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Chapter 4

Molecular Mechanisms Controlling Dormancy and Germination in Barley

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1. Introduction

1.1. History of barley

Barley (*Hordeum vulgare* L.) is amongst the oldest crops within cereals. Archaeological remains of this crop have been discovered at different locations in the Fertile Crescent (Zohary & Hopf, 1993) indicating that barley is being cultivated since 8,000 BC. The wild relatives of barley were recognized as *Hordeum spontaneum* C. Koch. However, in the recent literature of taxonomy, *H. spontaneum* C. Koch, *H. vulgare* L., as well as *H. agriocrithon* Åberg, are believed to be the subspecies of *H. vulgare* (Bothmer & Jacobsen, 1985). Studies with molecular markers have confirmed that barley was brought into cultivation in the Isreal-Jordan area but barley diversification occurred in Indo-Himalayan regions (Badr et al., 2000).

1.2. Importance of barley in Canada

Barley, a gladiator's food in Athens and the only crop to be used as a form of money in early Sumerian and Babylonian cultures, is the fourth largest cultivated crop in the world after wheat, rice and maize. Barley is one of the most fundamental plants in human nutrition and it is one of the most widely cultivated cereal grown in various climatic regions of world; starting from sub-Arctic to subtropical (Zohary & Hopf, 1993). Depending on the physical arrangement of the kernels on the plant, it is categorized into two different types as six-row and two-row barley. Based on the presence or absence of covering on the kernels, it is also classified as hulled or hull-less.

In Canada, it was first cultivated in Port Royal in 1606. Today, Canada is the 4th biggest barley producer after the European Union, Russia and Ukraine (Taylor et al., 2009). Most farmers

grow barley for sale as malting barley. If the grain does not meet malting quality, it is sold as feed barley. Malting quality is somewhat subjective and depends upon the supply of good malting barley and its price. In the past couple of years, barley crops have suffered great loss in yield and quality due to lower germination potential and water sensitivity (Statistics Canada, 2007). Despite significant losses in barley production and yield in the year 2006-2007 (9.5 million tonnes (Mt)), the total production of barley increased (11.8 Mt) in 2007-2008 due to larger cropping area at the expense of wheat acerage (Statistics Canada, 2007).

Total barley production decreased by 10% and the harvested area by 1.5% in 2009 compared to 2008. Domestic use has increased by 4% due to a decline in corn imports. Total exports have increased by 12.5% in 2009 after a drastic decline of 47% in 2008 from the previous year (USDA Report, 2009). Average price for malt barley has gone down significantly from $208 to $179 per tonne (Agric. & Agri-Food Canada, 2009).

1.3. Challenges related to barley production

Malting quality characteristics (beta-glucan content, protein breakdown, fermentability, hull adherence and even germination) are extremely important aspects for barley improvement. While considerable progress has been achieved, much remains to be done in terms of improving the quality and production of malting barley. Quality of barley significantly affects its end utilization. Statistical data indicate that approximately 19% of total barley produced is used in malting process, 8% is consumed as food, 2% in industrial processes and about 73% is used for animal feed due to inadequate malting quality (e-malt.com, 2007). The issues linked with germination of malting barley have acquired substantial global attention for the last few years. It is evident from the literature that storage conditions and pre-harvest sprouting have major consequences on germination. The underlying causes for varietal differences in these characteristics is still unclear. Secondary dormancy greatly reduces the germination and marketability of grains used for malting purposes. Therefore, there is dire need to address this issue that malting barley sustains its germination without prolonged dormancy and pre-harvest sprouting.

2. Seed dormancy

2.1. Seed dormancy: Definition

Seed dormancy is a common characteristic of wild plants which ensures their continued existence/survival under unfavourable conditions, decreases competition with other species and prevents damage to seedlings from out-of-season germination of the seed. Domesticated species, on the other hand, are selected for uniform germination and rapid seedling establishment often leading to selection of genotypes with less dormancy. This can lead to pre-harvest sprouting (PHS), a phenomenon in which the seed germinates on the parent plant causing extensive loss of grain quality to crops like wheat, barley and maize (Bewley & Black, 1994).

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Seed dormancy is defined as "*inhibition of germination of an intact viable seed under favourable conditions*" (Hilhorst, 1995; Li & Foley, 1997; Bewley, 1997). The germination block has developed in a different way from one species to another depending upon their habitat and conditions of growth. These dormancy mechanisms have evolved because these germination blocks have been operated in a variety of climates and habits. In light of these complex nature of germination blocks, another definition of dormancy has been defined as, a "*dormant seed cannot germinate in a specified period of time under any combination of conditions that are otherwise sufficient for its germination*" (Baskin & Baskin, 2004). It is reported that dormancy must not be linked with lack of germination, but dormancy is the combination of characteristics of the seed which decide physical and environmental circumstances needed for germination (Finch-Savage & Leubner-Metzger, 2006). Germination can be defined as appearance of radicle from seed coat. The requirement of germination may include one or more of the processes like mobilization of stored food, overcoming the physical barrier by activation of cell wall degrading enzymes followed by resumption of active growth by cell elongation and division (Finkelstein et al., 2008).

2.2. Classification of seed dormancy

Although almost all kinds of dormancy cause delay in germination, the principal of this delay may vary from species to species. The variation can be due to embryonic immaturity or due to the existence of physical or physiological constraints caused by the presence of a hard seed coat or some inhibitory chemicals that interfere with embryo growth (Finch-Savage & Leubner-Metzger, 2006). Dormancy can be primary dormancy that is acquired in the later developmental phases of embryo development and seed maturity. There are also conditions in which after-ripened, imbibed seeds enter into secondary dormancy when exposed to unfavourable temperature, light or low moisture conditions (Bewley, 1997).

Despite the progress in understanding the mechanisms controlling dormancy, it can be treated as the least recognized event (Finch-Savage & Leubner-Metzger, 2006). Both physiologists and ecologists have studied the factors controlling dormancy but the outcome is far from clear due to the fact that dormancy is affected by numerous environmental conditions (an ecologist's dilemma) and the model species like Arabidopsis studied by molecular physiologists and geneticists tend to have a very shallow dormancy (Walck et al., 2005). The molecular controls that regulate dormancy can be of two different components i.e., an embryo or a seed coat. However, dormancy is a entire seed trait and on this basis, can be classified into the five classes namely physiological, morphological, morpho-physiological, physical and combinatorial dormancy (Nikolaeva, 1969; Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006).

2.3. Factors affecting dormancy

Dormancy is affected by various factors and the potential regulators are identified by their effect on depth of dormancy or by analysis of genetic lines that have varying levels of dormancy. The factors that affect dormancy are classified into two broad categories, embryo- and seed coat imposed dormancy. A hard seed coat manifests its effect on dormancy by prevention of water uptake during imbibition (waxy or lignified tissues in legume seeds), mechanical

constraint due to hard seed coat (nuts) or endosperm (lettuce) causing inhibition of radicle protrusion, interference with gas exchange (cocklebur) and retention of inhibitors (*Xanthium*) and production of inhibitors like abscisic acid (ABA). Genetic variation in seed coat components such as testa layer, pericarp and pigmentation also cause altered dormancy and seed longevity (Debeaujon et al., 2000; Groos et al., 2002; Sweeney et al., 2006). Pigmented seeds are generally more dormant although hormone levels and their sensitivity to them may increase dormancy of non-pigmented seeds (Gale et al., 2002; Walker-Simmons, 1987; Flintham, 2000). Many nitrogenous compounds like nitrite (NO_2^-), nitric oxide (NO), and nitrate (NO_3^-) cause dormancy release. NO could promote germination by cell wall weakening and instigating vacuolation (Bethke et al., 2007). Genomic studies in rice to identify loci controlling seed colour, dormancy and shattering resistance show a tight linkage between the responsible genes and single locus can also control these traits (Ji et al., 2006).

Embryo dormancy is controlled by inherent characteristics of the embryo. The presence or absence of embryo dormancy has mainly been attributed to the content and sensitivity of phytohormones ABA and gibberellic acid (GA) (Bewley, 1997). Dormancy and germination are also affected by environmental factors such as light, moisture and temperature (Borthwick et al., 1952; Gutterman et al., 1996). The intensity of dormancy in the mature seed and its onset during seed development vary considerably due to genotype by environmental interaction during the entire process of seed development (Corbineau et al., 2000; Crome et al., 1984; Bewley, 1997;).

2.4. Hormonal control of dormancy

The plant hormone abscisic acid is required for setting dormancy during embryo maturation and its deposition associate with the commencement of primary dormancy (Kermode, 2005). Another plant hormone, gibberellic acid is antagonistic in action to ABA. Gibberellins promote post-germinative growth by activating hydrolyzing enzymes that break cell walls, mobilize seed storage reserves and stimulate embryo cell expansion (Bewley, 1997). Ethylene also promotes germination by antagonizing ABA signalling. Ethylene receptor mutants have higher ABA content and are hypersensitive to ABA (Ghassemian et al., 2000; Beaudoin et al., 2000; Chiwocha et al., 2005). Plant steroidal hormones, brassinosteroids, enhance the germination potential of embryos in a GA-independent manner (Leubner-Metzger, 2001). The germination completion and establishment of seedling is accomplished by Auxin (Carrera et al., 2007; Ogawa et al., 2003; Liu et al., 2007a). Auxin accumulates at the radicle tip during embryo development and in seeds after imbibition (Liu et al., 2007a). Although various hormones may affect dormancy and germination, the general consensus is that ABA is the primary mediator of dormancy (Koornneef et al., 2002; Holdsworth et al., 2008; Finkelstein et al., 2008).

2.5. ABA and GA regulate dormancy and germination

The functions of ABA in dormancy maintenance and initiation are firmly established and widely reviewed (Koornneef et al., 2002; Finch-Savage & Leubner-Metzger, 2006; Finkelstein et al., 2008). In cereals like wheat, barley and sorghum, ABA controls the onset of dormancy

(Walker-Simmons, 1987; Jacobsen et al., 2002). Genetic studies show that the *de novo* synthesis of ABA in embryo or endosperm is required to induce dormancy (Nambara & Marion-Poll, 2003). Other studies with ABA-deficient mutants have suggested that ABA in the embryos and not the maternal ABA is crucial for induction of dormancy (Karssen et al., 1983). Dormancy may be maintained by renewed post-imbibition synthesis of ABA (LePage-Degivry & Garello, 1992; Ali-Rachedi et al., 2004). The reduction in seed dormancy has been seen for ABA biosynthetic enzymes, that have ABA sequestration with expressed antibodies in the seeds and in seeds that are treated with chemicals for inhibition of ABA biosynthesis (Nambara & Marion-Poll, 2003; Lin et al., 2007). The content of ABA and resulting dormancy are controlled by interaction of ABA biosynthetic and ABA catalyzing enzymes. The most critical enzyme in ABA biosynthesis is the 9-*cis*-epoxycarotenoid dioxygenase (NCED) that is essential for ABA synthesis in endosperm and embryo (Lefebvre et al., 2006). Rate-limiting enzyme during ABA biosynthesis, NCED regulates ABA biosynthesis during induction of secondary dormancy (Leymarie et al., 2008). During the transition from embryo maturation to germination, ABA is catabolised by ABA 8'-hydroxylases which are encoded by cytochrome P450 CYP707A gene family causing a decline in dormancy (Okamoto et al., 2006). Imbibition of embryos in water also causes leaching of ABA resulting in reduced dormancy (Suzuki et al., 2000). After-ripening, which is occurring during dry storage of seeds, causes a decline in embryo ABA content and sensitivity (Grappin et al., 2000). In a study conducted on pre-harvest sprouting (PHS) in susceptible and resistant wheat cultivars, after-ripening occured prior to harvest ripeness in the majority of PHS-susceptible cultivars, whereas it was slowest in cultivars that were most PHS-resistant. However, no direct relationship could be found between timing of caryopsis after-ripening and dormancy or ABA responsiveness in wheat (Gerjets et al., 2009).

ABA content as well as ABA sensitivity are critical components of embryo dormancy. ABA-insensitive mutants that are deficient in ABA perception or signalling have lower dormancy and exhibit viviparous germination (Koornneef et al., 1984; Robichaud & Sussex, 1986; Koornneef et al., 1989). Analysis of sprouting-susceptible and sprouting-resistant cultivars of wheat for ABA content and ABA sensitivity showed larger differences in ABA sensitivity than ABA content measured by capability of ABA to block embryo germination (Walker-Simmons, 1987).

The role of GA in modulating dormancy is highly debated (Finkelstein et al., 2008). The treatment with GA may not direct germination in few species or in fully dormant seeds of Arabidopsis. The decline of ABA content is usually needed prior to embryo GA content or sensitivity to the hormone increases (Ali-Rachedi et al., 2004; Jacobsen et al., 2002). After-ripening, which leads to a decline in ABA content and ABA sensitivity, results in increased sensitivity to GA and light in Arabidopsis (Derkx & Karssen, 1993). So the ratio of ABA to GA seems to be critical, where a higher content of ABA overrides the growth-promoting effect of GA. In cereals, although the GA signalling components seem to be similar to dicots, redundant GA signalling pathways may exist. This is evident from the fact that in rice, the mutation in the only known receptor of GA, *Gibberellin-Insensitive Dwarf 1* (*GID1*) leads to decreased α-amylase production (Ueguchi-Tanaka et al., 2005); however mutating all three homologues of *GID1* in Arabidopsis inhibits germination (Willige et al., 2007). Therefore, it can be concluded

that the embryo dormancy in case of cereals, for the most part, is controlled by ABA content and sensitivity.

2.6. Effect of light on dormancy occurs through ABA and GA metabolism

The role of light in regulation of dormancy was first identified when germination was induced by exposing the dark-imbibed seeds with red (R) light pulse and the successive far-red (FR) light pulse cancelled the effect of red light (Borthwick et al., 1952). This response is mediated by the R/FR phytochromes, UV-A/blue light receptor cryptochromes, the phototropins and the recently identified blue light receptor zeitlupes (Bae & Choi, 2008).

The induction of germination by red light can be substituted by the application of GA (Kahn et al., 1957), whereas red light application do not induce germination in mutants deficient in GA (Oh et al., 2006). Toyomasu et al., (1998) reported that the GA biosynthetic gene's expression encoding GA3ox (*LsGA3ox1* in lettuce and *AtGA3ox1* and *AtGA3ox2* in Arabidopsis) is generated by R light and its activation is inhibited by FR light. On the other hand, transcripts of a GA-deactivating gene *GA2ox* (*LsGA2ox2* in lettuce and *AtGA2ox2* in Arabidopsis) are reduced by R light (Yamauchi et al., 2007; Oh et al., 2006; Nakaminami et al., 2003; Seo et al., 2006).

Similar to modulation of GA content, ABA biosynthetic and deactivating enzymes are also regulated by light. Genes encoding ABA biosynthetic enzymes NCED (*LsNCED2* and *LsNCED4* in lettuce and the Arabidopsis *AtNCED6* and *AtNCED9*) and zeaxanthin epoxidase (AtZEP/AtABA1 in Arabidopsis) are reduced by R light treatment (Seo et al., 2006; Sawada et al., 2008; Oh et al., 2007) whereas, transcript levels of ABA-deactivating genes encoding CYP707A (*LsABA8ox4* in lettuce and CYP707A2 in Arabidopsis) are elevated by R light (Sawada et al., 2008; Oh et al., 2007; Seo et al., 2006).

The phytochromes regulate the levels of ABA and GA by one of the interrelating proteins *PHYTOCHROME INTERACTING FACTOR3-LIKE 5* (*PIL5*) which belongs to a family of helix-loop-helix (bHLH) family of proteins containing 15 members (Yamashino et al., 2003; Toledo-Ortiz et al., 2003;). Studies of *PIL5* over-expressing and mutant lines show that it regulates ABA and GA content by regulating their metabolic genes (Oh et al., 2006).

3. Molecular networks regulating dormancy

3.1. Perception and transduction of ABA signal

3.1.1. ABA receptors

Physiological studies in different plant species indicate that accumulation of ABA is required for induction and maintenance of dormancy (Finkelstein et al., 2008). The perception of ABA and its downstream signalling to inigtiate ABA-regulated responses is an area of active research. Various lines of evidence suggest multiple sites of ABA perception, thus, multiple ABA receptors (Allan & Trewavas, 1994; Gilroy & Jones, 1994; Huang et al., 2007). The first

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ABA-specific binding protein, a 42 kDa ABAR, was identified and isolated from *Vicia faba* leaves and the pretreatment of their guard cell protoplasts with a monoclonal antibody against the 42 kDa protein reduced ABA induced phospholipase D activity in a manner that was dose-dependent (Zhang et al., 2002). Another 52kDa protein, ABAP1 was shown to bind ABA and was up-regulated by ABA in barley aleurone layer tissue (Razem et al., 2004). The ABA "receptor", Flowering Time Control Locus A (FCA) in Arabidopsis was identified based on its high sequence similarity to barley ABAP1 and was shown to bind ABA and affect flowering (Razem et al., 2006). Another ABA receptor from Arabidopsis, the Magnesium Protoporphyrin-IX Chelatase H subunit (CHLH) regulates classical ABA-regulated processes like stomatal movements, post germination growth and seed germination (Shen et al., 2006).The CHLH also shared very high sequence similarity to ABAR (Shen et al., 2006). In 2008, questions about FCA being a receptor for ABA arose in both the laboratory of the original authors and, independently, in laboratories in New Zealand and Japan. This culminated in the simultaneous publication of a letter questioning the original results (Risk *et al.* 2008) and a retraction of the claim that FCA was an ABA receptor (Razem et al., 2006). Subsequent studies have confirmed that the findings of Razem et al., (2006) were not reproducible (Risk et al., 2009; Jang et al., 2008). Questions have also been raised regarding CHLH and its effect on feedback regulation of ABA synthesis and the apparent lack of a mechanism for its ABA receptor function (Shen et al., 2006; Verslues & Zhu, 2007). CHLH binding to ABA was proven using more than one method (Wu et al., 2009). Yet the barley homologue of CHLC (magnesium chelatase 150 kD subunit) does not bind ABA (Muller & Hansson, 2009). Two classes of plasmamembrane ABA receptor, a G-protein-coupled receptor (GPCR), the GCR2, and a novel class of GPCR, the GTG1 and the GTG2 have been discovered. They regulate major ABA responses such as seed germination, seedling growth and stomatal movement (Liu et al., 2007b; Pandey et al., 2009). However, the GCR2 mediation of ABA-controlled seed germination and post-germination growth are controversial as the ABA-related phenotypes are lacking or weak in *gcr2* mutants (Gao et al., 2007; Guo et al., 2008). GTGs regulate ABA signalling positively and interact with the only Arabidopsis G-protein α-subunit, GPA1, which can negatively regulate ABA signalling by nullyfying the activity of GTG-ABA binding (Pandey et al., 2009). The ABA insensitive mutants *abi1* and *abi2* belong to Mg^{2+}- and Mn^{2+}-dependent serine-threonine phosphatases type 2C (PP2Cs) and are known to be negative regulators of ABA signalling (Merlot et al., 2001; Gosti et al., 1999; Rodriguez et al., 1998; Meyer et al., 1994). The 14 member gene family of Regulatory Components of ABA Receptor (RCARs), which interact with ABI1 and ABI2, bind ABA, mediate ABA-dependent inactivation of ABI1 and ABI2 *in vitro* and antagonize PP2C action *in planta (Ma et al., 2009)*. PYRABACTIN RESISTANCE 1 (PYR/PYL family of START proteins) were shown to inhibit the PP2C mediated ABA signaling (Park, 2009). In Arabidopsis, the PYR/PYL/RCAR family proteins constitute the major in vivo phosphatase 2C-interacting proteins (Noriyuki et al., 2010). The crystal structure of Arabidopsis PYR1 indicated that the molecule existed as a dimer, and the mechanism of its binding to ABA in one of the PYR1 subunits was recently established (Nishimura et al., 2009; Santiago et al., 2009). Finally, the whole ABA signalling cascade that includes PYR1, PP2C, the serine/threonine protein kinase SnRK2.6/OST1 and the transcription factor ABF2/AREB1 was reconstituted *in vitro* in plant protoplasts resulting in ABA responsive gene expression (Fujii et al., 2009).

3.1.2. ABA signalling components

To identify the different ABA signalling components, various Arabidopsis mutants were screened for insensitivity to ABA for germination and were termed ABA insensitive (abi) (Koornneef et al., 1984; Finkelstein, 1994). The ABI1 and ABI2 encoded protein phosphatase 2C (type 2C phosphatases, PP2C) regulate ABA signalling (Leung et al., 1997). ABI3, ABI4 and ABI5 control mainly seed related ABA responses (Parcy et al., 1994; Finkelstein & Lynch, 2000).

The process of dormancy initiates during early seed maturation and continues until the seed matures completely (Raz et al., 2001). In Arabidopsis, the seed maturation and induction of dormancy is mainly controlled by four transcription factors namely FUSCA3 (FUS3), ABSCISIC ACID INSENSITIVE 3 (ABI3), LEAFY COTYLEDON 1 (LEC 1) and LEC 2 (Stone et al., 2001; Baumlein et al., 1994; Giraudat et al., 1992; Lotan et al., 1998). The plant specific transcription factors with the conserved B3-binding domain include ABI3, FUS3 and LEC2 (Stone et al., 2001). LEC1 encodes the HAP3 subunit of a CCAAT-binding transcription factor CBF (Lotan et al., 1998). Common mutant phenotypes such as decreased dormancy at maturation occur due to abi3, lec1, lec2 and fus3 and they affect seed maturation severely (Raz et al., 2001) as well as cause reduced expression of seed storage proteins (Gutierrez et al., 2007). A study, using Arabidopsis cultivars that differed in dormancy, showed no correlation between LEC1, FUS3, ABI3 and Em expression and dormancy (Baumbusch et al., 2004). Although all four genes affect embryo maturation, they also play a unique role in regulating each other's functionality and expression pattern (Holdsworth et al., 2008). FUS3 controls formation of epidermal cell identity and embryo derived dormancy (Tiedemann et al., 2008). Loss of LEC1 causes germination of excised embryos similar to lec2 and fus3 mutants (Raz et al., 2001). LEC2 controls the transcription program during seed maturation and affects DELAY OF GERMINATION 1 (DOG1), the first seed dormancy protein accounting for variation in natural environment as identified by quantitative trait loci (QTL) analysis (Bentsink et al., 2006; Braybrook et al., 2006). Both LEC1 and LEC2 regulate the expression of FUS3 and ABI3 (Kroj et al., 2003; Kagaya et al., 2005). ABI3 and FUS3 positively auto-regulate themselves and each other creating a feedback loop (To et al., 2006). Interestingly, none of these four transcription factors (LEC1, FUS3, ABI3 and LEC2) contains motifs to interact with an ABA response element (ABRE), but do contain a B3 domain that interacts with the RY motif present in the promoters of genes that produce RNA during the late maturation phase of the seed (Ezcurra et al., 1999; Reidt et al., 2000; Monke et al., 2004; Braybrook et al., 2006). The transcription factor ABSCISIC ACID INSENSITIVE 5 (ABI5) is a basic leucine zipper (bZIP) domain-containing protein that interacts with ABRE and activats ABA-mediated transcription in seeds (Finkelstein & Lynch, 2000; Carles et al., 2002). ABI3 activates RY elements, physically interacts with ABI5 and this physical interaction seems to be necessary for ABA-dependent gene expression (Nakamura et al., 2001).

Although much information on dormancy regulation is available for dicots like Arabidopsis, the molecular control of dormancy in cereals is not very clear. One of the key genes in regulating seed maturation, dormancy and desiccation in maize is Viviparous1 (VP1), an ortholog to ABI3 in Arabidopsis (McCarty et al., 1989; McCarty et al., 1991; Giraudat et al., 1992). It is also responsible for transcriptional control of the LATE EMBRYOGENESIS

ABUNDANT (LEA) class of proteins (Nambara et al., 1995; Nambara et al., 2000). VP1 is involved in root growth-related interaction between ABA and auxin (Suzuki et al., 2001). QTL analysis showed VP1 to be responsible for seed dormancy and PHS (Flintham et al., 2002; Lohwasser et al., 2005). VP1 is responsible for controlling embryo maturation and dormancy as well as inhibition of germination (McCarty & Carson, 1991; Hoecker et al., 1995). Like ABI3, ABI5 and VP1 interac to regulate embryonic gene expression and sensitivity of seed to ABA (Lopez-Molina et al., 2002). VP1/ABI3 has been cloned from various dicot and monocot species (Hattori et al., 1994; Jones et al., 1997; Rohde et al., 2002) and contains three basic domains designated B1, B2 and B3 and a N-terminal acidic domain (A1) (Giraudat et al., 1992). The A1 domain is responsible for ABA-mediated transcriptional activation, B2 for ABRE-mediated transcriptional activation and B3 for RY/G-box interaction (Hoecker et al., 1995; Ezcurra et al., 1999). VP1/ABI3 is also alternatively spliced in various plant species and its mis-splicing causes PHS in wheat (McKibbin et al., 2002; Wilkinson et al., 2005; Gagete et al., 2009). ABI5 undergoes alternative splicing forming two variants which interact with each other and each having distinct binding affinity to VP1/ABI3 (Zou et al., 2007). In barley, ABA-dependent up-regulation of ABI5 is positively regulated by a feed-forward mechanism that involves ABI5 itself and VP1 (Casaretto & Ho, 2005).

Our work on FCA and FY, two key components in regulation of flowering, suggest that commonalities exist in germination and flowering pathways. The transcript levels of barley FCA are positively correlated to dormant state of the embryos and are involved in regulation of VP1 and Em gene promoters (Kumar et al., 2011). The Arabidopsis FY, which regulates the autonomous floral transition pathway through its interaction with FCA, is also involved in seed germination in Arabidopsis (Jiang et al., 2012). The fy-1 mutant has lower ABA sensitivity and may be involved in development of dormancy (Jiang et al., 2012). These reports suggest a very prominent role of transcriptional regulation in fine tuning ABA responses.

3.2. Inhibition of GA signalling by DELLA proteins

Components of GA signalling regulate seed germination (Peng & Harberd, 2002). Nuclear transcriptional regulators, the DELLA proteins, control GA signalling (Itoh et al., 2002; Richards et al., 2000; Wen & Chang, 2002; Dill et al., 2001). DELLA proteins are negative regulators of GA signalling (Wen & Chang, 2002). Arabidopsis has five DELLA proteins (GA-INSENSITIVE [GAI], REPRESSOR OF GA1-3 [RGA], RGA-LIKE1 [RGL1], RGL2, and RGL3), while rice SLENDER1 (SLR1) and other species such as barley SLENDER1 (SLN1), maize, and wheat have only one DELLA protein (Dill et al., 2001; Chandler et al., 2002; Itoh et al., 2002; Peng & Harberd, 2002). Downstream of the DELLA proteins, GA regulates Myb-like (GAmyb) transcription factor binding to promoter of α-amylase genes (Gubler et al., 1995). The GA-signal is recepted by a soluble GA receptor which has homology to GA-INSENSITIVE DWARF1 (GID1), a human hormone-sensitive lipase (Ueguchi-Tanaka et al., 2005). The bioactive GAs bind to GID1 which in turn promotes interaction between GID1 and the DELLA-domain of DELLA protein (Willige et al., 2007; Ueguchi-Tanaka et al., 2007). This interaction enhances the affinity between DELLA-GID1-GA complex and a specific SCF E3 ubiquitin–ligase complex, SCFSLY1/GID2 which involves the F-box proteins AtSLY1 and OsGID2 in

Arabidopsis and rice, respectively (Sasaki et al., 2003; McGinnis et al., 2003; Willige et al., 2007; Griffiths et al., 2006). The ubiquitinylation and subsequent destruction of DELLAs is promoted by SCFSLY1/ GID2 through the 26S proteasome (Fu et al., 2002; McGinnis et al., 2003; Sasaki et al., 2003). The DELLA genes are transcriptionally controlled by the light-labile transcription factor PIL5 which increases the transcription of GAI and RGA genes by binding to its promoters on the G-Box (Oh et al., 2007).

DELLA degradation is GA-dependent and is inhibited by ABA in barley and by both ABA and salt (NaCl) in Arabidopsis (Gubler et al., 2002; Achard et al., 2006). Plant development through the two independent salt-activated hormone signalling pathways (ABA and ethylene) integrates at the level of DELLA function (Achard et al., 2006). DELLA also affects flowering in an ABA-dependent manner (Achard et al., 2006); however, its function in regulation of dormancy and germination is not clear. Germination in tomato, soybean and Arabidopsis is not dependent on down-regulation of DELLA genes (Bassel et al., 2004). Despite a high content of RGL2, the DELLA protein that specifically represses seed germination, Arabidopsis sly1 mutant seeds can germinate (Ariizumi & Steber, 2007). Far-red light is known to inhibit germination through DELLA dependent induction of ABI3 activity and ABA biosynthesis while DELLA mediates expansion of cotyledon leading to breaking the coat-imposed dormancy (Penfield et al., 2006; Piskurewicz et al., 2009).

4. Epigenetic regulation of dormancy related genes

Despite the lack of complete information about ABA signalling, it is amply clear that ABA responses are regulated by transcriptional regulation, except for the quick responses in stomatal closure (Wasilewska et al., 2008). Besides transcriptional regulation, ABA mediates epigenetic regulation to control plant responses (Chinnusamy et al., 2008). ABA-mediated epigenetic regulation of gene expression in seeds is now being studied extensively. Polycomb group-based gene imprinting and DNA methylation/demethylation control seed development in plants (Eckardt, 2006). Seed specific physiological processes like dormancy and germination are being studied in the context of epigenetic regulation. A cDNA-AFLP-based study showed epigenetic regulation of transcripts during barley seed dormancy and germination (Leymarie et al., 2007). During seed development and germination inhibition, gene regulation is also regulated by ABA through transcription factors such as ABI3, VP1, LEC2, FUS3 as well as the APETELA2 (ABI4), HAP3 subunit of CCAAT binding factor (LEC1) and the bZIP (ABI5) (Finkelstein et al., 2002). ABA regulates the B3 domain transcription factors through PICKLE (PKL) which encodes putative CHD3 type SWI/SNF-class chromatin-remodeling factor (Ogas et al., 1999). ABA-mediated stress responses occur through Histone Deacetylase (HDACs)-dependent chromatin modifications and ATP-dependent chromatin remodelling complexes that include SWI3-like proteins (Wu et al., 2003; Rios et al., 2007). Stress-related memory is also inherited through epigenetic mechanisms (Boyko et al., 2007). ABA also regulates non-coding small RNAs (siRNA and miRNA) that can regulate DNA methylation resulting in epigenetic changes (Bond & Finnegan, 2007; Yang et al., 2008).

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5. Tillering and bud dormancy

Tillering is a key agronomic trait contributing to grain yield. Tillers are formed from axillary buds that grow independent of the main stem. The levels of dormancy in buds determine the timing and extent of tillers in most monocot crops. Various proteins such as MONOCULM 1 (MOC1) (Li et al., 2003) have been implicated in regulation of bud dormancy but recent studies suggest the involvement of autonomous pathway (flowering) genes in regulation of bud dormancy. The first clue regarding the commonality between factors controlling flowering and bud dormancy arose from environmental signals that regulated them (Chouard, 1960). The signalling events responsible for regulation of flowering and bud dormancy converge on FLOWERING LOCUS T (FT) (Bohlenius et al., 2006). Day length is an important determinant in regulation of flowering acting through its photoreceptor PHYTOCHROME A (PHYA). PHYA affects the floral induction pathway through its effect on CONSTANS (CO), a gene involved in flowering pathway, which in turn affects FT(Yanovsky & Kay, 2002). FT is negatively regulated by FLC which regulates temperature-dependent seed germination in Arabidopsis (Helliwell et al., 2006; Chiang et al., 2009). FCA and FVE regulate FT under high and low temperatures in a FLC-dependent manner (Sheldon et al., 2000; Blazquez et al., 2003). The transcript levels of *FCA* have also been correlated to bud dormancy in poplar (Ruttink et al., 2007). Although limited, the information regarding the intricate network of signalling events that regulate the two most important events, namely the transition from vegetative to reproductive state, and from non-germinated to germinated state suggests some common factors (Horvath, 2009).

6. Breeding for pre-harvest resistance in barely

Seed dormancy is a quantitatively inherited trait in several plant species such as rice, popular, Arabidopsis, wheat and barley (Ullrich et al., 1996; Li et al., 2004). In barley, seed dormancy and germination have been important breeding objectives since its domestication and malt utilization. Malting barley must rapidly germinate upon imbibition. Endosperm starch and proteins hydrolysis within 3 to 4 days is an important characteristic for malting quality in barley. To assure rapid and complete germination for malting industry, barley breeders have stringently selected against seed dormancy resulting in barley varieties that are highly susceptible to pre-harvest spouting after early fall rains or heavy dew, which is an undesirable trait (Prada et al., 2004). A moderate level of seed dormancy is desirable for proper malting. In order to achieve suitable level of seed dormancy, several studies reported seed dormancy QTLs in barley (Edney & Mather, 2004; Zhang et al., 2005), different dormancy genes however responsible in different population of various pedigrees. Levels of seed dormancy that vary in different genetic backgrounds are also affected by environmental factors and their interaction with genetic factors. Various studies have identified the major QTLs (SD1 and SD2) that can be used in combination with other minor QTL of local germplasm to achieve moderate level of seed dormancy for malting barley (Li et al., 2004). Few QTL identified in barley for dormancy and preharvest sprouting are listed in Table 1. In addition hormonal cross talk can be explored for seed dormancy and germination as breeding prospect for better barley values and end utilization.

Chromosome	Marker interval	Variability (%)	References
Cross: Setptoe x Morex			
5H	*Ale* - ABC324	50	Ullrich et al., 1993 Obethur et al., 1995 Han et al., 1996 Ullrich et al., 2002 Gao et al., 2003
5H	MWG851D - MWG851B	15	
7H	*Amy2 - Ubi1*	5	
4H	WG622 - BCD402B	5	
Cross: Chebec x Harrington			
5H	CDO506 - GMS1	70	Li et al., 2003
Cross: Hordeum spontaneum (Wadi Qilt) x *Hordeum vulgare* (Mona)			
$1H_1$	ABC160-3	13	Zhang et al., 2005
$5H_2$	BMAG812-1 – E35M59mg-4	14	
$1H_2$	EMBAC659-3 – EE38M55ob-1	45	
$7H_1$	AF22725-3 – BMAG341A-2	13	
$7H_2$	BMAG135-4 – HVPR1B-2	39	
$1H_1$	EMBAC659-3 – EE38M55ob-1	50	
Cross: Stirling x Harrington			
1Hq	Hvglvend – Awbms80	1.6	Li et al., 2003, Bonnardeaux et al., 2008
2Hqa	GBMS244 – Emag174	-	
3Hqa	GBM1043 – Bmag0013	2.2	
4Hqa	GBM1501 – Bmag741	-	
5Hqa	Bmag0337 – GBM1399	3.7	
5Hqb	Scsst09041a – scssr03901	52.2	
Cross: Harrington x TR306			
1HL	iPgd2 – TubA2	10	Ullrich et al., 2009
2HS	ABC019 – ABG716	7	
2HC	MWG865	6	
3HL	ABG609B – MWG838	13	
5HL	MWG602 – ABC718	40	
7HS	dRPG1 – ABG077	6	
7HC	MWG003 – Ris15	7	
Cross: Triumph x Morex			
1HS	GMS21	10	Ullrich et al., 2009 Prada et al., 2004
3HL	E39M49_j – E39M48_c	13	

Chromosome	Marker interval	Variability (%)	References
5HC	E39M49_f – MWG522	54	
7HC	E32M48_c – E39M48_p	7	
7HL	E37M60_g	7	
Cross: BCD47 x Baronesse			
1H	Bmag504 - Bmag032	10	
4H	HvSnf2 – HvAmyB	9	
5H	Bmag222 – GMS001	34.5	Castro et al., 2010
6H	Bmag500 - Bmag009	9	
7H	Bmag120 – Ris44	23	
Cross: ND24260 x Flagship			
3H	bPb – 0619	6	
3H	bPb – 2630	4	
4H	bPb – 9251	4	
5H-2	bPb – 9191	15	Hickey et al., 2012
5H-2	bPb – 5053	31	
5H-2	bPb – 1217	35	
5H-2	bPb – 1217	28	
6H-2	bPb - 1347	4	

Table 1. Dormancy and preharvest sprouting related QTLs in barley.

7. Future perspective

The plethora of information on molecular control of dormancy and germination is ever increasing with studies performed on model plants. Little information is available from agriculturally important crops such as wheat and barley as they are tedious systems due to their genome complexity and ploidy levels. However, these economically important crops do bring out the unique variations of the biological systems that improve our understanding.

The recent pieces of evidence from our studies in barley and Arabidopsis (Kumar et al., 2011; Jiang et al., 2012) lay a foundation for looking deeply into the bigger picture involving flowering and dormancy as connected pathways. Genetic studies in Arabidopsis also identified DOG1, a key component in dormancy pathway, as quantitative trait loci for flowering (Atwell et al., 2010). The improvements in next generation sequencing and its decreasing cost has made it the technology of choice for looking at entire genomes for various transcriptome and epigenetic studies in crop plants. A refocused approach using

all interconnected pathways and improved technologies to study them will certainly enhance our understanding of dormancy and germination as well as flowering and in turn promote crop improvement.

Abbreviations

ABA Abscisic Acid

ABAP1 ABA Binding Protein 1

ABI3 Abscisic Acid Insensitive 3

ABI5 Abscisic Acid Insensitive 5

DOG1 DELAY OF GERMINATION 1

FCA Flowering Time Control Protein A

FLC Flowering Control Locus C

FT Flowering Locus T

GA Gibberellic Acid

GID1 GA-INSENSITIVE DWARF1

LEA Late Embryogenesis Abundant

LEC 1 LEAFY COTYLEDON 1

PHS Pre-harvest Sprouting

SLN1 Slender 1 (DELLA protein)

VP1 Viviparous 1

EM Early Methionine

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