed size and space within the pod capacity are correlated (Fukuta et al., 2006), suggesting physical limitations restrict the extent of cotyledon expansion. Thereafter, cotyledon biomass accumulation continues until seed maturation processes prevent further storage product biosynthesis accompanied by the onset of seed desiccation (Weber et al., 2005; Gallardo et al., 2008). In contrast to the pre-storage phase, during the storage phase rates of biomass accumulation are less sensitive to alterations in leaf photosynthesis in faba bean (Toker, 2004) and also in soybean (*Glycine max* (L.) Merr.) (Borrás et al., 2004).

Within the protective confines of pod walls, rates of evaporative loss of water from seed coat surfaces are low or nil, so there is little or none of the tension necessary to drive transpirational inflow through the xylem, and nutrients and water are imported into developing seed coats predominantly through the phloem (Zhang et al., 2007). Embryo, endosperm and seed coat each forms an independent symplasmic domain (Patrick and Offler, 2001), so nutrient flows to these structures necessitate transport from and into cells across their plasma membranes at organ interfaces. Specialized transfer cells develop at these interfaces to support the high membrane fluxes of nutrients required to meet the demands for storage product biosynthesis occurring within cotyledons. Studies of cellular pathways of nutrient flows and membrane transport mechanisms largely have been confined to the storage phase of seed development. Several recent reviews have dealt with development and nutrient loading of seeds (for example, see Weber et al., 2005; Zhang et al., 2007).

In order to achieve a more coherent account of these issues, where critical information is not available for faba bean, reference is made to other species, especially pea (*Pisum sativum* L.) on account of its close phylogenetic relationship with *V. faba*.

2. Induction of flowering

Progress to flowering in Mediterranean and spring faba bean follows a photothermal model. Aspects of vernalization, daylength and thermal time have been assessed in a range of experiments.

The vernalization requirement of winter faba bean is considered quantitative, rather than absolute, as unvernalized plants eventually flower (Link et al., 2010). Vernalization of spring and Mediterranean types of faba bean accelerated flowering (Ellis et al., 1988a), but only in line with the accumulated thermal growing time above the base temperature of 0 °C (Ellis et al., 1988b, 1990).

Faba bean is considered either day-neutral or long-day requiring. The minimum photoperiod for one Mediterranean landrace was as short as 9.5 h (Ellis et al., 1990) and this may help explain the lack of detection of photoperiod response in other materials. Some Italian cultivars did not flower until both a minimum daylength requirement of 12 h and a minimum thermal time of 833 °C-d were fulfilled (Ianucci et al., 2008). When two English spring faba bean cultivars were grown in the unsuitable environment of South Australia, they did not flower until daylength exceeded 12 h, long after thermal time requirements would have been met, while Mediterranean types flowered at much shorter days (Stoddard, 1993a).

Thermal time is the most important contributor to progress to flowering in faba bean. Variation in response to thermal time among six diverse genotypes (five from the Mediterranean basin and one English spring type) was not statistically significant (Ellis et al., 1988c, 1990), with about 1000 °C-d required for flowering above a base temperature of 0 °C. This base temperature has been confirmed in independent studies (Boote et al., 2002), but variation in thermal time to flowering has, not surprisingly, been found (compare Ianucci et al., 2008, with Ellis et al., 1990 and see also McDonald et al., 1994).

The optimum temperature for progress to flowering was proposed as 18–28 °C (Ellis et al., 1988a) and subsequently refined to 20–25 °C (Ellis et al., 1988c). For modelling purposes it has been set at 22 °C (Boote et al., 2002) or 23 °C (Turpin et al., 2002) and this optimum may be lower in cool-climate-adapted germplasm such as winter types.

The contributions of genes *E* (early initiating), *Hr* (high response to vernalization), *Lf* (late flowering) and *Sn* (sterile nodes) to earliness of flowering, photoperiod response and thermal response have been analysed in pea (Alcalde et al., 1999) but their homologues have not been reported in faba bean. Analysis of the molecular genetics of flowering genes in grain legumes has been initiated in pea (Hecht et al., 2007) and the molecular physiology is as yet little explored in the legumes. More direct management of these genes may allow us to breed cultivars with better adaptation to stressful environments where the window for plant growth is narrow, such as semi-desert or high-latitude conditions.

3. Retention of flowers

The lack of retention of flowers by faba bean plants has vexed growers for many years, as many find it alarming to see apparently healthy flowers dropping off apparently healthy plants. Three factors contribute to this loss of flowers.

The first factor is pollination and fertilization, as the crop has a mixed breeding system (reviewed by Stoddard and Bond, 1987). When a flower remains unpollinated, due to lack of either autofertility or bee activity, it cannot produce seeds. The adequacy of autofertility and of bee activity have been investigated in many situations (Stoddard, 1986a; Suso et al., 2001). Investigations on the anatomy and physiology of autofertility have identified