CHAPTER

12

Genetic and environmental effects on crop development determining adaptation and yield

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1 INTRODUCTION

Crop development is a sequence of phenological events controlled by the genetic background and influenced by external factors, which determines changes in the morphology and/or function of organs (Landsberg, 1977). Although development is a continuous process, the ontogeny of a crop is frequently divided into discrete periods, for instance 'vegetative', 'reproductive' and 'grain-filling' phases (Slafer, 2012).

Patterns of phenological development largely determine the adaptation of a crop to a certain range of environments. For example, genetic improvement in grain yield of wheat has been associated with shorter time from sowing to anthesis in Mediterranean environments of western Australia (Siddique et al., 1989), whereas no consistent trends in phenology were found where drought is present but not necessarily terminal, including environments of Argentina, Canada and the USA (Slafer and Andrade, 1989, 1993; Slafer et al., 1994a) (Fig. 12.1). Even in agricultural lands of the Mediterranean Basin where wheat has been grown for many centuries, breeding during the last century did not clearly change phenological patterns (Acreche et al., 2008).

This chapter focuses on two major morphologically and physiologically contrasting grain crops: wheat and soybean. For both species, we have an advanced understanding of development and

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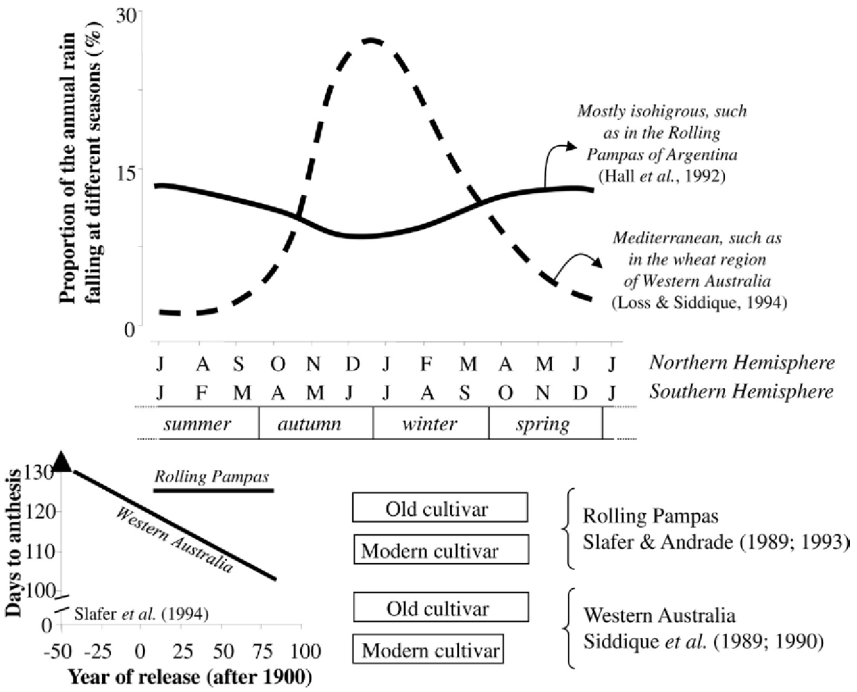


FIG. 12.1 Comparison of the patterns of seasonal rainfall in western Australia and Rolling Pampas of Argentina (top), and the changes in days to anthesis of wheat cultivars released in these regions during the 20th century (bottom). The bars cover, for each type of cultivar and region, common periods from sowing to anthesis. *Souce: Araus et al. (2002).*

physiology in general. Wheat is a determinate, long-day grass of temperate origin, which is responsive to vernalization. Soybean is a typically indeterminate (but with determinate intermediate variants), short-day grain legume of tropical origin, which is insensitive to vernalization. Comparisons with other species are used to highlight the similarities and differences. The aims of this chapter are to outline the developmental characteristics of grain crops and the links between phenology and yield, to revise the mechanisms of environmental and genetic control of development and to explore the possibilities of improving crop adaptation and yield potential through the fine-tuning of developmental patterns.

2 CROP DEVELOPMENT

In this section, we briefly describe the major developmental stages or phases of wheat and soybean separately (as developmental features are in many cases unique), and then discuss the relationships between crop phenology and yield determination.

2.1 Major developmental stages or phases

2.1.1 Wheat

The development of the wheat plant comprises phases defined in terms of microscopic and macroscopic changes that have been integrated into several phenological scales (Miralles and Slafer, 1999). Figure 12.2 shows developmental progress of wheat based on easily recognizable events including microscopic (e.g. double ridges, terminal spikelet initiation) and macroscopic (e.g. crop emergence, heading, anthesis, maturity, harvest) delimiters of phases. In this simple scheme, development involves three major phases:

1. vegetative, when the leaves are initiated
2. reproductive, when first spikelet and then floret development (including floret

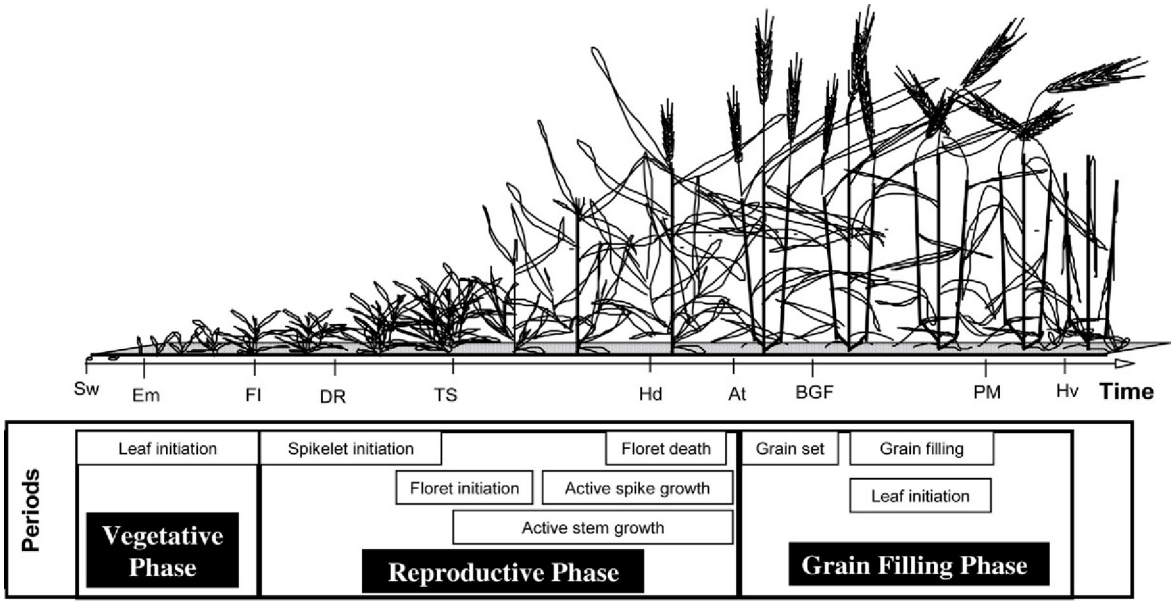


FIG. 12.2 Diagram of wheat growth and development showing the stages: sowing (Sw), seedling emergence (Em), floral initiation (Fl), initiation of the first double ridge (DR), terminal spikelet initiation (TS), heading (Hd), anthesis (At), beginning of the grain-filling period (BGF), physiological maturity (PM), harvest (Hv). Boxes indicate the periods of differentiation or growth of some organs within the vegetative, reproductive, and grain-filling phases. *Source: Slafer and Rawson (1994a).*

mortality) occurs, until the number of fertile florets is determined

3. grain filling, when the grain first develops endosperm cells, and then grows to its final weight.

These phases are delimited by sowing–floral initiation, floral initiation–anthesis and anthesis–maturity (Fig. 12.2). Although they do not delimit major developmental phases, the initiation of both the first double ridge and the terminal spikelet are important early reproductive markers. The former is the first (microscopically) visible sign that the plant is reproductive, while the latter marks the end of the spikelet initiation phase, when the final number of spikelets per spike is determined which, under most field conditions, coincides with the onset of stem elongation.

A mature wheat seed normally contains four leaf primordia (Kirby and Appleyard, 1987; Hay and Kirby, 1991). After sowing, seed imbibition and initiation of leaf primordia is reassumed; a typical seedling has six differentiated leaves at emergence under non-stressful field conditions. Leaf initiation continues until the onset of floral initiation, when the maximum number of leaves in the main shoot is determined. Measured in thermal time, the rate of leaf initiation (or its reciprocal, the plastochron) is relatively constant between different leaf primordia (Kirby et al., 1987; Delécolle et al., 1989), but genetic variation has been reported (e.g. Evans and Blundell, 1994). The timing of floral initiation is therefore a major driver of the length of the crop cycle to anthesis, as all leaf primordia appear at a certain rate (the reciprocal of phyllochron) before the last internode elongates and the crop reaches heading. Phyllochron is approximately constant, although under circumstances of slow development inducing the initiation of a large number of leaf primordia in the main shoot (>10), the phyllochron of later leaves tends to

be longer than that of early leaves (Miralles and Slafer, 1999). Although it is frequently assumed that phyllochron is approximately 100°Cd (base temperature 0°C), it is affected by both genetic and environmental factors (e.g. Halloran, 1977; Rawson et al., 1983; Rawson, 1986, 1993; Stapper and Fischer, 1990; Kirby, 1992; Slafer et al., 1994a,b; Slafer and Rawson, 1997).

Cereals develop the capacity to produce a tiller at each phytomer. The process of emergence and growth of tillers, termed tillering, starts when the first tiller bud is mature to grow. The onset of tillering is approximately three phyllochrons after seedling emergence; from then on, the emergence of tillers is closely related to leaf emergence (Masle, 1985; Porter, 1985). Under favorable conditions, the pattern of potential tiller emergence is exponential (Miralles and Slafer, 1999; Alzueta et al., 2012) for a short period up to growth resources become limiting to maintain all tillers. Some tillers die in the reverse order of their emergence, thus contributing to the synchrony and convergence of development in a crop (Hay and Kirby, 1991). This process stabilizes during the period immediately before anthesis, when the number of spikes per unit land area is defined.

In each shoot after floral initiation, the apex starts initiating spikelet primordia; later on, floral initiation starts in the earliest initiated spikelets. Although the double ridge stage has been used as a morphological indication of floral initiation, the first spikelet primordium is normally initiated before double ridge (e.g. Delécolle et al., 1989; Kirby, 1990), so that floral initiation can only be dated *a posteriori* by relating total number of primordia with time (or thermal time), considering the final leaf number (Miralles and Slafer, 1999). The phase of spikelet initiation finishes with the initiation of the terminal spikelet in the apical meristem, when the maximum number of spikelets is fixed. Floral initiation, which had started in the earliest developed spikelets (in the middle third of the spike) before this 'terminal spikelet initiation'stage, continues in all spikelets. Floret development starts in the proximal (to the rachis) positions of each spikelet, and progresses towards the distal positions (e.g. Sibony and Pinthus, 1988). This is why the carpels (at anthesis) and the grains (at maturity) of proximal florets are larger than those in more distal positions (e.g. Rawson and Evans, 1970; Calderini et al., 2001). Floret initiation within each spikelet continues approximately until booting (Kirby, 1988; González et al., 2003b, 2005b; Ferrante et al., 2010, 2013a), reaching a maximum of 6 to 12 floret primordia per spikelet (Sibony and Pinthus, 1988; Youssefian et al., 1992; Miralles et al., 1998), mostly depending on the spikelet position. The development is then arrested in a huge proportion (normally 70–80%) of florets, leading to a large rate of floret mortality coincident with the onset of rapid growth of stems and spikes shortly before anthesis (Kirby, 1988; González et al., 2003b, 2005b). This suggests that competition for assimilates would determine the rate of floret mortality (González et al., 2005b; Ghiglione et al., 2008) as well as the onset of this mortality (González et al., 2011; Ferrante et al., 2013b). Thus, the more the spike can grow at these critical stages, the more florets can reach the stage of fertile florets (and grains afterwards), irrespective of whether this growth is dependent on crop growth or partitioning, or whether it is due to agronomy or genetic improvement (see Slafer (2003); Slafer et al. (2005) for an extended discussion and further references). Just before anthesis, pollination and fertilization occur in fertile florets. Grain set – the proportion of fertile florets producing 'normal' grains – normally ranges between 70 and 90%, likely due to competition for assimilates (Savin and Slafer, 1991; Ferrante et al., 2013a). The period of grain set is characterized by substantial grain development with virtually no grain growth, and is therefore described as the 'lag phase' (Stone and Savin, 1999).

Grain growth and development are normally partitioned into three phases: the above-mentioned lag phase, the effective grain-filling period and the maturation and drying phase (e.g. Bewley

and Black, 1985; Savin and Molina-Cano, 2002). Most of the endosperm cells develop during the lag phase, when grains rapidly accumulate water but almost no dry matter (Evers, 1970; Nicolas et al., 1984). The effective grain-filling period involves rapid accumulation of dry matter in the form of seed reserves; water content continues to increase rapidly, and eventually establishes the maximum volume of the seed. During the maturation and drying phases, seeds lose water, reach 'physiological maturity' (maximum dry matter accumulation) and enter a quiescent state (Bewley and Black, 1985). Thus, physiological maturity is the phenological stage that indicates the end of grain growth. The most precise method to determine the timing of physiological maturity is therefore establishing when grain growth ceases (Egli, 1998). However, this laborious method requires frequent consecutive samples to determine that constant grain weight has been reached; hence it only serves to indicate physiological maturity several days after the event (Rondanini et al., 2007). The apparent consistency between the dynamics of water and dry matter in grains of all major crops has led to a reliable, simple method to estimate grain development towards maturity based on the water content of the grains (Box 12.1; see also Fig. 15.4 in Chapter 15).

BOX 12.1

QUANTIFYING GRAIN DEVELOPMENT THROUGH ITS MOISTURE CONTENT

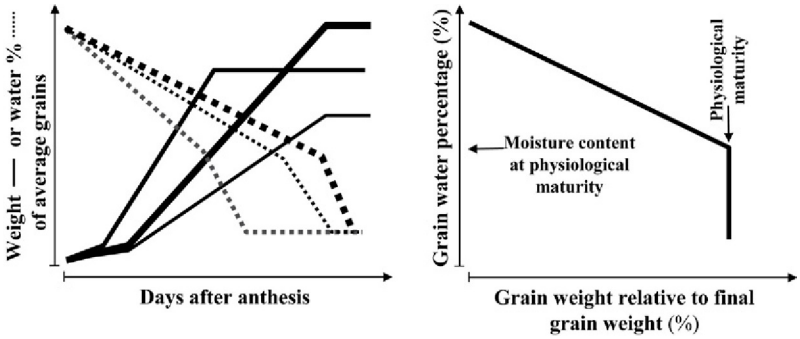
The most common characterization of post-flowering development progress towards maturity has been qualitative, dividing the development into loosely defined grain stages, such as 'aqueous', 'milky', 'dough', and 'hard' grain. As this characterization is based on the proportion of water in grains, it is possible to put forward a quantitative developmental estimate based on the actual grain water content, reflecting the proportion of the time to maturity already elapsed at any time the moisture content of growing grains is measured. For this to be realistic there must be a steady change in this variable during the whole post-flowering period, and for it to be of universal application (a developmental scale applicable to all genotypes of a particular species and to different crop managements), there should be uniform performance across cultivars and environmental conditions.

The scheme indicates that grain growth and grain moisture content dynamics are strongly variable depending on the genotype and the environment, determining large differences in final grain weight. However, the relationship between grain growth and its water content seem much more stable, as there is a positive relationship between the rate of grain growth and the rate of water percentage reduction (the higher the slope of grain dry matter gain the smaller – more negative – the rate of water percentage in grains). If the final grain weight is normalized (by referring in each case the grain weight at any time between anthesis and maturity as a percentage of the final grain weight), there seems to be a universal sharp negative relationship between the grain moisture percentage and grain weight normalized; so that disregarding profound differences in final grain weight and in the dynamics of grain growth, all crops within a particular species reached physiological maturity at a rather similar water content in the grains. Evidences in maize (Saini and Westgate, 2000; Borrás et al., 2003; Borrás and Westgate, 2006), wheat (Schnyder and Baum, 1992; Calderini et al., 2000), barley (Alvarez Prado et al., 2013), sorghum (Gambín and Borrás, 2005), soybean (Swank et al., 1987) and sunflower (Rondanini et al., 2007) have shown that final grain weight is achieved at, or near to, a particular

BOX 12.1 *(cont.)*

moisture content irrespective of the actual size of the grains (affected by genetic or environmental factors)*, revealing that dry matter accumulation in developing grains and the concurrent loss of water are closely related phenomena.

content just after anthesis and ≈40% at physiological maturity (Calderini et al., 2000), it can be directly established what proportion of the grain-filling period has elapsed at any time we measure grain moisture content in the field. This



Thus, it seems that duration of grain filling is determined by the interaction between reserve depositions and declining cellular water content, where deposition of reserves such as starch replaces water until critical minimum moisture content is reached. As, for each crop, (1) water percentage at flowering and at maturity are rather constant (for a wide range of grain growing conditions and of final grain weights) and (2) it decreases linearly across the range from flowering to physiological maturity, it can be proposed that the progress of grain development towards maturity may be trustworthily based on the water content of the grains. For instance, if for wheat the limits are ≈80% water

quantitative assessment allowing determination of how much of the grain filling has been already completed may be instrumental in management decisions such as when applying a desiccant to the crop to advance harvest without losing yield (e.g. Calviño et al., 2002). Chapter 15 presents the application of the model relating grain growth and grain moisture content dynamics in the analysis of genetic control of grain size in maize.

* In some extreme conditions moisture content at maturity may also be affected within a crop, though assuming a constant value for a particular crop seems quite stable for realistic agronomic conditions.

2.1.2 Soybean

External development in soybean is described in terms of the number of leaves or nodes on the main stem (V-stages) or the presence or growth of reproductive organs in the upper nodes on the main stem, i.e. R-stages (Fig. 12.3). After seedling emergence (VE), the cotyledons open and the two unifoliate leaves unroll (VC); then trifoliate leaves appear and expand at a rate that depends mainly on temperature (Hesketh et al., 1973;

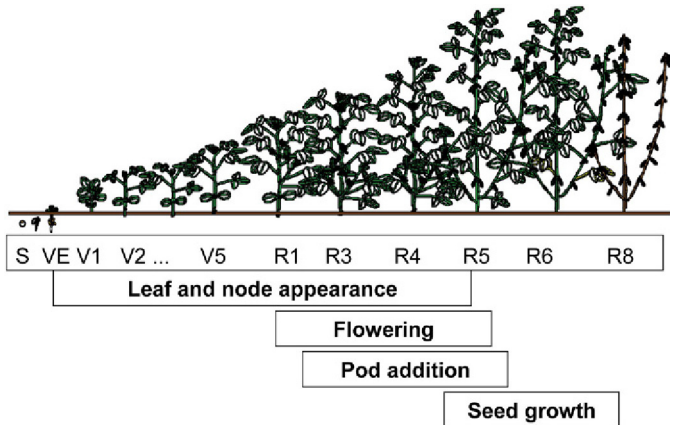


FIG. 12.3 Diagram of soybean growth and development showing the stages: sowing (S), seedling emergence (VE), appearance of different leaves (V1–Vn), until the appearance of the first open flower (R1), followed by different reproductive phases in which flowers become pods, seeds start to grow inside pods (R3–R7) until maturity (R8). Boxes indicate the periods of appearance of leaves, nodes, flowering-pod addition, seed growth.

Thomas and Raper, 1976; Sinclair, 1984a), defining the successive V-stages (V1, V2, Vn), with a phyllochron of approximately 50°Cd (base temperature 11°C; Sinclair et al., 2005). Under many field conditions, approximately one leaf expands every three to four days (Fehr and Caviness, 1977; Bastidas et al., 2008). The opening of the first flower, usually in an axillary raceme on the main stem, defines the flowering stage R1. When flowers open at one of the two uppermost nodes on the main stem, the full bloom stage R2 is defined. Subsequent stages are defined by the presence and size of reproductive organs on one of the four uppermost nodes on the main stem with a fully developed leaf, irrespective of the organs present in other positions of the plant: a pod of 5 mm (R3: beginning pod) or 2 cm (R4: full pod), a seed 3 mm long within the pod (R5: beginning seed) or seeds filling the pod cavity (R6: full seed). Maturity begins when one normal pod on the main stem reaches its mature pod color (R7), and full maturity (R8) is attained when 95% of the pods have reached their mature pod color.

The dormant plumule in the soybean seed has two unifoliate leaves and the first trifoliate leaf primordia initiated during seed development in the mother plant (Lersten and Carlson, 2004). After germination, the pre-formed leaves resume their growth and new foliar primordia are differentiated from the shoot apex; shortly afterwards, branches are differentiated from axillary meristems (Borthwick and Parker, 1938; Sun, 1957; Thomas and Kanchanapoom, 1991). Flower initiation is determined by the appearance of a knob-like primordium in the axil of a bract that precedes the differentiation of floral cycles (Guard, 1931; Carlson and Lersten, 2004). From axillary buds, floral primordia are produced in racemes, while the terminal meristems of the main stem continue differentiating foliar primordia (Borthwick and Parker, 1938). In determinate plants, the terminal apex ceases to differentiate leaf primordia soon after flower initiation and forms a pronounced terminal raceme (Thomas and Kanchanapoom, 1991). In indeterminate plants, the terminal meristem remains vegetative for a longer time and differentiates new foliar primordia, while floral differentiation progresses from the lower to the upper nodes (Saitoh et al., 1999). Eventually, the terminal meristem of indeterminate plants forms a floral primordium and ceases the differentiation of leaves (Caffaro et al., 1988), but does not develop a terminal raceme like determinate genotypes. After floral initiation, the flower primordia progress into complete flowers. Soybean flowers are typically self-pollinated on the day when the corolla opens (Fehr, 1980). From anthesis to pod set, pistil length and weight increase

and fertilized ovules develop into embryos (Peterson et al., 1992; Carlson and Lersten, 2004). After a fairly long lag-phase, the seeds begin to accumulate reserves in the cotyledons while water concentration progressively decreases to 55–60%, when physiological maturity is achieved (Swank et al., 1987; Egli, 1998). There are positive correlations between pistil length during early stages of pod development, ovule size and embryo cell numbers, suggesting that changes in external characteristics of flower or pod are correlated with seed development (Peterson et al., 1992). Moreover, seed growth rate during grain filling is highly correlated with the number of cells differentiated in the cotyledons (Egli et al., 1981, 1989; Munier-Jolain and Ney, 1998).

A large proportion of soybean reproductive structures aborts and abscises. Abortion can occur at several stages, including flowers (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986), immature pods (Hansen and Shibles, 1978; McBlain and Hume, 1981; Egli and Bruening, 2005) or young seeds (Duthion and Pigeaire, 1991; Westgate and Peterson, 1993); when seeds enter the linear phase of growth, the chance of pod abortion decreases (Egli, 1998). Combined flower and pod abscission may range from 32 to 82% (van Schaik and Probst, 1958; Hansen and Shibles, 1978; Wiebold et al., 1981). Reductions in crop photosynthesis increase abortion (Hardman and Brun, 1971; Schou et al., 1978; Egli and Zhen-wen, 1991; Jiang and Egli, 1995); pod age, position and timing of development modify the chances of surviving (Egli, 2005). Abortion and abscission are higher in nodes at the top and the bottom of the canopy than in those in the middle (Heindl and Brun, 1984). Within a node, secondary inflorescences (Piegaire et al., 1988) and distal flowers in the raceme (Peterson et al., 1992) are more likely to abort than primary racemes or proximal flowers, while late developing pods have less chance of surviving than early pods (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986; Egli and Bruening, 2002, 2006b). Despite its relative long flowering period, the soybean does not have much capacity to recover from flower and pod abortion induced by relatively short-term (≥14 d) reductions in assimilate supply, and final seed number is reduced even though the rest of the period of production of new pods occurs under optimal conditions (Egli, 2010).

Two characteristics in soybean development highly contrast with wheat: (1) the period of leaf appearance and node elongation partially overlaps with the phases of flowering and pod-addition; and (2) reproductive development is highly asynchronous. Both characteristics are related to the difference in growth habit. In determinate soybean, leaf appearance in the main stem ceases soon after R1 (Bernard, 1972). In contrast, indeterminate plants may produce more than two-thirds of main stem nodes after flowering (Heatherly and Smith, 2004); leaf appearance cessation roughly coincides with R5 (Sinclair, 1984b; Bastidas et al., 2008). In semi-determinate types, stem growth ends suddenly after a flowering period, which is almost as long as that of indeterminate plants (Bernard, 1972). Besides these differences, overlapping still exists in determinate soybeans at the plant level, as the production of nodes on the branches is maximum between R1 and R5 in both extreme types (Egli et al., 1985; Board and Settimi, 1986). The degree of overlap and the differences between extreme growth habits are also dependent on environmental conditions. Short photoperiods or very adverse growing conditions reduce the number of nodes appearing on the branches after R1 in indeterminate (Bernard, 1972; Caffaro and Nakayama, 1988) and determinate cultivars (Settimi and Board, 1988; Frederick et al., 2001).

Asynchronous development at the plant level includes inter-nodal and intra-nodal variations. Continued node production on the main stem of the indeterminate cultivars delays flowering of the upper nodes (Saitoh et al., 1999). This in turn leads to high inter-nodal differences

in post-flowering development (Munier-Jolain et al., 1993, 1994; Kantolic, 2006; Egli and Bruening, 2006a). In determinate plants, most main stem nodes and the basal nodes of the branches begin to flower near simultaneously (Bernard, 1972; Gai et al., 1984), but flowering at a node level is longer than in indeterminate plants (Gai et al., 1984). At whole-plant level, flowering (defined as the time from R1 until the opening of the last flower) and pod-addition (defined as the period when new pods are formed) phases are generally longer in indeterminate than in determinate plants (Egli and Leggett, 1973; Foley et al., 1986; Egli and Bruening, 2006a). Under normal field conditions, asynchronism declines as the plant approaches maturity (Munier-Jolain et al., 1993; Kantolic, 2006). Seeds developing from flowers opening at later growth stages tend to have shorter seed-fill duration (Egli et al., 1987), and reach maturity only a few days after the first pods lose their green color (Spaeth and Sinclair, 1984).

3 DEVELOPMENTAL RESPONSES TO ENVIRONMENTAL FACTORS

The processes regulating crop development are complex due to interactions between genetic and environmental factors. Water deficit delays phenological development in some species such as sorghum (*Sorghum bicolor*) and quinoa (*Chenopodium quinoa*) (Donatelli et al., 1992; Geerts et al., 2008). Availability of resources, that is water, nutrients, radiation and CO_2, may affect the rate of development (Rawson, 1992, 1993; Evans, 1987; Rodriguez et al., 1994; Arisnabarreta and Miralles, 2004), but these effects are quantitatively minor (Slafer, 1995; Hall et al., 2014). In this section, the analysis of environmental control of development will therefore be restricted to the main environmental drivers of crop development: temperature, including temperature *per se* and vernalization, and photoperiod.

3.1 Temperature *per se*

Of the three major environmental factors, temperature *per se* is the only one that has a universal impact on the rates of development (Aitken, 1974). This means that all crops and all phases of development are sensitive to temperature (Miralles and Slafer, 1999). In general, the higher the temperature, the faster is the rate of development and, consequently, the shorter is the time to complete a particular developmental phase (Slafer and Rawson, 1994a). In all species, developmental responses to temperature start as soon as the seed imbibes (Roberts, 1988), and continue until maturity (Hesketh et al., 1973; Angus et al., 1981; Del Pozzo et al., 1987; Porter et al., 1987; Jones et al., 1991; Slafer and Savin, 1991; Cober et al., 2001; Setiyono et al., 2007). From the various models that have been proposed to predict the timing of development affected by temperature, the most widely accepted is the thermal time (with units of degree days, °Cd; Monteith, 1984). The thermal time model is the calendar time weighted by the thermal conditions; it assumes that the rate of development increases linearly with temperature between the cardinal thresholds of base and optimum temperatures. At temperatures higher than the optimum, there may or may not be a plateau followed by a sharp decrease in rate of development until it becomes zero at the theoretical maximum temperature at which development ceases. Although the general model is universal, the actual cardinal temperatures are generally higher for crops of tropical origin (e.g. soybean, rice, maize, sorghum) than for their temperate counterparts (e.g. wheat, barley, canola). Intra-specific, stage-dependent variation in cardinal temperatures has also been reported (e.g. Angus et al., 1981; Del Pozzo et al., 1987; Porter et al., 1987; Slafer and Savin, 1991; Grimm et al., 1993; Rawson and Richards, 1993; Slafer and Rawson, 1994b, 1995a; Boote et al., 1998; Cober et al., 2001; Setiyono et al., 2007). During the growing cycle, cardinal temperatures

increase for wheat (e.g. Slafer and Savin, 1991) but decrease for soybean (Grimm et al., 1994, Setiyono et al., 2007). This reflects the adaptation of wheat to increasing temperatures during its reproductive development, while the opposite occurs in soybeans. Consistent with this proposition, cardinal temperatures decrease with ontogeny in sunflower (Goyne and Hammer, 1982; Chimenti et al., 2001).

3.2 Photoperiod

In comparison to temperature, photoperiod responses are more complex. The degree of variation within species and across stages of development also includes complete insensitivity. Although photoperiodic stimulus is perceived by leaves and transmitted to the apex since the emergence of the crop, many species exhibit a juvenile phase of insensitivity to photoperiod immediately after seedling emergence that imposes a lower limit for the length of the vegetative phase and thus for the final number of leaves. A juvenile phase has been demonstrated for at least some cultivars of soybean (Collinson et al., 1993), maize (Kiniry et al., 1983), barley (Roberts et al., 1988) and sunflower (Villalobos et al., 1996). Other crops such as wheat do not appear to possess a juvenile phase before it becomes sensitive to photoperiod (Hay and Kirby, 1991; Slafer and Rawson, 1995c). These plants perceive the photoperiod stimulus immediately after seedling emergence, and therefore the minimum number of leaves may coincide with the number of leaf primordia initiated by seedling emergence. For example, if photoperiod is sufficiently long after emergence, spring wheat may only have six leaves in the main shoot from seedling emergence to anthesis, which includes the four leaves already present in the embryo plus a couple of leaves initiated from sowing to seedling emergence, when the photoperiod can be perceived (section 2.1.1). Most soybean cultivars have a juvenile phase of variable duration, from 8 to 33 days under optimum temperature (Shanmugasundaram and Tsou, 1978; Board and Settimi, 1988; Ellis et al., 1992; Collinson et al., 1993) but some genotypes have no juvenile phase (Wilkerson et al., 1989; Wang et al., 1998).

Sensitivity to photoperiod is generally quantitative rather than qualitative; that is development is delayed rather than prevented when photoperiod is not optimum (Major, 1980; Summerfield et al., 1993; Slafer and Rawson, 1994a). Most plants are classified by their quantitative photoperiodic response according to the changes in the rate of development and thereby in the length of the phases in response to photoperiod. The two most common categories are 'short-day' and 'long-day' plants. Short-day plants reduce their rates of development (and extend the duration of phases which are sensitive) when photoperiod is lengthened, while long-day plants reduce the duration of their phases when photoperiod is lengthened. Crop species of temperate origin (e.g. wheat, barley, oats, canola, linseed, peas) are long-day plants, while crops of tropical origin (e.g. maize, sorghum, rice, soybean) are short-day plants. Within a particular crop species, genotypes could be classified as follows:

1. Photoperiod insensitive or neutral, if they do not respond to photoperiod in any of its developmental phases; therefore, thermal time to flowering is fairly constant across locations or sowing dates (if insensitive to vernalization), or
2. Photoperiod sensitive, if duration of at least some of its developmental phases increases (short-day species) or decreases (long-day species) in line with photoperiod. Within the sensitive genotypes, there is normally a huge range of genotypic variation.

The optimum photoperiod maximizes the rate of development and, consequently, minimizes the duration of the sensitive phases; photoperiod sensitivity is the delay in duration of a certain stage of development per hour difference between actual and optimum photoperiod. Both

optimum photoperiod and photoperiod sensitivity vary among genotypes (e.g. Major, 1980; Davidson et al., 1985; Worland et al., 1994; Slafer and Rawson, 1996; Summerfield et al., 1998; Kantolic and Slafer, 2005). In soybean, cultivars from low maturity groups present a lower sensitivity and a higher photoperiod threshold than genotypes of high maturity groups (Cober et al., 2001; Boote et al., 2003).

Photoperiod sensitivity could be different throughout the crop ontogeny. For instance, while wheat reduces the length of different phases from seedling emergence to flowering as photoperiod is increased, without any sensitivity described for the duration of grain filling, soybean shows photoperiod sensitivity during the whole crop cycle, including grain filling. The variation in sensitivity during different phases has been in fact proposed as a breeding goal to increase the duration of critical phases for yield determination at the expense of the duration of earlier phases (section 5). Highly sensitive cultivars during early phases (e.g. before double ridges in wheat and before R1 in soybean) are usually highly sensitive during later phases (stem elongation in wheat and post-flowering phases in soybean), but the association is not strict (Kantolic and Slafer, 2001); combinations of different sensitivities at different phases might be possible (Slafer et al., 2001).

Both in wheat and in soybean, less-stimulating photoperiods, that is short in wheat and long in soybean, delay both floral initiation and flowering and increase the number of vegetative primordia generated in the apex (Borthwick and Parker, 1938; Rawson, 1971, 1993; Wall and Cartwright, 1974; Halloran, 1977; Thomas and Raper, 1977; Major, 1980; Hadley et al., 1984; Pinthus and Nerson, 1984; Raper and Kramer, 1987; Roberts and Summerfield, 1987; Caffaro and Nakayama, 1988; Sinclair et al., 1991; Evans and Blundell, 1994; Slafer and Rawson, 1994a,b, 1995d, 1996; Upadhyay et al., 1994a,b; Fleming et al., 1997; Kantolic and Slafer, 2001, 2005; Kantolic et al., 2013; Zhang et al., 2001; Miralles et al., 2001, 2003; González et al., 2002). In line with the extended periods, non-stimulating photoperiods modify the number of tillers and the number of leaves per tiller in wheat and the number of branches and the number of nodes in the branches of soybean (Thomas and Raper, 1983; Board and Settimi, 1986; Settimi and Board, 1988; Caffaro and Nakayama, 1988; Miralles and Richards, 2000; Kantolic and Slafer, 2001, 2005, 2007; Kantolic et al., 2013).

Photoperiod also affects developmental rates of soybean after flowering: the duration of the flowering, pod addition phases and the time from R1 to full maturity are increased by direct exposure to long photoperiod (e.g. Johnson et al., 1960; Lawn and Byth, 1973; Major et al., 1975; Thomas and Raper, 1976; Raper and Thomas, 1978; Guiamet and Nakayama, 1984a; Morandi et al., 1988; Summerfield et al., 1998; Kantolic and Slafer, 2001; Han et al., 2006; Kantolic and Slafer, 2007; Kumudini et al., 2007). During seed filling, long photoperiods increase the duration of the lag phase (Zheng et al., 2003; Kantolic, 2006) and delay leaf senescence (Han et al., 2006). It has been proposed that the synchronization in seed maturation, which contrasts with the low synchronism that prevails during the early stages of flowering and pod set, is attributable to photoperiod responses: late developing seeds are generally exposed to short photoperiods that increase their development rate (Gbikpi and Crookston, 1981; Raper and Kramer, 1987). In fact, asynchronous maturity has been described in soybeans exposed to long days under both controlled (Guiamet and Nakayama, 1984b) and field conditions (Mayers et al., 1991). In field experiments that included photoperiod manipulations, asynchronism was quantitatively affected by photoperiod, and the response could be partially reverted by exposure to short photoperiod (Kantolic, 2006).

As photoperiod modulates flowering time and potential plant size, pre-flowering responses to photoperiod have a strong impact on adaptation and potential yield (Roberts

et al., 1993). In fact, the classification of soybean cultivars in maturity groups defining broad-sense adaptation is based on pre-flowering developmental response to photoperiod (Summerfield and Roberts, 1985; Boote et al., 1998; Heatherly and Elmore, 2004).

3.3 Vernalization

Vernalization is the acceleration of development by exposing sensitive cultivars to cool temperature during the early stages of crop ontogeny. The plant apex may sense vernalizing temperatures from seed imbibition, throughout the vegetative phase. Vernalization requirements are typical of crops with a temperate origin. In many of these crops, there are 'winter' and 'spring' cultivars. It is frequently assumed that vernalization requirements are characteristic of winter genotypes within a particular species. The difference between spring and winter types may be restricted, however, to the magnitude of vernalization responsiveness (e.g. Levy and Peterson, 1972; Slafer and Rawson, 1994a).

Vernalization may be reversed if the period of low temperature is interrupted, an effect known as 'devernalization'. This was experimentally proven in wheat by Gregory and Purvis (1948) and Purvis and Gregory (1952). Dubert et al. (1992) showed that devernalization may occur at temperatures between 20 and 30°C.

Excluding the effects of temperature *per se* by the calculation of the length of the phases in degree days, photoperiod and vernalization are generally considered to account for most of the differences in development rate among cultivars; any 'residual' difference after the vernalization and photoperiod requirements were satisfied would be the consequence of differences in 'basic development rate' or 'intrinsic earliness' (Major, 1980; Flood and Halloran, 1984; Masle et al., 1989, Slafer, 1996), which are discussed in section 4.1.3.

4 GENETIC CONTROL OF DEVELOPMENT

4.1 Genes affecting development in wheat and related species

The life cycle in wheat is determined by genes that regulate (1) photoperiod response (*Ppd*), (2) vernalization response (*Vrn*) and (3) developmental rates independent of these two environmental factors, called either intrinsic earliness, earliness *per se* or developmental rate genes (*Eps*). The latter are also affected by temperature depending on the gene and allele considered (Slafer and Rawson, 1995b; Appendino and Slafer, 2003). Most of the variation in developmental rates is explained by vernalization and photoperiod response genes, with smaller, more subtle effects of *Eps* alleles (Slafer, 2012; Gomez et al., 2014).

Wheat is an allohexaploid with three genomes, A B and D (Table 12.1): the simultaneous presence of more than one locus implicated in a particular trait (homeologous loci) generates a more complex inheritance pattern than in diploid related species. This polyploid nature prompted an early interest on genetic research in wheat, through a cytogenetic approach, taking advantage of the use of aneuploid genetic stocks. In this way, genetic variability in characters such as vernalization and photoperiod responses are well documented (Worland et al., 1987; Law et al., 1991). Interest in earliness *per se* is more recent, owing to smaller effects and more complex interactions requiring new molecular approaches to understand the *Eps* alleles (Table 12.1).

Understanding genes affecting development in wheat has gained further relevance recently with the development of models using particular gene effects rather than generalized genetic coefficients in crop simulation exercises (Chapter 14). This approach makes models more suitable for developing and testing hypotheses on the genetic improvement value of particular

developmental traits based on quantitative predictions of G × E interactions for particular genes (Yin et al. 2000; Hoogenboom and White, 2003; White et al., 2008; Zheng et al., 2013).

4.1.1 Vernalization response genes

Vernalization requirement is the need of fulfillment of a low temperature period in sensitive genotypes to avoid delays in development to reach floral initiation. This requirement prevents the exposure of developing flowers to frost in sensitive cultivars. Most studies about the genetic systems controlling these requirements have been concentrated in the major genes *Vrn1* of *Triticum aestivum*, which explains a large amount of the qualitative variability observed in germplasm and cultivars grown around the world. They are located on homeologous chromosomes 5A (*Vrn-A1*, formerly *Vrn1*); 5B (*Vrn-B1*, formerly *Vrn2*) and 5D (*Vrn-D1*, formerly *Vrn3*) (Flood and Halloran, 1986; Snape et al., 2001); and they map to equivalent position to *Vrn-H1* in *Hordeum vulgare*, *Vrn-R1* in *Secale cereale* and *Vrn-A^{m}1* in diplod wheat *T. monococcum* (Laurie, 1997; Dubcovsky et al., 1998). Additional loci like *Vrn2* (Yan et al., 2004a; Distelfeld et al., 2009a), *Vrn3* (Yan et al., 2006) and *Vrn4* (Yoshida et al., 2010) are also involved in the gene pathway of vernalization (Table 12.1). However, variability on these loci is less known.

TABLE 12.1 *Ppd*, *Vrn* and *Eps* loci of *Triticum aestivum* (T.a.; allohexaploid: A, B and D genomes); *Triticum monococcum* (T.m; diploid: A^m genome) and *Hordeum vulgare* (H.v; diploid: H genome)

	Genomes				
	***T.a* 2n = 6x**			***T.m* 2n = 2x**	***H.v* 2n = 2x**
Chromosome group	**A**	**B**	**D**	**A^m**	**H**
1					*Ppd-H2*
				Eps-A^m 1	
2	*Ppd-A1*	*Ppd-B1*	*Ppd-D1*		*Ppd-H1*
		Eps2-B			*Eps2-HL* *Eps2-HS*
3	*Eps-AL*				*Eps3-HS*
4					*Eps4-HS*
					Vrn-H2
5	*Eps5*	*Eps5-BL $_{1-2}$*			*Eps5-HL*
	Vrn-A1	*Vrn-B1*	*Vrn-D1*	*Vrn-A^m 1*	*Vrn-H1*
	Vrn-A2	***Vrn.B2***	***Vrn-D2***	*Vrn-A^{m}2*	
6					*Eps6-HL1* *Eps6-HL2*
7					*Eps7-HS* *Eps7-HL*
		Vrn-B3	*Vrn-D4*		*Vrn-H3*

Numbers from 1 to 7 at the left indicate the chromosome group. Main genes, genetically mapped either as QTL or major genes are in normal type, while not genetically mapped are in bold. Genes are grouped by character. The gene order in the table does not indicate the gene order in the respective chromosome. For gene nomenclature see text in Sections 4.1.1, 4.1.2 and 4.1.3.

The presence of dominance in one or more *Vrn1* loci results in partial or complete elimination of the vernalization requirement, giving rise to spring phenotypes, while winter wheat normally carries recessive alleles. Early studies indicated that the *Vrn-A1* locus has the greatest effect in the elimination of the vernalization requirement (Law et al., 1976; Snape et al., 1976), with some alleles like *Vrn-A1a* conferring insensitivity to vernalization (Appendino and Slafer, 2003; Yan et al., 2004a). Variability in these loci is spread in commercial germplasm but the allelic frequencies may vary depending on the region of cultivation in the world (Stelmak, 1990; Yan et al., 2004a).

A gene primarily detected in the diploid wheat *T. monococcum* is *Vrn-A^{m}2* (mapped on chromosome 5A^m) is also present in *H. vulgare* (*Vrn-H2*). This gene is, in contrast to *Vrn1*, a dominant repressor of flowering and is downregulated by both vernalization and short day (Yan et al., 2004b; Dubcovsky et al., 2006). This genetic factor also regulates flowering by vernalization in polyploid winter wheat. There is no evidence of phenotypic variability in hexaploid wheat but its presence has been demonstrated through RNAi transgenic wheats in winter cultivar Jagger (Yan et al., 2004b) and through chromosome engineering in tetraploid (*T. durum*) wheat (Distelfeld et al., 2009a). Both in barley and diploid wheat, the determination of the vernalization requirement involves an epistatic interaction between *Vrn1* and *Vrn2* (Tranquilli and Dubcovsky, 2000).

Vrn3 is a locus involved in the pathway of vernalization requirement, upregulated by long days. It is located on chromosome 7B (*Vrn-B3*, formerly *Vrn5*), is orthologous to the barley gene *Vrn-H3* located on chromosome 7H, and shows a dominant spring inheritance. The mutation that generates spring genotypes in wheat is not widely spread in commercial germplasm representing a potentially valuable source of genetic diversity (Yan et al., 2006).

Vrn4 is a less characterized gene, and natural variability has been reported only in the D genome (*Vrn-D4*). It promotes flowering and the presence of a dominant *Vrn-D4* allele determines spring growth habit, with a residual response to vernalization. *Vrn-D4* has recently been mapped on chromosome 5D (Yoshida et al., 2010).

Interactions between these genes have been observed, suggesting that all of them integrate the same regulatory pathway of flowering initiation mediated by vernalization. Based on the knowledge acquired from the isolation of *Vrn1*, *Vrn2* and *Vrn3* genes, a model of molecular regulation has been proposed, which integrates also the vernalization and photoperiod pathways (Box 12.2).

4.1.2 Photoperiod response genes

In bread wheat, photoperiod sensitivity is mainly determined by a group of genes located on chromosome group 2 (Table 12.1), namely *Ppd-D1*, formerly *Ppd1* (chromosome 2D), *Ppd-B1*, formerly *Ppd2* (chromosome 2B), and *Ppd-A1*, formerly *Ppd3* (chromosome 2A). Photoperiod insensitivity is of dominant effect, and *Ppd-D1* is the main source of photoperiod insensitivity conferred by the *Ppd-D1a* allele (Worland and Law, 1985; Worland, 1999). *Ppd-B1* is also an important source of photoperiod insensitivity (Scarth and Law, 1984). Although chromosome 2A influences photoperiod sensitivity (Law et al., 1978; Scarth and Law, 1984), to the best of our knowledge *Ppd-A1* has not been genetically mapped. Chromosomes of other groups (1, 3, 4 and 6) may also be involved in photoperiod response, either via modifiers or via major genes (Law, 1987). Law (1987) demonstrated the adaptive roles of *Ppd-D1* and *Ppd-B1* loci using substitution lines with contrasting genotypes in photoperiod response genes.

Two major loci regulating the photoperiod response in barley are *Ppd-H1* and *Ppd-H2* located on chromosomes 2H and 1H, respectively

BOX 12.2

FLOWERING TIME: MODEL OF THE REGULATORY PATHWAY MEDIATED BY VERNALIZATION

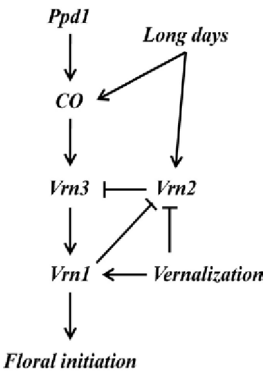
Vrn1, *Vrn2* and *Vrn3* genes have been cloned, providing important hints to unravel the regulatory pathway of the spike initiation in response to seasonal cues. These vernalization genes interact and integrate the day-length response to prevent or promote the reproductive stage (reviewed by Trevaskis et al., 2007; Distelfeld et al., 2009b).

Vrn1 encodes a transcriptor factor highly similar to the meristem identity gene *Apetala 1* (*Ap1*) from *Arabidopsis thaliana*, which regulates the transition of the shoot apical meristem from vegetative to reproductive. Sequence changes (insertions or deletions) in regulatory regions have naturally occurred in the three homoeologous *Vrn1* genes giving rise to dominant alleles for spring growth habits.

The *Vrn2* locus includes two tightly linked and related genes (*ZCCT1* and *ZCCT2*), which both repress flowering initiation under long days. In diploid species, like barley or *T. moncoccum*, simultaneous deletion or non-functional mutations of both genes were associated with recessive alleles for spring growth habits.

Vrn3 is a functional homolog to the *Flowering Locus T* (*FT*) formerly described as a flowering promoter in *A. thaliana*. The coded protein moves from leaf to shoot apex through the phloem. *Vrn3* accelerates flowering promoting the transcription of *Vrn1* under long days. *Vrn3* (*FT*) is considered a central flowering integrator, since the vernalization and photoperiod signals converge on it. The day-length response is mediated by *Ppd1*, which acts in conjunction with the homologs of the *Arabidopsis* photoperiod gene *CONSTANS* (*CO*). In *Arabidopsis*, long days result in the stabilization of CO proteins, which upregulate *FT* resulting in the acceleration of flowering. This *CO* function would be conserved in temperate cereals.

The model proposes that for a winter, photoperiod-sensitive wheat (ancestral phenotype) sown early in the fall, floral initiation inducted by *Vrn1* is prevented mainly by the action of *Vrn2*, which represses the expression of *Vrn3*, otherwise expected to show a high transcript level under long days. As winter progresses, cold temperatures and short days downregulate *Vrn2*. Low levels of *Vrn2* release *Vrn3* from its repression which, in turn, is induced during the long days of the spring under the regulation mediated by *Ppd1*. *VRN3* protein moves from leaf to apex, where it promotes *Vrn1* transcription leading to the initiation of the reproductive stage. *Vrn1* also acts as a direct or indirect repressor of *Vrn2*, completing the regulatory feedback loop among these genes, which ensures that, once started, the flowering phase progresses steadily. Under this model, any mutation (as those mentioned above) limiting the repressive action of *Vrn2*, either by its own non-functional protein, or by alterations in the repressor recognition sites, will determine a spring wheat.



(Table 12.1; Laurie et al., 1995). *Ppd-H1* has been cloned (Turner et al., 2005), and the region of chromosome 2H that contains *Ppd-H1* is collinear with the region of chromosome 2D of wheat where *Ppd-D1* has been mapped (Laurie, 1997; Borner et al., 1998). However, these genes have important differences in the photoperiod response of barley and wheat. In the presence of *Ppd-D1a* (a semi-dominant allele), wheat flowers rapidly on either short or long days, but the recessive genotype delays flowering on short days. In barley, the recessive *Ppd-H1* delays flowering on long days, but has no effect on short days (Laurie et al., 1995; Turner et al., 2005). According to Beales et al. (2007), these wheat and barley *Ppd* genes have contrasting types of mutations, which cause, in wheat, the induction of *Vrn3* (Yan et al., 2006), irrespective of day length, and in barley, the failure to induce this gene correctly on long days (Box 12.2).

Although sowing to heading or anthesis is often considered as a single phase, it is clear that sensitivity to photoperiod changes with developmental phases (e.g. Slafer and Rawson, 1996; Miralles et al., 2000; González et al., 2002). Understanding and manipulating the differential sensitivity to photoperiod at different stages might be useful in increasing yield potential (section 5). However, most attempts to identify genes of photoperiod sensitivity, in particular phases using near-isogenic or recombinant inbred lines for *Ppd* alleles have failed (Scarth et al., 1985; Whitechurch and Slafer, 2001, 2002; Foulkes et al., 2004; González et al., 2005c). This is likely because we only know (and have worked with) a few of the hypothesized genes for photoperiod sensitivity (Table 12.1; Snape et al., 2001). There are other approaches to determine what genes are down- or up-regulated in response to photoperiod (Ghiglione et al., 2008) or to identify genes or quantitative trait loci (QTL) for differences in length of different phases within mapping populations (Borràs-Gelonch et al., 2010) to allow breeding for developmental partitioning (García et al., 2011).

4.1.3 *Earliness* per se *genes*

Time to heading can differ among cultivars by several weeks depending on the interaction between photoperiod, vernalization requirement and the ambient temperature. Where the vernalization and photoperiod requirements have been adequately satisfied, significant differences in time to heading may still persist. The genetic factors underlying these differences have received different names: narrow sense earliness, earliness *per se*, intrinsic earliness or basic development rate genes (e.g. Slafer, 1996, and references quoted therein).

In polyploid species such as *T. aestivum* or diploid species such as *H. vulgare* or *T. monococcum*, this character exhibits a complex genetic base. Earliness *per se* genetic effects have been identified mainly on *T. aestivum* chromosomes of groups 2, 3 and 5 (Table 12.1); a few of them have been mapped as QTL (Scarth and Law, 1984; Miura and Worland, 1994; Worland, 1996; Kato et al., 2002; Toth et al., 2003).

In *T. monococcum*, a QTL for earliness *per se* is located on the distal region of chromosome $1A^mL$ (*Eps-A^{m}1*) (Bullrich et al., 2002). Allelic variation at this locus modified flowering time with fully vernalized plants grown under long day in a controlled environment. Also, smaller differences under natural conditions, in interaction with photoperiod and vernalization requirements were evidenced. *Eps-A^{m}1* was then mapped within a 0.8 cM interval using a high-density mapping population and markers generated from the rice collinear region (Valarik et al., 2006). In *H. vulgare*, Laurie et al. (1995) mapped several QTL for *Eps* (Table 12.1), giving evidence of a wide dispersion of candidate genetic factors underlying this character in barley. Future studies will help in the identification of these potential *Eps* genes that, according to Snape et al. (2001), would also be expected to be present in wheat.

4.2 Genes affecting development in soybean

4.2.1 Photoperiod response genes

Genetic control of flowering has been widely used to improve crop adaptation in classical soybean breeding programs (Curtis et al., 2000). The control of time of flowering involves at least eight major loci, each with two alleles: *E1/e1*, *E2/e2* (Bernard, 1971), *E3/e3* (Buzzell, 1971), *E4/e4* (Buzzell and Voldeng, 1980), *E5/e5* (McBlain and Bernard, 1987), *E6/e6* (Bonato and Vello, 1999) and *E7/e7*, closely linked to *E1/e1* (Cober and Voldeng, 2001) and *E8/e8* (Cober et al., 2010). In most cases, the dominant or partially dominant allele lengthens time to flowering in response to photoperiod (McBlain et al., 1987; Saindon et al., 1989; Cober et al., 1996); an exception to this is *E6*, in which early flowering is dominant (Bonato and Vello, 1999). Apparently, the genes of the E series, also known as maturity genes, have no effects on the response of development to temperature (Upadhyay et al., 1994a).

Sensitivity of genotypes to photoperiod depends on the allelic composition of E-genes. Photoperiod sensitivity tends to increase with the number of dominant alleles (Summerfield et al., 1998; Cober et al., 2001; Stewart et al., 2003; Kumudini et al., 2007). The number and type of dominant alleles also seem to modify the photoperiod threshold for response (Messina et al., 2006). Lines with the dominant allele *E1* tended to have a longer juvenile period (Upadhyay et al., 1994b); modeling also supports the role of *E1* in extending the juvenile phase (Messina et al., 2006). Besides their direct effect on photoperiod response, some combinations of alleles seem to have additional advantages in crop adaptation; for instance, the allelic combination of *E1e3e4* is preferable to *e1E3E4* to enhance yield under chilling conditions (Takahashi et al., 2005).

Several QTL associated with flowering time and maturity have been mapped in soybean (Keim et al., 1990; Mansur et al., 1996; Lee et al., 1996; Tasma et al., 2001; Abe et al., 2003; Matsumura et al., 2008); molecular markers are available for marker-assisted breeding for photoperiod sensitivity. Although some association has been found between some loci E and those controlling flowering time in *Arabidopsis thaliana* (Tasma and Shoemaker, 2003), the molecular basis of photoperiodic response in soybean has not been elucidated.

Near-isogenic lines have been developed for the genes of the E-series by back-crosses with different commercial lines (Bernard, 1971; Saindon et al., 1989; Voldeng and Saindon, 1991; Voldeng et al., 1996; Cober and Morrison, 2010). Although the genes that control pre- and post-flowering development are apparently the same, their individual effects may differ depending on the developmental phase. For instance, the allele *E1* alone has a considerable effect on delaying flowering under long days, but has virtually no effects on delaying maturity. In contrast, the effects of *E2*, *E3*, *E4*, *E5* and *E7* on delaying flowering are less marked than those of *E1* but they are effective in delaying maturity under long photoperiods (Bernard, 1971; McBlain and Bernard, 1987; Saindon et al., 1989; Upadhyay et al., 1994a; Cober et al., 1996; Summerfield et al., 1998; Cober and Voldeng, 2001; Xu et al., 2013). The effects of the genes are not purely additive; interactions between them differ depending on developmental stage (Bernard, 1971; Buzzell and Bernard, 1975; Buzzell and Voldeng, 1980; Upadhyay et al., 1994a).

In addition to these major genes, many QTL associated with flowering time and maturity have been mapped in soybean (Keim et al., 1990; Mansur et al., 1996; Lee et al., 1996; Tasma et al., 2001; Abe et al., 2003; Watanabe et al. 2004; Matsumura et al., 2008; Liu and Abe 2010; Cheng et al., 2011). Recent efforts to understand the molecular bases of the major genes and QTL have identified and characterized the soybean orthologs of *Arabidopsis* photoreceptors, clock-associated genes, and flower-identity genes as flowering genes (Watanabe et al., 2012). The

functional genes underlying the loci *E3* and *E4* were found to code for phytochrome A3 (Watanabe et al., 2009) and A2 (Liu et al., 2008), respectively. *E2* is a soybean ortholog of the *GIGANTEA* gene (Watanabe et al., 2011). The nuclear protein *GIGANTEA* is involved in the expression of *CONSTANS* (*CO*) and *FLOWERING LOCUS T* (*FT*) in the photoperiodic pathway in *Arabidopsis* (Sawa and Kay 2011); *CONSTANS* (*CO*) is a central regulator of this pathway, triggering the production of the mobile florigen hormone FT that induces flower differentiation (Valverde, 2011). Some studies have suggested that *E1* protein might function as a transcription factor in the phytochrome A signaling pathway, controlling two *GmFTs* genes, orthologs of the *Arabidopsis FT* (Kong 2010; Xia et al., 2012). In fact, soybean not only possesses orthologs for most of the *Arabidopsis* flowering genes but also has multiple copies of most of them; the functions of these multiple orthologs in the control of soybean flowering should be still clarified (Watanabe et al. 2012).

Some QTL have also been identified to control post-flowering photoperiod responses (Watanabe et al., 2004; Cheng et al., 2011; Komatsu et al., 2012). In coincidence with the role of phytochromes mediating some photoperiod responses after flowering (Han et al., 2006), post-flowering photoperiod sensitivity has been associated with *E3* and *E4*, but not with *E1* (Xu et al., 2013). It has been proposed that the *E3* and *E4* alleles inhibit pod development and seed maturation through the activation of a still unknown factor and directly control the persistence of the vegetative activity of the stem apex (Xu et al., 2013).

4.2.2 Long-juvenile genes

Some soybean genotypes delay flowering under short days (Hartwig and Kiihl, 1979). This trait was first identified in a plant introduction designated as P1 159925, and has been subsequently referred to as 'long-juvenile' (Parvez and Gardner, 1987; Hinson, 1989; Wilkerson et al., 1989), although there is no evidence that the trait alters the length of the juvenile period. The long-juvenile trait retards the overall development towards flowering, so that under short days the emergence-to-flowering period is longer in long-juvenile compared with normal genotypes (Sinclair et al., 1991, 2005; Sinclair and Hinson, 1992; Cairo and Morandi, 2006). This trait is useful in tropical and subtropical areas, as flowering can be delayed in spite of the prevailing conditions of high temperature and short photoperiod.

Examining the segregation pattern of this trait in six F2 populations, from crosses between conventional lines and P1 159925, Ray et al. (1995) concluded that the trait is controlled by a single recessive gene (J/j): the conventional phenotype (JJ) has normal photoperiodic response, while the long-juvenile phenotype (jj) delays flowering under short days. Studying the inheritance of the long-juvenile trait under short days for BR80-677 and MG/BR 22 soybeans, Carpentieri-Pípolo et al. (2000, 2002) proposed that the long-juvenile trait may be controlled by three recessive genes; a genotype with a single pair of recessive alleles did not show the long-juvenile characteristic. The recessive genetic combination in three loci causes a longer pre-flowering period than recombination in two loci.

Differences between normal and long-juvenile lines are small under long days (Cregan and Hartwig, 1984; Parvez and Gardner, 1987; Sinclair and Hinson, 1992; Cairo and Morandi, 2006). The genetic background has important effects on the quantitative expression of the trait (Sinclair and Hinson, 1992; Ray et al., 1995; Sinclair et al., 2005). To avoid environmental and genetic effects in the expression of the character, Cairo et al. (2002) have generated molecular markers linked to the juvenile locus in two genetic backgrounds of soybean that can be used for an early discrimination of long-juvenile plants in a segregating population.

4.2.3 *Growth habit genes*

The growth habit or stem termination in soybean is affected by two loci (*Dt1*, *Dt2*) (Bernard, 1972). Determinate growth habit is conditioned by the recessive allele (*dt1dt1*); the dominant gene pair *Dt1Dt1* produces the indeterminate phenotype. A second gene (dominant *Dt2*), independent of the *Dt1* locus, produces a semi-determinate phenotype in the presence of *Dt1*; *dt1* is epistatic to *Dt2-dt2*. However, Bernard (1972) observed that, in some genetic backgrounds, *Dt2* and *dt1dt1* produce indistinguishable phenotypes, and that *Dt1Dt1* may be modified by other genetic factors. A third allele (*dt1-t*) was reported at the *dt1* locus (Thompson et al., 1997); plants with this allele present a tall determinate phenotype. Although *dt1-tdt1-t* and *Dt2Dt2* phenotypes are similar in plant height, *dt1-tdt1-t* is more similar to *dt1dt1* when considering leaf and stem traits at the top of the plant.

Isogenic lines for indeterminate/determinate growth habit alleles at the *Dt1* locus in combination with different photoperiod sensitive/insensitive alleles at loci *E1*, *E2*, *E3*, *E4*, and *E7* have been developed to allow comparison of differences between the two growth habits in a wide range of maturity (Cober and Morrison, 2010). When comparing isogenic lines of the same maturity group, determinate lines were always shorter than indeterminate ones but determinate and indeterminate isogenic lines had similar seed yields (Cober and Morrison, 2010).

The *Dt1* gene is an ortholog of *Arabidopsis TERMINAL FLOWER1* (*TFL1*), *GmTFL1b* (Liu et al., 2010; Tian et al., 2010). The *Dt1* expression is under the control of the two phyA-genes, *E3* and *E4*. When photoperiod-sensitive plants having *E1* and a dominant allele at either the *E3* or *E4* locus (or both) are exposed to non-inductive long days, the vegetative activity at the stem apex meristem is retained to produce more nodes due to the enhanced expression of *Dt1* (Xu et al., 2013).

5 CAN WE IMPROVE CROP ADAPTATION AND YIELD POTENTIAL THROUGH FINE-TUNING DEVELOPMENTAL RATES?

Although yield components are being formed all the time from sowing to maturity (e.g. Slafer et al., 1996; Slafer, 2003), there are particular phases that are more relevant for yield. This means that there is scope for improving yield through manipulation of phenology. The prerequisites for this to be effective is that we must (1) recognize the phases which are actually critical, (2) be able to manipulate development to avoid stressful conditions (adaptation) or take advantage of resource availability (yield potential) in these critical phases and (3) evaluate trade-offs between yield components when the developmental phases are modified. In wheat and soybean, yield relates with number of grains rather than average grain size (Slafer and Andrade, 1993; Magrin et al., 1993; Egli, 1998). Evolutionary principles explain the dominant role of grain number and the secondary influence of grain size (Sadras, 2007; Sadras and Slafer 2012; Slafer et al. 2014).

Number of grains per unit area is largely determined by the events during the stem elongation phase in wheat, while in soybean, the critical phase for seed number goes from soon after flowering to early seed filling. These species-specific periods are known as 'critical period' for yield determination. Thus, crop ontogeny should be tailored to avoid stress during the most critical stages (Lawn and Imrie, 1994) and to capture the environmental conditions that favor grain number; environmental characterizations quantifying likelihood of stress in critical period are therefore important (Chapter 13). With good supply of nutrients and water, the number of grains per unit area is proportional to the amount of solar radiation affecting growth and negatively related

to mean temperature affecting development. Thus, their combined effect can be described by the photothermal quotient defined as the ratio of radiation and temperature (Nix, 1976). Fischer (1984, 1985) demonstrated a strong correlation between the number of grains per unit area and the photothermal quotient during the critical period of wheat. In soybean, capture of solar radiation during the pod-setting stage is closely associated with the number of grains per unit area (Kantolic and Slafer, 2001; Calviño et al., 2003).

5.1 Crop development and adaptation

An important objective of crop adaptation is to match crop development phases with optimum environmental conditions, particularly, the timing of flowering is critical. If flowering is too early, plant growth may be insufficient to produce a minimum amount of biomass compatible with reasonable yields (Mayers et al., 1991). This is why early vigor of the crop is much more important for 'short-season' crops (e.g. spring cereals grown at high latitudes) than for 'full season' crops. Chapter 4 discusses in detail the challenges of growing temperate crops in northern Europe, including the role of phenology as the key adaptive trait in these extreme environments. On the other hand, if flowering is too late, the period available for grain growth may be too short and/or too stressful (Lawn et al., 1995). Therefore, the above-mentioned extremes (early and late flowering) define the length of the growing season, and the pre-flowering development may be manipulated to improve adaptation by balancing the optimum time of flowering (Rhone et al., 2010) and the consequent duration of pre- and post-flowering phases.

Phenological adaptation is particularly critical in stressful environments. When water or nutrients are scarce, vegetative growth may become limiting, increasing the length of the pre-flowering phase, which may increase the size of both canopy and root system. Cultivars with a longer vegetative period may have deeper root systems and better capacity of extracting water from deeper soil layers than early flowering ones (e.g. Giménez and Fereres, 1986; Dardanelli et al., 2004), which may be useful provided the soil holds water deep in the profile. In contrast, long-cycle cultivars may deplete more water before the critical periods (Edwards and Purcell, 2005), risking more severe stress when crop yield is most sensitive; under these circumstances, early-flowering cultivars may produce larger yields when moisture stress develops late in the season (Fig. 12.1; Kane and Grabau, 1992).

Crop development may also improve cultivar adaptation by reducing the risk of biotic stresses. Early-maturing wheat had been useful for escaping rust damage in Australia (Park et al. 2009), while management techniques based primarily on early-maturing cultivars of soybean effectively reduced the impact of stem rot (*Sclerotinia sclerotiorum*) in Argentina (Ploper, 2004).

In soybean, the stem-termination habit, which modifies the length of the phase of node production independently of the duration of pre-flowering stages, is not directly associated with potential yield, but confers some characteristics that may modify cultivar adaptation. Determinate growth habit is useful in reducing plant height and lodging but can result in excessive dwarfing in early-maturing soybean (Cober and Tanner, 1995). Indeterminate cultivars tend to yield better than determinate ones in yield-restricted environments and late plantings (Beaver and Johnson, 1981; Robinson and Wilcox, 1998; Kilgore-Norquest and Sneller, 2002). However, the adaptive value of stem termination types to particular environments may also depend on genetic background (Heatherly and Elmore, 2004).

5.2 Crop development and yield potential

A large body of evidence indicates that reduction in canopy photosynthesis before the onset of stem elongation in wheat or before

R1 in soybean seldom reduces the final number of seeds, while crop growth reduction after stem elongation in wheat or from R2 to R5 in soybean is directly related with the number of seeds or pods set (Fischer, 1985, 2011; Egli and Zhen-wen, 1991; Savin and Slafer, 1991; Jiang and Egli, 1993, 1995; Board et al., 1995; Board and Tan, 1995; Abbate et al., 1997; Demotes-Mainard and Jeuffroy, 2004; González et al., 2005a; Miralles and Slafer, 2007; Ferrante et al., 2012). In wheat, where grain filling is mostly sink limited (Slafer and Savin, 1994; Borrás et al., 2004), reduction in grain number cannot be compensated by an increase of grain weight, except for small compensations that might occur if the decrease in grain number brings about increases in carpel size and concomitantly greater grain weight potential (Calderini and Reynolds, 2000; Calderini et al., 2001; Ugarte et al., 2007). In soybeans, where seed filling is usually more limited by the source (Egli, 1999, 2004; Borrás et al., 2004; Egli and Bruening, 2006b), reductions in seed production by stresses during R1–R3 may be partially compensated by favorable conditions during seed filling.

Within this context, from the developmental point of view, it has been proposed that the length of the critical phase might be extended at the expense of the duration of earlier phases as a means of increasing yield potential both in wheat (Slafer et al., 2001, 2005; Miralles and Slafer, 2007) and soybean (Kantolic et al., 2007). Briefly, the length of the critical phase in both crops is (1) highly relevant in the determination of seed number per unit land area (Fig. 12.4a) and (2) sensitive to photoperiod (Fig. 12.4b). In experiments where crops were exposed to different day lengths, the number of grains metre^{-2} increased with increasing duration of the critical phase (Fig. 12.4c). In soybean, the increase in seed number in response to long photoperiod is related to both more nodes per plant and more seeds per node, which actively accumulate during the critical period; this is strongly supported by experiments both in controlled environments (Guiamet and Nakayama, 1984a,b; Morandi et al., 1988) and in the field (Kantolic and Slafer, 2001, 2005, 2007; Kantolic et al., 2013). In wheat, the increase in seed number in response to short photoperiod is mainly related to the fate of floret primordia during the 'floret mortality' period: with longer photoperiod and shorter phase, the proportion of floret primordia that develops towards fertile florets is consistently reduced (González et al., 2003b, 2005b; Ghiglione et al. 2008; Serrago et al., 2008). Early studies where the duration of the stem elongation phase was modified demonstrated that increasing assimilate allocation to the spike can improve survival of florets in the middle of the spikelet, mostly in the third to fifth position from the rachis within the spikelet (González et al., 2005a). Furthermore, recent evidence supports that both the onset and rate of floret death are strongly linked to resource availability for the developing (and growing) florets (González et al., 2011; Ferrante et al., 2013b). More detailed studies suggest that mortality is linked to autophagy (Box 12.3). From the association between seed set, duration of critical phases and the photoperiodic control of these phases, it has been proposed that selecting for photoperiodic sensitivity could increase grain set (Fig. 12.4d).

6 CONCLUDING REMARKS

In this chapter, the particularities of development of wheat and soybean have been discussed to highlight the importance of identifying the genetic and environmental controls of the phenological pattern. This knowledge is a prerequisite to understand, predict and manipulate the association between crop cycle, the resources and the environmental constraints to favor the coincidence of the critical period with the most favorable conditions. Although the cycle to match crops and environmental factors has been determined in most production systems, further improvement is feasible by manipulation of critical periods.

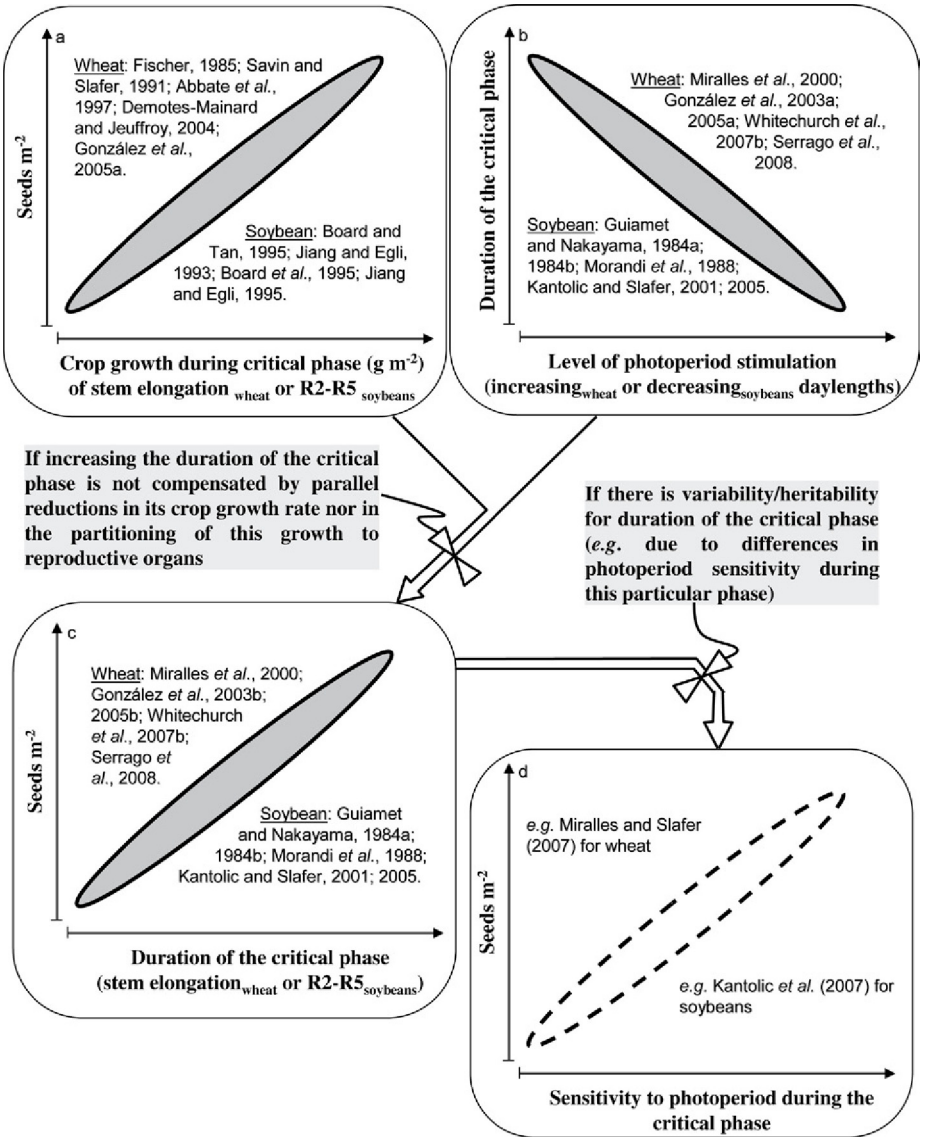


FIG. 12.4 The top two panels summarize two principles: seed number is strongly responsive to crop growth during a critical phase for seed number determination ((a) with some of the many references evidencing this relationship), and these phases in wheat and soybean are sensitive to photoperiod so that the less inductive the photoperiod the longer the phase (b). Lack of or incomplete compensation between crop duration and growth rate during the critical phase, means that longer duration favor higher seed set, as shown when the duration of the critical phase is altered by manipulating photoperiod only during this phase (c). Thus, increasing sensitivity to photoperiod during this particular phase would increase seed number m^{-2} through increasing growth, allowing in turn the set of more inflorescences, more seeds per inflorescence or both (d). A more comprehensive treatment can be found in Slafer et al. (2001), Miralles and Slafer (2007) and Slafer et al. (2014) for wheat, and Kantolic et al. (2007) for soybeans.

BOX 12.3

LIVE AND LET DIE: LIKELY MECHANISMS OF FLORET MORTALITY IN WHEAT

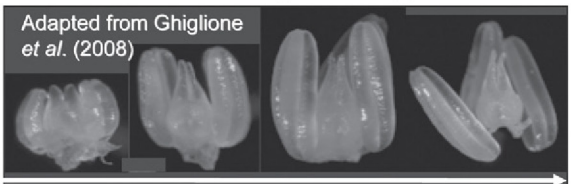
As in many other species, the number of grains per unit land area is the main yield component explaining the variations in wheat yield. Although each spikelet within the wheat spike has the capacity to produce a very large number of floret primordia (≈10–12 in central spikelets), many of these developing florets fail to reach the stage of fertile floret at anthesis. As (1) the number of floret primordia developed in each spikelet is enormously higher than the number of fertile florets at anthesis and (2) the proportion of grain set (grains per fertile floret) is normally quite high, the capacity of floret primordia to survive and continue developing all its floret organs constitutes a major bottleneck process for reaching a high number of fertile florets, and thereby grains, in wheat.

Understanding the mechanisms of floret mortality from a combined approach including (1) anatomy changes of the primordia at cellular level, (2) physiological development and (3) gene expression (transcriptomic patterns) during the active spike growth period would be a way to gain insight into the process for increasing floret survival in wheat. In a study where a combination of microarray, biochemical and anatomical approaches were used to investigate the origin of floret mortality, Ghiglione et al. (2008) modified the duration of the spike growth period by modifying the photoperiod only during the phase of spike growth (until then all plants were in the same condition). They found that the acceleration of floret primordia mortality induced by extending photoperiod (e.g. González et al., 2003b; 2005b), which is illustrated below, was associated with the expression of genes involved in photosynthesis, photo-protection and carbohydrates metabolism. The expression of marker genes associated with floral development cell proliferation and programmed cell death were activated with long photoperiod, i.e. the signal that determined the mortality of distal floret within the spikelets.

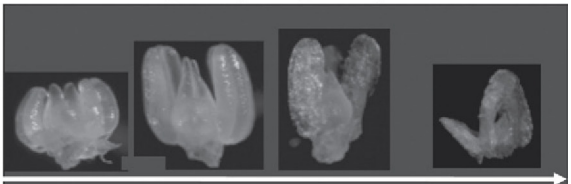
Anatomy and morphological changes in the primordia were found and cells of the ovaries of aborting florets revealed the formation of the vacuoles that become dense and increased in size, the development of dense globular bodies (authophagosomes), chromatin condensation of the nucleus and vanishing of nucleolus in the

Plants grown under field conditions (i.e. relatively short days)

Plants grown under extended photoperiod during the spike growth period



Floret development in a plant growing under normal field conditions through stages 6, 7, 8 and 8.5 of the Waddington *et al.* (1983) scale



Floret mortality in a similar floret that reached the stage 7 normally, illustrating the decay of floret organs and floret abortion, due to accelerated development

BOX 12.3 *(cont.)*

cells of the ovaries of aborting florets suggesting that floret abortion was a programmed cell death by authophagy rather than passive death or necrosis. Finally, another mechanism involved in floret abortion is the level of soluble carbohydrates as the decrease of soluble sugars (glucose and fructose) during the spike growth period enhanced the floret abortion of the primordia previously initiated. This agrees with previous studies showing that the fate of florets was largely determined by the acquisition of assimilates by the growing spike when affected by either genetic (Miralles et al., 1998; González et al., 2005c) or environmental (González et al., 2005a; Ferrante et al., 2010) factors.

The study of floret initiation and mortality in wheat from a multidisciplinary approach allows the exploration of different mechanisms involved in the process under study improving the understanding of the process. Thus, the identification of candidate genes controlling the process of survival of the floret primordia previously initiated might constitute a major step to improve further the number of grains per unit land area and yield in cereals and in other crops.

The critical period may occur before (e.g. in wheat) or after (e.g. in soybean) flowering, but it is clear that, in both species, in spite of their large morphological and physiological differences, the growth during this period defines crop yield in most environments. Improving our knowledge of genetic and environmental drivers of the expression of genes that control flowering time should improve our precision in positioning the critical period when the highest level of resources is expected, and stresses are less likely (Chapter 13).

In both species, the length of the critical phase is positively related with the number of seeds, and its duration is modified by photoperiod. Manipulative experiments described in this chapter showed that increasing sensitivity to photoperiod during the critical phase for grain number determination may actually raise yield potential. The longer the critical phase, the more the crop may grow, supporting more grains to be set. So yield could be improved if this phase is lengthened without modifying the whole crop cycle duration. In wheat and barley, there is a large variation in duration of stem elongation independently of the total duration to anthesis (Kernich et al., 1997; Whitechurch et al., 2007a) which is partially due to variation in photoperiod sensitivity during this phase (Whitechurch et al., 2007b). In fact, in exceptional cases, empirical breeding may have made use of this variability (Abeledo et al., 2001). In soybean, simulation studies have shown that shortening the pre-flowering period, without changing the duration of the whole cycle, could increase yields in a broad range of latitudes and environmental conditions (Kantolic et al., 2007). The main problem to manipulate this trait is to identify clearly the genetic basis of photoperiod sensitivity of the critical phase. This is not simple. However, even though no single major allele has been particularly linked with photoperiod sensitivity during the critical phase for yield determination, different sources of evidence reinforce the idea that photoperiod sensitivity of individual phases may be independent of each other. This would allow exploiting this trait to change the length of the critical period without altering the duration of the whole crop cycle. Moreover, identifying the genes involved in floret survival (e.g. Ghiglione et al., 2008) is the first step to understanding their environmental modulation.

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