PLANT DEVELOPMENT REGULATION: OVERVIEW AND PERSPECTIVES

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ABSTRACT

Plant development, as occur in other eukaryotes, is conducted through a complex network of hormones, transcription factors, enzymes and micro RNAs, among other cellular components. They control developmental processes such as embryo, apical root and shoot meristem, leaf, flower, or seed formation, among others. The research in these topics has been very active in last decades. Recently, an explosion of new data concerning regulation mechanisms as well as the response of these processes to environmental changes has emerged. Initially, most of investigations were carried out in the model eudicot *Arabidopsis* but currently data from other plant species are available in the literature, although they are still limited. The aim of this review is focused on the current knowledge of main molecular actors involved in plant development regulation in diverse plant species. A special attention will be given to the major families of genes and proteins participating in these mechanisms. The information on the regulatory pathways where they participate will be briefly cited. Additionally, the importance of certain structural features of such proteins that confer ductility and flexibility to these mechanisms will also be reported and discussed.

Keywords: plant development, regulation, monocots, eudicots, disordered/ductile proteins.

1. INTRODUCTION

The life cycle of a plant begins with a single cell zygote that develops an embryo by asymmetric cell division and subsequently new plant organs. In the eudicot *Arabidopsis* embryo includes a basal root meristem, a central region hypocotyl and two seed leaves or cotyledons, flanking a shoot apical meristem (SAM). The SAM is a reservoir of undifferentiated stem cells that functions as a continuous source of new cells yielding the adult root architecture. The two meristems formed during embryogenesis give rise to the root and shoot systems of the plant. The root stem cell niche (SCN) is a part of the cell proliferation domain (Ivanov and Dubrovsky, 2013). The SAM is the source of cells for all aerial organs produced after germination (Nakayima and Benfey, 2002). The SAM has a highly organized structure. It is subdivided into three domains: the central zone (CZ) of pluripotent stem cells, the peripheral zone primordia that contributes to the production of lateral organs, and the rib zone (RZ). The CZ is maintained by an underlying organizing center (OC). Below the OC is the rib zone (RZ), which is responsible for the elongation of the stem. Cells in the peripheral zone and the rib zone are rich in cytoplasm and divide rapidly. In flowering plants like *Arabidopsis thaliana* during the vegetative phase the primordia develop into leaves. Shoot meristems produce leaves on their flanks in regular patterns called phyllotaxy. Therefore, the primary SAM produces all the aerial structures of the adult plant, and alterations in SAM organization or function can have profound effects on vegetative and reproductive plant morphology. Development of leaves from the flanks of the SAM involves specification of proximodistal, dorsoventral and mediolateral axes. Differential growth and morphogenesis along these axes results in a planar organ specialized for photosynthesis. The

final shape and complexity of leaves varies greatly between species and within a plant leaf shape and size can also vary depending on developmental stage and growth conditions. The change to the subsequent generative phase is called floral transition, which is regulated by multiple flowering pathways that are controlled by environmental and endogenous factors. Particularly, the transition from vegetative to reproductive growth controlled by day length is crucial. Day length is perceived in leaves and induces a systemic signal, called florigen that moves through the phloem to the shoot apex. At the SAM, florigen causes changes in gene expression that reprogram the SAM to form flowers instead of leaves. This switch from vegetative to reproductive growth is one of the most important plant developmental decisions because the right timing of the floral initiation is essential for the optimal production of fruits and seeds that ensures reproductive processes. Additionally, normal patterns of organogenesis in plants require coordination between growth direction and growth magnitude.

Organogenesis in plants, as occur in animals, requires coordination of complex transcriptional networks that regulate the differential distribution of hormones. For instances, auxins are fundamental plant hormones in embryonic development (Möller and Weijers, 2009), organogenesis (Vanneste and Friml, 2009), and root cell patterning (Friml et al., 2003). Additionally, the transition from vegetative to reproductive growth controlled by day length is crucial. This switch from vegetative to reproductive growth is important because of the right timing of the floral initiation is essential for the optimal production of fruits and seeds in flowering plants. The exposure to cold (vernalization) is also an important factor. In this review, we give an overview of the main molecular actors regulating developmental processes in plants. Most investigations have been focused to regulatory mechanisms functioning in *A. thaliana*, an angiosperm and eudicot model plant, but in the last decade new data have been obtained in other plant species, either monocots or eudicots including legumes. In this review a special attention

will be given to list the major families of genes and proteins that participate in these mechanisms (Fig 1). Additionally, the importance of structural features that confer ductility and flexibility to the regulatory proteins has been pointed out in the last years.

2. EMBRYO, ROOT AND SHOOT APICAL MERISTEMSDEVELOPMENT

Several factors are implicated in controlling the different functional zones of the root meristem to modulate root growth, among these, plant hormones auxins and cytokinins play crucial roles. Auxin in root development has been established as a master regulator (Saini et al., 2013). Other hormones such as abscisic acid, cytokinins, ethylene, jasmonic acid as well as brassinosteroids, gibberellins, and strigolactones interact either synergistically or antagonistically with auxin. The hormone synthesis as well as the control of hormone levels involve the regulation of many different genes and protein families. In this section, a briefly information about main components participating in the regulatory pathways controlling embryo, root and shoot apical meristem development are reviewed.

2.1 *Auxin* response regulators

The phytohormone auxin (indole-3-acetic acid, IAA) regulates plant morphogenesis during all stages of development. It affects cell division and elongation, differentiation, tropisms, apical dominance, senescence, abscission, and flowering including embryogenesis and post-embryonic development (Davies 1995; Reinhardt et al., 2000; Ludwig et al., 2013). Its synthesis and transport influences plant morphogenesis. During many years multiple pathways have been proposed for the biosynthesis of IAA. It is well established that both TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA/TAR) and YUCCA (YUC) flavin monooxygenase-like proteins are required for biosynthesis of IAA (Zhao et al., 2001; Cheng et al., 2006; Mashiguchi et al., 2011). The YUC genes are mainly expressed in meristems, young

primordia, vascular tissues, and reproductive organs. Overexpression of each YUC gene leads to auxin overproduction. YUC proteins catalyze a rate-limiting step of the indole-3-pyruvic acid (IPA) pathway, which is the main IAA biosynthesis pathway in Arabidopsis. The mechanism of IAA synthesis in *Oryza sativa* (rice) may be different from that in Arabidopsis (Yamamoto et al., 2007). Some *YUCCA* genes involved in this mechanism do not have orthologues outside the Angiosperms. *YUCCA* orthologues have been identified and characterized in *Zea mays* (maize) (Gallavotti et al., 2008), *Triticum aestivum* (wheat) (Li et al., 2014a) and *Vitis vinifera* (grapevine) (Böttcher et al., 2013). An interaction between IAA and ethylene biosynthesis genes mediated by *YUCCA* genes has been suggested (Böttcher et al., 2013).

The AUXIN INFLUX CARRIER PROTEIN 1 (AUX1) / LIKE-AUX1 (LAX) proteins, the p-glycoprotein (PGP) auxin ABC-type transporters, and the PIN-FORMED auxin efflux carriers (PIN) are involved in active auxin transport (Ongaro and Leyser, 2008; Swarup et al., 2008). Some differences have been found between monocots and eudicots. For instance, the function of PIN1 appears to be different in *A. thaliana* and *O. sativa* (Wang et al., 2014). AUXIN RESPONSE FACTORS (ARFs) can act either as activators or repressors of transcription of these AUX/IAA proteins (del Bianco and Kepinski, 2011; Saini et al., 2013). High levels of auxin promote the proteasome-mediated degradation of the AUX/IAA proteins, acting as repressors of auxin response by binding members of ARFs family. ARF proteins having a Q-rich middle region, such as ARF5, ARF7, ARF8 and ARF19, are transcriptional activators, whereas those without the Q-rich middle region, such as ARF1 and ARF2 are thought to act as transcriptional repressors. Auxin binds to its intracellular auxin receptor TRANSPORT INHIBITOR RESPONSE 1 (TIR1) protein, the F-box component of the SCF(TIR1) E3 ubiquitin ligase complex. The SCF(TIR1) E3 ubiquitin ligase complex regulate root and hypocotyl growth, lateral root formation, cell elongation, and gravitropism. TIR1 ubiquitinates AUX/IAA repressors

and triggers their degradation, thus releasing the inhibition of ARF transcriptional activity (Dharmasiri et al., 2005). The presence of 23 ARFs and 29 AUX/IAAs in Arabidopsis represents a complex matrix configuration of the auxin signaling pathway (Guilfoyle and Hagen 2007; Lokerse and Weijers 2009). The role of ARF–AUX/IAA and auxin-AUX/IAA interactions have been also reported in *O. sativa* (Shen et al., 2010; Zhu et al. 2012), *P. trichocarpa* (Kalluri et al., 2007), *V. vinifera* (Kohno et al., 2012) and *Z. mays* (Zhang et al., 2014a).

The control of embryonic root initiation is crucial to cell identity in plants. In Arabidopsis, the auxin-dependent transcriptional activator ARF5/MONOPTEROS (MP) drives hypophysis specification by promoting the IAA transport from the embryo to the hypophysis precursor (Schlereth et al., 2010; Tian et al., 2014). Its transcriptional activity is inhibited by BODENLOS (BDL)/IAA12 protein (Hamann et al., 2002). In addition, MP positively regulates the expression of *PIN1* (Friml et al., 2003). Cell-cell communication also mediates development. Five PIN family members (PIN1, PIN2, PIN3, PIN4, and PIN7), participate in the cell-to-cell transport of IAA in Arabidopsis. The PIN3 is also involved in the lateral root initiation (Tian et al., 2014). The information concerning IAA regulation and role of IAA transporters has increased in monocots species such as *O. sativa*, *Z. mays*, *Sorghum bicolor*, and *Brachypodium distachyon* in the last years (for a review see Balzan et al., 2014).

Other IAA transport regulators are MITOGEN ACTIVATED PROTEIN KINASES (MAPK) (Zhang et al., 2008). MAPK kinase-7 (MKK7) and MAPK 12 participate in the control of root system architecture through negative regulation of IAA signalling. MAPK kinases have been investigated in several plant species including *A. thaliana*, *O. sativa*, *P. trichocarpa*, *B. distachyon* and *Z. mays* (Agrawal et al., 2003; Rodríguez et al., 2010; Kong et al., 2013).

Auxin and PIN transporters also regulate gravitropism. Changes of the relative orientation of the gravity vector require the relocation of PIN3 and PIN7 to the lower side of the gravity-

sensing cells (Petrášek et al., 2006; Harrison and Masson, 2008; Kleine-Vehn et al., 2010). PIN2 mediates the directional auxin flow from the root tip to the elongation zone where control of elongation occurs (Abas et al., 2006; Wiśniewska et al., 2006).

A connection between the Arabidopsis carotenoid cleavage dioxygenases *MORE AXILLARY GROWTH (MAX)* genes and auxin has been proposed. *MAX* genes are involved in strigolactone biosynthesis and perception with important roles in regulating shoot and root architecture. Mutations in the *A. thaliana* *MAX* genes and orthologous genes in *Pisum sativum*, *O. sativa* and *Petunia hybrid* lead to increased branching (Hayward et al., 2009, de Saint Germain et al., 2013; Czarnecki et al., 2014). The *MAX* pathway acts regulating auxin transport capacity in the main stem. This is achieved at least in part by modulation of the levels of PIN auxin efflux carriers. The findings link high auxin transport to high shoot branching (Ongaro and Leyser, 2008). For shoot activation, shoots must be able to export auxin mediated by *MAX* gene regulation. *AtMAX3*, *AtMAX4*, and *AtMAX1* act in the synthesis of the mobile hormone regulating PIN1 levels through *MAX2*. In addition, the concentration of auxin in the polar transport stream is monitored by the *AXR1/AFB* pathway to regulate cytokinin synthesis. Thus, high auxin down-regulates cytokinin synthesis, inhibiting shoot activation.

Additionally, the MADS-box gene *AGL14/XAANTAL2/XAL2*, closely related to the flowering gene, *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1 (SOC1)* is required for root stem-cell niche (SCN) and meristem patterning (Martínez-Castilla and Álvarez-Buylla, 2003). It up-regulates *PIN1* and *PIN4* mediated by auxin levels (Garay-Arroyo et al., 2013). *AGL12/XAANTAL1* also regulates root development (Gan et al., 2005; Tapia-López et al., 2008). The characterization of *SOC1-like* genes in *O. sativa* (Lee et al., 2004), *T. aestivum* (Shitsukawa et al., 2007), *Citrus sinensis* (citrus) (Tan et al., 2007), *Hordeum vulgare* (Papaefthimiou et al., 2012) and Orchidaceae such as *Dendrobium Chao Parya Smile* (Ding et al., 2013) have been

reported.

2.2 Cytokinin response regulators

Roots are a major source of cytokinin in plants, which is synthesized in the root and transported to the shoot. In *Arabidopsis*, cytokinin biosynthesis is dependent on AUXIN RESISTANT1 (AXR1)-mediated signalling (Müller and Leyser, 2011) and the activation of *ARABIDOPSIS RESPONSE REGULATOR 5* (ARR5) (Müller and Sheen, 2008). The cytokinin/auxin antagonistic interaction is crucial to position the root meristem transition zone (TZ) and to maintain root meristem size. Cytokinin-mediated up-regulation of the *SHORT HYPOCOTYL 2* (SHY2/IAA3), a member of the *AUX/IAA* family repressors, contributes also to cell differentiation at TZ and root meristem growth (Dello et al., 2008). Other regulators such as ARR1 and DELLA protein REPRESSOR OF GA1-3 (RGA) and UPBEAT1 (UPB1), a basic helix–loop–helix bHLH151 transcription factor, participate in this mechanism (Moubayidin et al., 2010).

In *A. thaliana*, cytokinins are perceived by a family of histidine kinase receptors, such as *Arabidopsis* histidine kinase2 (AHK2), AHK3 and AHK4/woodenleg (WOL1)/cytokinin response1 (CRE1) (Bishopp et al., 2011; Saini et al., 2013). In *O. sativa* the cytokinin oxidase/dehydrogenase4 integrates the interaction between cytokinin and auxin signaling to control the crown root formation (Gao et al., 2014a). Response regulators (RRs) have been also characterized in *O. sativa* (Tsai et al., 2012) and *T. aestivum* (Chitnis et al., 2014).

2.3 Gibberellins response regulators

Gibberellins (GAs) regulate different aspects of plants growth from seed germination through leaf expansion, stem elongation, flower induction, and development to seed. For that, the interaction between GA and other hormones exists and involve different signaling pathway

components. The most extensively characterized among these are the DELLA proteins. In the TZ, DELLA proteins (DELLAs) of GRAS family, ARR1, SHY2 and PIN modulate cell differentiation, and in the root meristem, GAs increase the stability of PIN1, PIN2 and PIN3 mediated by DELLAs (Claeys et al., 2013). GA biosynthesis is linked to the transport of auxin by PIN1 (Saini et al., 2013). Other DELLAs such as GA-INSENSITIVE (GAI), REPRESSOR of GA1-3 (RGA), or GAI-ASSOCIATED FACTOR1 (GAF1) regulates GAs signalling and GAs homeostasis in Arabidopsis (Peng et al., 1997; Fukazawa et al., 2014) and rice (Fu et al., 2001).

During vegetative growth, DELLAs also inhibit cell proliferation by inducing expression of the cell cycle inhibitors SIM, SIM-RELATED1 (SMR1), SMR2, and KIP-RELATED PROTEIN 2 (KRP2) (Claeys et al., 2013). DELLAs also interact with SPATULA (SPT/bHLH24) that inhibits cotyledon cell expansion. Other member of GRAS family involved in root growth is SCARECROW-like protein 3 (AtSCL3) that acts as an attenuator of GAI and RGA and controls root cell elongation. GA signaling maintains the interaction between AtSCL3 and DELLA, in conjunction with the SHR/SCR pathway, which modulates the timing and extent of the formative division in the meristem zone (MZ) (Heo et al., 2011). RGA-like proteins such as AtRGL1 and AtRGL2, members of DELLA subfamily, are also regulators of GA responses (Wen and Chang, 2002; Lee et al., 2002). AtRGL2 affects seed germination, and AtRGL1 and AtRGL2 modulate floral development. In *O. sativa*, *SLENDER RICE1* (*SLR1*), a member of DELLA subfamily, acts as a repressor of the GA signaling pathway (Itoh et al., 2002; 2005; Ueguchi-Tanaka et al., 2007).

2.4 Other hormone response regulators

Crosstalk between brassinosteroids and auxin also regulates various aspects of plant root growth and development (Saini et al., 2013). In *A. thaliana*, *BRAVIS RADIX* (*BRX*) is required for

interaction between brassinosteroids and auxins for optimum root growth. Brassinosteroids induce the expression of various *ARFs* genes (*IAA17/XAR3*, *IAA7/XAR2*, *IAA14/SLR*) and affect the cellular localization PIN3, PIN4 and AUX1/LAXs.

Synergistic interactions take place between auxin and ethylene in the regulation of root gravitropism and root growth (Saini et al., 2013; Santisree et al., 2011). *PIN2/AUX1* is up-regulated by ethylene leading to the stimulation of basipetal auxin transport towards the elongation zone of the root in *A. thaliana*. Mutation of *ABA INSENSITIVE3 (ABI3)* inhibits lateral root initiation by attenuating auxin response, and the expression of *ABI4* affects the expression of *PIN1*. ABA also up-regulates the expression of *ARF2* resulting in the inhibition of root growth.

Jasmonic acid (JA) is also implicated in the regulation of root growth. In *A. thaliana* *ARF6* and *ARF8* are positive regulators of adventitious rooting. They regulate the expression of three *AUXIN-INDUCIBLE GRETCHEN HAGEN3 (GH3)* genes, *GH3.3*, *GH3.5* and *GH3.6*. that modulate JA homeostasis. In *O. sativa*, JA induces the expression of auxin efflux carrier genes *OsPIN1c*, *OsPIN5a*, *OsPIN10a* and *OsPIN10b* in the roots (Wang et al., 2009b).

2.5 Class 1 KNOX homeodomain transcription factors

KNOX genes fall into two subclasses, Class I *KNOX* (*KNOXI*) and Class II *KNOX* (*KNOXII*) based on sequence similarity, gene structure, and expression pattern (Scofield and Murray, 2006; Hay and Tsiantis, 2010; Arnaud and Pautot, 2014; Zhou et al., 2014). *Class I KNOX* genes, evolutionarily close to *Z. mays* *KN1*, are expressed in the SAM of both monocot and eudicot plants and play crucial roles in the maintenance of SAM, as well as in cell expansion, differentiation associated with organogenesis, and in the regulation of leaf. Class II *KNOX* genes display diverse expression patterns but their function is still not clear. In *A. thaliana*, the Class I

KNOX genes is comprised of *SHOOT MERISTEMLESS (STM)*, *KNAT1* (*KNAT* = *Knotted* in *Arabidopsis thaliana* – also called *BREVIPEDICELLUS (BP)*, *KNAT2* and *KNAT6*. Activation of *STM* expression requires the function of the *CUP-SHAPED COTYLEDON (CUC)* genes, which encode NAC-domain transcriptional regulators.

MYB domain transcription factors, and members of *BLADE ON PETIOLE (BOP)*, *YABBY (YAB)*, *BEL1-like*, *GROWTH-REGULATING FACTOR (GRF)* and *Class I BASIC PENTACYSTEINE (BPCs)* families are negative regulators of KNOX gene expression. MYB factors are conserved between *Z. mays*, (*ROUGH SHEATH2*), *Antirrhinum* (*PHANTASTICA*, *PHAN*) and *Arabidopsis* (*ASYMETRIC LEAVES1*, *AS1*). *AtMYB93* is a negative regulator of lateral root development (Gibbs et al., 2014). *AtMYB93* homologues have been found in diverse crop species. *GRF* exhibit conserved function in monocot and eudicot plant species (Kuijt et al., 2014). *AtGRF4*, -5 and -6 from *A. thaliana* could repress *KNAT2* promoter activity. In *O. sativa*, *OsKN2* is down-regulated by *OsGRF3* and *OsGRF10* *in vivo* and *OsGRF1* seems to play a regulatory role in stem elongation (Kim et al., 2003). In *Hordeum vulgare* (barley), *BGRF1* probably act as a repressor (Kuijt et al., 2014). BPCs are direct regulators of the *INNER NO OUTER (INO)*, *SEEDSTICK (STK)*, and *LEAFY COTYLEDON 2 (LEC2)*, and have a role in the fine regulation of the cytokinin content in the meristem, as both *ISOPENTENYLTRANSFERASE 7 (IPT7)* and *ARABIDOPSIS RESPONSE REGULATOR 7 (ARR7)*. The BPCs also deregulate the expression of the *STM* and *BP/KNAT1* (Simonini and Kater, 2014). KNOX genes have also been characterized in legume species such as *PsKN1* and *PsKN2* in *P. sativum* (Tattersall et al., 2005), orthologues of *STM* and *KNAT1/BP*, respectively, and *LjKN1*, *LjKN2* and *LjKN3* in *Lotus japonicus* (Luo et al., 2005). In *Medicago truncatula* KNOX genes present important differences compared with other characterised legume KNOXs (Di Giacomo et al., 2008; Zhou et al., 2014).

Positive regulators of *KNOX* expression have also been described, *CUC1*, *CUC2* and *JAGGED LATERAL ORGANS (JLO)*, which belong to *CUC* and the *LATERAL ORGAN BOUNDARY DOMAIN (LBD)* gene families (Kuijt et al., 2014).

2.6 *BEL1*-like *TALE* homeodomain proteins

In *A. thaliana*, the *BEL1*-like *TALE* Homeodomain (BLH) protein *BELLRINGER (BLR)* functions together with *STM* and *BP* in the shoot apex to regulate meristem identity promoting correct shoot architecture. The BLH proteins, *SAWTOOTH1 (BLH2/SAW1)* and *SAWTOOTH2 (BLH4/SAW2)* negatively regulate *BP* expression. *BEL1*-type orthologues have been identified in *T. aestivum* and *Solanum tuberosum* (potato) (Sharma et al., 2014). BLH form heterodimeric complexes with *STM* and *BP*. This *KNOX*-BLH interaction is conserved among various plant species (Mizumoto et al., 2011; Arnaud and Pautot, 2014; Sharma et al., 2014).

2.7 *CUP-SHAPED COTYLEDON (CUC)* transcription factors

CUC genes, which belong to the *NAC (NAM, CUC3)* gene family, are involved in embryonic SAM formation via *STM* activation and in the separation of cotyledons and floral organs, which is critical for proper leaf and flower patterning (Vroemen et al., 2003; Nardmann and Werr, 2007). Orthologues in *Z. mays*, *ZmNAM1*, *ZmNAM2*, *ZmCUC3* together with *NO APICAL MERISTEM (NAM)* from *Petunia hybrida (PhNAM)*, *Antirrhinum majus CUPULIFORMIS (AmCUP)*, *PaNAC01* and *PaNAC02* from *Picea abies* or *MtNAM* from *M. truncatula* have been studied (Zimmermann and Werr, 2005; Larsson et al., 2012; Cheng et al., 2012). *NAM*- and *CUC3*-related proteins are functionally equivalent between monocots and eudicots, although divergent expression patterns have been observed (Adam et al., 2011).

2.8 Lateral Organ Boundaries (LOB) containing domain proteins

The LOB-Domain protein family (LBD) (also named ASYMMETRIC LEAVES 2 proteins, AS2-like) encode a plant-specific family of transcriptional regulators conserved in a variety of evolutionarily divergent plant species (Matsamura et al., 2009). LBD proteins play a crucial role in defining organ boundaries and are involved in almost all aspects of plant development, including embryo, root, leaf, and inflorescence (Husbands et al., 2007). Furthermore, **several LBDs are regulated by a variety of phytohormones**. In Arabidopsis, *LBD16 / ASL18* and *LBD29 / ASL16* are involved in the auxin signal transduction cascade that leads to the formation of lateral roots (Majer and Hochholdinger, 2011). The *ASL19 / LBD30 (JLO)* regulates auxin transport via repression of the auxin efflux carriers PIN1, PIN3, PIN4 and PIN7 and contributes to the auxin dependent embryonic apical-basal polarity and patterning processes in the embryo. *ASL9 / LBD3*, close relative to *ASL6 / LBD29*, is regulated by cytokinin in the root.

In *O. sativa*, *CROWN ROOTLESS1 (CRL1)*, close relative of *ASL16 / LBD29*, is crucial for crown root formation (Inukai et al., 2005). ARF proteins directly regulate *CRL1* expression in the auxin signalling pathway. *ADVENTITIOUS ROOTLESS1* encodes an auxin-responsive protein that controls the initiation of adventitious root primordia (Liu et al., 2005). *CRL1*-regulated genes have been identified recently in rice (Coudert et al., 2014). The orthologue *RCTS* in *Z. mays* has been also characterized (Taramino et al., 2007).

2.9 WUSCHEL transcription factor

WUSCHEL (WUS) is a bifunctional homeodomain transcription factor expressed in cells of the organizing center of SAM. It regulates the maintenance of stem cell populations in shoot meristems. WUS acts mainly as a repressor in stem cell regulation, but becomes an activator

when is involved in the regulation of the *AGAMOUS* (*AG*) gene (Ikeda et al., 2009; Bleckmann et al., 2010; Yue et al., 2014). In *A. thaliana*, stem cell fate in the SAM is controlled by a regulatory network that includes the *CLAVATA* (*CLV*) ligand-receptor system (Leibfried et al., 2005). *WUS* restricts its own levels by activating a negative regulator, *CLAVATA3* (*CLV3*) (Stahl and Simon, 2010; Yadav et al., 2011). *WUS* / *CLV3* regulatory system is linked to cytokinin signalling by direct transcriptional control of *ARABIDOPSIS RESPONSE REGULATOR* genes (*ARRs*). *WUS* directly represses the transcription of several *ARRs* (*ARR5*, *ARR6*, *ARR7* and *ARR15*), which act in the negative-feedback loop of cytokinin signalling (Buechel et al., 2010).

The *ARGONAUTE* related protein *ZWILLE* (*ZLL*) is required for *WUS* / *CLV3* function. *ZWILLE* potentiates *WUS* function during shoot meristem stem cell development. In the absence of functional *ZLL*, stem cell-specific expression of *CLV3* is not maintained despite increased levels of *WUS* (Tucker et al., 2008). *ZLL* has overlapping functions with the *ARGONAUTE1* (Lynn et al., 1999). Additionally, *POLTERGEIST* (*POL*) and *POLTERGEIST-LIKE* (*PLL1*), two related protein phosphatases 2C, positively regulate *WUS* expression and also are essential to initiate the embryonic root meristem (Stahl and Simon, 2010). *ARGONAUTE* has been recently investigated in *O. sativa* (Yang et al., 2013). Orthologous to Arabidopsis *ZLL* were isolated also from *Brassica napus* (Elhiti et al., 2011). Ectopic expression of the Brassica *BnZLL* did not have any effects on Arabidopsis somatic embryogenesis.

WUS function can be replaced by the *WUSCHEL*-related *Homeobox* *WOX5*, usually expressed in the QC of the root meristem (Sarkar et al., 2007). *WUSCHEL-RELATED HOMEBOX* (*WOX*) family, is also critical for embryo development. *O. sativa*, genome encodes at least 13 *WOX* genes. Four of these (*OsWOX5*, *OsWOX11*, *OsWOX12B* and *OsWOX12A*) were up- or down-regulated by plant hormones (auxin, cytokinin and gibberellin) (Chen et al., 2014).

WOX11 is involved in the activation of crown root emergence and growth. It may be an integrator of auxin and cytokinin signaling during crown root development (Zhao et al., 2009). WOX genes in *Populus trichocarpa* may have expanded differently from the WOX genes in *A. thaliana*. In *Populus tomentosa*, a poplar specie physiologically close to *P. trichocarpa*, 18 WOX genes were identified (Liu et al., 2014). The characterization of WOX5 genes from *Triticum sp.* and its relatives have been also reported recently (Zhao et al., 2014). Members of this family have also been investigated in *P. sativum* (Zhuang et al., 2012), *P. P. abis* (Zhu et al., 2014), *Solanum lycopersicum* (tomato) (Ji et al., 2010) and *Rosa canina* (Gao et al., 2014b).

2.10 Other relevant transcription factors

The bHLH transcription factor TARGET OF MP 7 (TMO7/bHLH135) is required for MP-dependent root initiation (Schlereth et al., 2010). TMO7 transcription is limited to the pro-embryo cells adjacent to the future hypophysis and it is directly activated by MP. Therefore, MP activates two mobile factors, auxin and TMO7, which are both transported to the hypophysis. How these two signals converge to regulate stem cell specification remains unclear. In addition, BDL interacts with TOPLESS (TPL), a transcriptional co-repressor (Szemenyei 2008).

Expression of GRAS proteins SCARECROW (SCR) and SHORTROOT (SHR), and AP2-like ethylene-responsive PLETHORA (PLT) and BABY BOOM (BBM) is also necessary for the formation and maintenance of the SCN and SAM in Arabidopsis (Helariutta et al., 2000; Aida et al., 2004) . The *PLT* repress the CLASS III HOMEODOMAIN-LEUCINE ZIPPER (HD-ZIP III) transcription factors, master regulators of embryonic apical fate (Grigg et al., 2009; Smith and Long, 2010).

TEONSITE BRANCHED 1 CYCLOIDEA (TCP) transcription factors are critical for the morphogenesis of shoot lateral organs (Koyama et al., 2007; Ikeda and Ohme-Takagi, 2014).

TCPs regulate the expression of *CUC* genes. Similarly to *CUC*, the *LATERAL SUPPRESSOR* (*LAS*), which is a member of the GRAS family acts in shoot branching upstream of *REVOLUTA* (*REV*) (Greb et al., 2003). *LAS* in concert with the bHLH-protein-encoding Arabidopsis gene *REGULATOR OF AXILLARY MERISTEM FORMATION* (*ROX*), which is the ortholog of the branching regulators *LAX PANICLE1* (*LAX1*) in *O. sativa* and *BARREN STALK1* (*BA1*) in *Z. mays*, and the *REGULATOR OF AXILLARY MERISTEMS 1* (*RAX1*) in Arabidopsis modulate axillary meristem formation (Yang et al., 2012). Other GRAS protein such as HAIRY MERISTEM (*HAM*) is involved in meristem formation and maintenance in *P. hybrida* (Stuurman et al., 2002).

ULTRAPETALA1 (*ULT1*) is a key negative regulator of cell accumulation in Arabidopsis shoot and floral meristems. *REBELOTE* (*RBL*) and *SQUINT* (*SQN*) function redundantly in the temporal regulation of floral meristem termination in *A. thaliana* (Early and Poething, 2011). In *O. sativa*, *MONOCULM1* (*MOC1*), a member of GRAS family proteins, initiates axillary buds and promote their outgrowth (Li et al., 2003).

2.11 Small signaling peptides and receptor kinases

Small signaling peptides and receptor kinases are also essential for both primary and lateral root initiation and maintenance. *ROOT GROWTH FACTOR* (*RGF*)/*GOLVEN* (*GLV*)/*CLE-LIKE* (*CLEL*) peptides maintain the root SCN mediating the regulation of *PLT* transcription factors (Matsuzaki et al., 2010; Meng et al., 2012). The receptor-like kinase *ARABIDOPSIS CRINKLY4* (*ACR4*) promotes formative cell division in the pericycle (de Smet et al., 2008). In the primary root tip, *ACR4*, together with *CLV1* and their putative ligand *CLE40*, controls the number of columella stem cell divisions. The leucine-rich repeat receptor-like kinases (*LRR-RLKs*), *RECEPTOR-LIKE PROTEIN KINASE1* (*RPK1*) and *TOADSTOOL2* (*TOAD2*), are

redundantly required for central domain radial pattern formation and basal pole differentiation during embryogenesis (Nordine and Tax, 2008). Furthermore, both proteins RPK1 and TOAD2 are required to generate cotyledon primordial. The receptor-like protein kinase in Arabidopsis, CURVY1 (CVY1), regulates cell morphogenesis, flowering time and seed production (Gachomo et al., 2014). In *O. sativa*, *OsRPK1*, negatively regulates polar auxin transport and root development (Zou et al., 2014).

3. LEAF DEVELOPMENT

Leaf development include positioning and initiation of leaf primordia, specification of leaf identity, establishment of dorsiventrality, the control of cell division and expansion or pattern formation or leaf polarity. A cellular perspective of leaf development can be found in Kalve et al. (2014).

3.1 Class 1 KNOX homeodomain transcription factors

In initiating organs, the ARP-KNOX I regulatory module is well established in simple-leaved species as Arabidopsis. However, in other compound-leaved species such as *S. lycopersicum*, *Cardamine hirsute*, or the legume *P. sativum* show a different *KNOX I* expression pattern during leaf development (Zhou et al., 2014). The *KNOX I* genes may not be involved in compound leaf formation in legumes. Accordingly, orthologues of *FLORICAULA/LEAFY* (*FLO/LFY*) such as *UNIFOLIATA* (*UNI*) from *P. sativum* and *SINGLE LEAFLET1* (*SGL1*) from *M. truncatula* function in place of *KNOXI* to regulate compound leaf development. These findings suggest that probably the ARP-KNOX I regulatory mechanism might not be conserved in all plant species (Zhou et al., 2014). In *M. truncatula*, *ARP* (*PHANTASTICA*) and *STM/BP-like KNOXI* exhibit conserved functions (Zhou et al., 2014; Ge et al., 2014).

3.2 Lateral Organ Boundaries (LOB) containing domain proteins

In Arabidopsis, the member of the LOB-containing domain gene family (LBD) *AtASL4/AtLBD23* is expressed at the base at the adaxial side of lateral organs and is involved in early leaf development. *AtASL2/AtLBD6* is involved in symmetric flat leaf formation by repression of cell proliferation in the adaxial domain (Majer and Hochholdinger, 2011). *AtASL1* interacts with *AtASL2/AtLBD6* and regulate negatively *BLADE-ON-PETIOLE1 (BOP1)*, which directly induces *AtAS2/AtLBD6* expression in the young leaf primordia and later in the adaxial domain and the inner region of the leaf including the vasculature between adaxial and abaxial domains. BOP2 protein also induces the expression of *AtASL2/AtLBD6* and *AtASL4/AtLBD23*. Additionally, *AtASL1/AtLBD36* is expressed at the boundary between the SAM and the newly developing leaf primordial; *AtASL38/AtLBD41* is involved in dorsoventral determination of leaf development as its overexpression in *Celosia cristata* (cockscomb) leads to the formation of abaxialized leaves (Majer and Hochholdinger, 2011); *AtASL9/AtLBD3* affects rosette leaves and inflorescences. A genome comparative analysis has been done in LBD gene family from Arabidopsis and *O. sativa* (Yang et al., 2006), and *Z. mays* (Zhang et al., 2014b).

3.3 FILAMENTOUS FLOWER transcription factors

FIL/YABBY genes function redundantly to maintain leaf dorsoventral polarity and are required for specification of the leaf marginal region and lamina growth in Arabidopsis (Bowman, 2000; Stahle et al., 2009; Bonaccorso et al., 2012). Four members of this gene family, *FILAMENTOUS FLOWER (FIL/YAB1)*, *YABBY2 (YAB2)*, *YAB3* and *YAB5*, are expressed on the abaxial side of leaves. *FIL/YABBY* orthologues have been found in *Cabomba caroliniana*, a member of the

earliest-diverging angiosperms (Yamada et al., 2011), *Opium poppy* (Vosnakis et al., 2012), *O. sativa* (Toriba et al., 2007), *Vitis pseudoreticulata* (Xiang et al., 2013) and *Lilium longiflorum* (Wang et al., 2009c). The orthologue *OsYAB1* is involved in the feedback regulation of GA biosynthesis and *OsYAB3* is required for rice leaf development (Dai et al., 2007). In *A. thaliana*, *FIL* is required for inflorescence, floral meristem establishment and flower development (Lugassi et al., 2010).

In mutants with reduced *FIL/YABBY* function, *CINCINNATA-like (CIN)* and *TEOSINTE BRANCHED1, CYCLOIDEA (TCP/PFC)* genes are down-regulated (Sarojam et al., 2010). *CIN-TCP* proteins regulate growth and promote differentiation, particularly in marginal regions of the leaf (Koyama et al., 2010). Additionally, *YABBY* proteins interact with *LEUNIG (LUG)*, *LEUNIG-HOMOLOG (LUH)*, *SEUSS (SEU)* and *SEUSS-LIKE (SLK)* (Stahle et al., 2009; Bao et al., 2010). *LUG* and *LUH* belong to the *Gro/TLE* family of transcriptional co-repressors and exhibit partially overlapping functions in embryo and flower development (Bonaccorso et al., 2012). *FIL/YABBY* transcription factors require expression of the transcription factor *LATERAL SUPPRESSOR (LAS)* in the boundary between organs and the meristem (Stahl and Simon, 2010).

4. SEED DEVELOPMENT

The endosperm cellularization is important for embryo viability. *FERTILIZATION INDEPENDENT SEED POLYCOMB COMPLEX2 (FIS-PRC2)* and *ENDOSPERM DEFECTIVE1 (EDE1)* control this process (Lafon-Placette and Köhler, 2014).

4.1 *MADS-domain-containing transcription factors*

Type I *MADS*-box genes in *Arabidopsis* have assigned crucial roles in gamete and seed

development (Kapazoglou et al., 2012). The transcription factor member AGL62 is a major regulator of endosperm cellularization. AGL62 is expressed under negative control of the FIS-PRC2 complex revealing that the timing of endosperm cellularization is epigenetically controlled. Additionally, PHERES 1 (PHE1) / AGL37 participates in gamete and seed development, DIANA / AGL61, and AGL80 in central cell and endosperm formation (Kapazoglou et al., 2012). Similarly to AGL62, PHE1, and AGL36 are under epigenetic regulation mediated, in part, by the chromatin repressive enzymatic complex PRC2. In *P. hybrida*, ARABIDOPSIS BSISTER / AGL32 (ABS) and FBP24 are necessary to determine the identity of the endothelial layer within the inner integument of the ovule. In *H. vulgare*, two type I MADS-box orthologues, *HvOS1* and *HvOS2*, have been studied in different seed developmental stages (Kapazoglou et al., 2012). *HvOS1* and *HvOS2*, are closest relatives to wheat *TaAGL-33* and *TaAGL-42*, as well as rice *OsMADS65* and maize *ZmB4FML1*. *HvOS1* was induced by the phytohormone ABA and *HvOS2* was detected in specific endosperm sub- compartments. An epigenetic regulation of *HvOS1* and *HvOS2* in accordance to Arabidopsis Type I MADS genes has been suggested.

The three MADS-box genes *SEEDSTICK* (*STK*), *SHATTERPROOF1* (*SHP1*), and *SHP2* redundantly regulate *VERDANDI* (*VDD*), a putative transcription factor that belongs to the plant-specific B3 superfamily. It interacts with the MADS domain ovule identity complex affecting embryo sac differentiation in Arabidopsis (Matías-Hernández et al., 2010). In *O. sativa*, *OsMADS87* is associated to endosperm developmental transitions caused by interspecific hybridization in contrast to the Arabidopsis homologue *PHERES1* (Ishikawa et al., 2011). A genomic study in conifers showed the ancestral role of *MADS-box* genes for seed plants (Gramzow et al., 2014).

4.2 Other relevant transcription factors

In *Arabidopsis* the *AtYUCCA1/AtYUC1* encodes a flavin monooxygenase that catalyzes a rate-limiting step of IAA biosynthesis (Zhao et al., 2001). The orthologue *YUC-like* gene in *Z. mays*, *SPARSE INFLORESCENCE1* (*ZmSPI1*) is specific-expressed in endosperm (LeClere et al., 2010). DNA methylation and demethylation are critical for proper cellular regulation during plant development. In plants demethylation is operated by specific DNA glycosylases such as DEMETER (DME) and REPRESSOR OF SILENCING1 (ROS1), which play important roles in seed development. The DME homologue from *H. vulgare* (HvDME) has been also identified (Kapazoglou et al., 2013).

Photoreceptors, especially the far-red light-absorbing phytochrome A (PHYA), play a crucial role in early seedling development, triggering the transition from etiolated to photomorphogenic growth. Two GRAS proteins from *A. thaliana*, SCARECROW-LIKE21 (SCL21) and PHYTOCHROME A SIGNAL TRANSDUCTION1 (PAT1), are specifically involved in phytochrome A signal transduction. Both SCL21 and PAT1 are required in germinating seedlings to perceive FR light via PHYA signal transduction (Torres-Galea et al., 2013). In *O. sativa*, two homologues to PAT1, OsCIGR1 and OsCIGR2 (for CHITIN-INDUCIBLE GA-RESPONSIVE) have been identified (Day et al., 2003).

ELONGATED HYPOCOTYL5 (HY5), which is a basic domain/leucine zipper (bZIP) transcription factor, together with its close homolog HY5 HOMOLOG (HYH) regulates seedling de-etiolation (Vandenbussche et al., 2007; Chang et al., 2008). HY5 positively regulates the expression of *LIGHT-REGULATED ZINC FINGER PROTEIN 1* (*LZF1*), which also mediates de-etiolation, and *HYPOSENSITIVE TO LIGHT* (*HTL*), an alpha/beta-fold family protein that regulates seedling de-etiolation. HY5 indeed binds to the promoters of cell elongation-related gene *PICKLE* (*PKL*), which apparently negatively modulates HY5 (Jing and Lin, 2013). In

Arabidopsis the DE-ETIOLATED 1 (DET1)-CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1)-ELONGATED HYPOCOTYL 5 (HY5)-dependent photomorphogenesis pathway transcriptionally regulates the bHLH transcription factor PHYTOCHROME INTERACTING FACTOR 4 (PIF4) to coordinate seedling growth in response to elevated temperatures (Delker et al., 2014). The function of zinc finger proteins in photomorphogenesis in rice has been also investigated (Zhang et al., 2012) (Table 1).

5. FLOWER DEVELOPMENT

Plants finely control flowering processes in response to both environmental and endogenous conditions. A number of cellular mechanisms including chromatin remodelling, selective protein degradation, and transcriptional regulation mediated by transcription factors are involved in controlling these processes. Photoperiodic control or the exposure to cold (vernalization) are environmental signals to time the initiation of flowering at the appropriate season. The vernalization response is often coupled to the ability of plants to respond to the light/dark cycle.

5.1 *CONSTANS* protein

The ability to distinguish long days (LD) from short days (SD) is mediated by *CONSTANS* (CO) (Michaelis, 2009). CO acts as a floral promoter being regulated at both the mRNA and protein levels. The circadian regulation of CO mRNA requires a number of proteins, which are themselves regulated by the circadian clock. CYCLING DOF FACTOR1 (CDF1) acts as a negative regulator of CO transcription (Imaizumi et al., 2005). The repression of CO by CDF1 is removed by the activities of GIGANTEA (GI) and FLAVIN-binding KELCH DOMAIN F BOX PROTEIN1 (FKF1) (Sawa et al., 2007; Fornara et al., 2009). Additionally, four FLOWERING bHLH (FBH) transcriptional activators control CO expression for photoperiodic flowering. This

mechanism probably is conserved in different plant species. FBH homologues in poplar and rice induce *CO* expression in *Arabidopsis* (Ito et al., 2012).

The *CO* protein is produced in long days in the vasculature of the leaves where activates the expression of *FLOWERING LOCUS T* (*FT*), a phosphatidyl-ethanolamine binding protein, and its homologue *TWIN SISTER OF FT* (*TSF*) (Bu et al., 2014; Yang et al., 2014). *FT* protein is then translocated to the meristem where it acts to promote floral induction. The *GI-CO-FT* regulatory pathway identified in *Arabidopsis*, is also present in *O. sativa*, a short day (SD) plant (Tsuji et al., 2011). This *GI-CO-FT* might be an ancient pathway conserved across the plant kingdom (Amasino 2010). Multiple photoreceptors are implicated in the regulation of *CO* protein; *PHYTOCHROME B* (*PHYB*) promotes the degradation of *CO* early in the day, whereas *PHYA*, *CRYPTOCHROME1* (*CRY1*), and *CRY2* stabilize *CO* late in the day (Valverde et al., 2004).

The role of *CO* in flowering induction is conserved among distantly related plants but considerable variations have also been reported. In *O. sativa*, *OsHD1*, orthologue to *CO*, is the major determinant of photoperiod sensitivity. It activates expression of the *FT-like* gene *HD3a*, one of two sources of florigen in *O. sativa*. The photoperiod sensitivity in *O. sativa* depends in part on differences in the activity of *OsHD1* in LD and SD. The orthologue *HvCO1* has been identified in *H. vulgare*. The peptides of *HvCO1*, *HvCO2*, and *OsHD1* show significant structural differences from *CO* suggesting an evolutionary divergence in the most *CO-like* cereal genes (Griffiths et al., 2003). The *CONSTANS-like* gene from *Z. mays*, *CONZ1*, exhibit diurnal expression patterns notably similar to their *Arabidopsis* and *O. sativa* homologues (Miller et al., 2008). Recently, Wu et al. (2014) have characterized the *CO* gene family in *Glycine max* (soybean). *GmCOL1a/GmCOL1b* and *GmCOL2a/GmCOL2b* showed the highest sequence similarity to *Arabidopsis CO*.

5.2 FLOWERING LOCUS T and related proteins

Arabidopsis FLOWERING LOCUS T (*FT*) encodes a small protein similar to mammalian phosphatidylethanolamine binding-domain protein (Takada and Goto, 2003). The induction of *FT* is LD dependent, and mainly occurs accompanying cells of leaves. *FT* interacts with *FD*, a bZIP transcription factor, to up-regulate the floral identity gene *APETALA1* (*AP1*) (Abe et al., 2005; Wigge et al., 2005). The *FT* family in *Arabidopsis* contains five other members: *TWIN SISTER OF FT* (*TSF*), *TERMINAL FLOWER 1* (*TFL1*), *BROTHER OF FT* (*BFT*), *MOTHER OF FT* (*MFT*), and *A. thaliana* *CENTRORADIALIS* homologue (*ATC*). Phylogenetic analyses indicated that *FT* homologues are grouped into three major clades: *FT*-, *TFL1*- and *MFT*-like clades. *FT*-like genes (*FT* and *TSF*) are floral activators, *TFL1*-like genes (*TFL1*, *ATC* and *BFT*) are floral inhibitors and *MFT*-like genes participate in regulation of seed germination (Yoo et al., 2004; Xi et al., 2010). Interestingly, *FT* may not be the only florigen. *TFL1* may move cell to cell to maintain shoot meristem identity (Huang et al., 2012). Other *FT* homologues such as *TSF* also act systemically to promote flowering. *CENTRORADIALIS* homologue (*ATC*) may act in a non-cell autonomous manner to inhibit floral initiation. *ATC* is a short-day-induced floral inhibitor. Photoperiodic variations may trigger functionally opposite *FT* homologues to systemically influence floral initiation.

Homologues of *Arabidopsis* clock genes have been identified in various plant species (Imaizumi, 2010). Both eudicot and monocot species possess similar molecular circadian clocks, although some species-specific modifications have been described (Song et al., 2010). In *P. sativum* *GIGAS/FTa1* is essential for flowering under LD conditions and promotes flowering under SD conditions but it is not required for other photoperiodic responses such as internode elongation, leaf size or axillary growth (Hecht et al., 2011). Two *Beta vulgaris* (sugar beet) *FT*

paralogues (*BvFT1* and *BvFT2*) have antagonistic functions in controlling flowering time (Pin et al., 2010). The *FT* genes have been also characterized in *B. distachyon* and *T. aestivum* (Lv et al., 2014), *H. vulgare* (Faure et al., 2007), *S. tuberosum* (Navarro et al., 2011) and *G. max* (Nan et al., 2014).

EARLY HEADING DATE1 (*OsEHD1*) and *HEADING DATE 7* (*OsGHD7*) from *O. sativa* have no counterpart in *Arabidopsis*, and contribute to the natural variation in flowering time. *OsEHD1* antagonizes *OsHD1* function as a repressor and enables rice plants to flower under long photoperiods. *OsGHD7* inhibits flowering through the repression of the *OsEHD1*–*HD3a* pathway under LD (Xue et al., 2008). *OsGHD7* expression is specifically up-regulated during LD and it functions to maximize the reproductive success of the *O. sativa* plants. *OsEHD1* and *OsGHD7*, are absent in *B. distachyon* (Higgins et al., 2010).

OsHD3A and its homologue *RICE FLOWERING LOCUS T1* (*OsRFT1*) act as floral repressors in the daylength-dependent control of those two florigen genes (Kim et al., 2007; Komiya et al., 2008; Xue et al., 2008; Lee et al., 2010). The expression of *OsRFT1* induces flowering in LD, and also promotes flowering in the absence of *OsHD3A* under SD. *OsEHD1* and *OsGHD7* are absent in *B. distachyon* (Higgins et al., 2010). This observation suggest that photoperiod pathway through FT might be modified in rice. The *EHD1*–*RFT1* pathway is negatively regulated by phytochrome B, indicating the importance of this photoreceptor as a floral repressor in *O. sativa* (Komiya et al., 2009). *OsGHD7* also regulates plasticity of tiller branching by mediating the PHYTOCHROME B - TEOSINTE BRANCHED1 pathway (Weng et al., 2014). Phytochrome C (PHYC) plays a major role in the acceleration of *T. aestivum* (wheat) flowering under LD (Chen et al., 2014b) through the activation of the central photoperiod gene *PHOTOPERIOD 1* (*PPD1*) and *FLOWERING LOCUS T*.

5.3 *MADS*-domain-containing transcription factors

The daylength and vernalization pathways converge in the regulation of floral promoters. In the

meristem, vernalization promotes flowering through the epigenetic repression of the floral repressor *FLOWERING LOCUS C* (*FLC*). This allows for the induction of floral integrators by *CO* under inductive long days. Additionally, *FT*, *TSF*, and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) / *AGAMOUS LIKE 20* (*AGL20*) act as strong floral promoters (He et al., 2003) being antagonistically regulated by *CO* and *FLC*. The vernalization response needs the interaction of *FLC* and *FRIGIDA* (*FRI*), which is required for high levels of *FLC* expression (Johanson et al., 2000; Michaels, 2009). The activation of *FLC* by *FRI* is coupled to changes in chromatin structure although the possible association between *FRI* and chromatin is still known. The genes, *FCA*, *FLOWERING LOCUS D* (*FLD*), *FLOWERING LOCUS K* (*FLK*), *FPA*, *FVE*, *FY*, and *LUMINIDEPENDENS* (*LD*) constitutively repress *FLC* (Michaels, 2009).

The MADS-domain containing genes *FLOWERING LOCUS M* (*FLM*) / *MADS AFFECTING FLOWERING 1* (*MAF1*) / *AGAMOUS-LIKE 24* (*AGL24*), *MAF2/AGL31* and *AGL19* are regulated by vernalization (Alexandre et al., 2008). *AGAMOUS-LIKE 6* (*AGL6*) is a floral promoter that negatively regulates the *FLC* / *MAF* clade genes and positively regulates *FT* in Arabidopsis (Yoo et al., 2011). MADS-domain-containing transcription factors often function in heteromultimeric complexes. *FLC* acts in a complex with *SHORT VEGETATIVE PHASE* (*SVP*) (Hartmann et al., 2000), which is involved in the repression of the floral integrators *FT* and *SOC1*. *SVP* homologues have been identified in *H. vulgare* (Trevaskis et al., 2007) and *O. sativa* (Lee et al., 2012). Recently, new pathways regulated by *SVP* have been described including that controlling meristem development and hormonal signalling during the vegetative growth (Gregis et al., 2014).

AGAMOUS-LIKE 42 (*AGL42* / *FYF*), *AGAMOUS-LIKE 71* (*AGL71*) and *AGAMOUS-LIKE 72* (*AGL72*) are phylogenetically closely related to *SOC1*, and are also involved in the floral

transition. They promote flowering at the shoot apical and axillary meristems and seem to act through a gibberellins-dependent pathway. SOC1 directly controls the expression of these genes (Dorca-Fornell et al., 2011). *EARLY FLOWERING 3 (ELF3)* and *TERMINAL FLOWER 1 (TFL1)* are also involved in the regulation of thermosensory flowering in *Arabidopsis*, playing complementary roles in this response to ambient temperature (Strasser et al., 2009).

Additionally, *STK* from *A. thaliana*, and *FLORAL BINDING PROTEIN 7 (FBP7)* and *FBP11* from *P. hybrida* control the initiation of ovule primordium formation. *SEPALLATA (SEP)* controls floral state by contributing to floral organ and meristem identity. *SEP* genes have not been detected in gymnosperms suggesting that they may be originated after the angiosperms/gymnosperms divergence (Parenicová et al., 2003). *APETALA1 (AP1)*, *CAULIFLOWER (CAL)* and *FRUITFULL (FUL)* are important for flower initiation, in part because of their roles in up-regulating *LEAFY (LFY)* expression. The *AP1*, *CAL* and *FUL* genes act redundantly to control inflorescence architecture by affecting the domains of *LFY* and *TFL1* expression as well as the relative levels of their activities (Ferrándiz et al., 2000). *APETALA3 (AP3)* and *PISTILLATA (PI)* are also required for the activities of *AP1*, *LFY*, and *UNUSUAL FLORAL ORGANS (UFO)* (Ng and Yanofsky, 2001; Yamaguchi et al., 2014). The regulation of *AP3* and *PI* has been investigated in *Papaver somniferum* (Singh et al., 2014), *S. lycopersicum* (Quinet et al., 2014) and *V. vinifera* (Fernández et al., 2013). Some differences have been found compared to *Arabidopsis*. The lateral inflorescence meristem fate in tomato is more similar to an immature flower meristem than to the inflorescence meristem of *Arabidopsis*.

In plants, *MADS-box* genes have acquired considerable phylogenetic diversity. *MADS-box* genes have been classified into $M\alpha$ (i.e. *AGL23*, *AGL61*, *AGL62*), $M\beta$ (i.e. *AGL51*, *AGL54*, *AGL76*, *AGL78*, *AGL81*, *AGL89*), $M\gamma$ (i.e. *AGL37*, *AGL80*), $M\delta$ (i.e. *AGL30*), *MIKC^c* (i.e. *AGL1*, *AGL2*, *AGL5*, *AGL6*, *AGL7*, *AGL12*, *AGL13*, *AGL15*, *AGL17*, *PI*, *AGL27*, *AGL31*,

AGL68) and MIKC* (i.e. *AGL30*, *AGL65*, *AGL67*, *AGL94*, *AGL104*) groups based on phylogeny (Parenicová et al. 2003; Becker and Theissen, 2003; Arora et al., 2007; Liu et al., 2013; Hsu et al., 2014). Numerous of these genes are involved in flower development. MIKC*-type genes except *AGL67*, are almost exclusively expressed during pollen development in *Arabidopsis* (Verelst et al., 2007). MIKC*-type genes are not only present in higher eudicots but have also been identified in representatives of all major groups of land plants, including bryophytes, lycophytes, ferns, gymnosperms, basal angiosperms, eudicots, and monocots. In *O. sativa* all three MIKC*-type genes, the S-clade genes *MADS62* and *MADS63* and the P-clade gene *MADS68* are specifically expressed late in pollen development (Liu et al., 2013). *OsMADS1* / *LHS1* controls floret meristem specification, *OsMADS14* and *OsMADS15*, highly homologous to *ZAP1* from *Z. mays* and *AP1*, control early flowering (Fornara et al., 2004). The *Ananas comonus* (pinapple) *AcMADS1* probably play a role in flower development and fruitlet ripening (Moyle et al., 2014). In *G. max*, *GmAP1* (Chi et al., 2011) and *GmMADS28* (Huang et al., 2014) participates in the regulation of floral organ number and petal identity. In trees, the like-AP1 (LAP1) protein, an orthologue of AP1, mediates in photoperiodic control of seasonal growth cessation (Azeez et al., 2014). Legume flower development system differs from that in *Arabidopsis* (Wong et al., 2013). A MADS-box comparative gene family analysis has been also done in *H. vulgare* and *B. distachyon* (Schmitz et al., 2000; Wei et al., 2014).

5.4 Lateral Organ Boundaries (LOB) containing domain proteins

In *Arabidopsis*, *ASL2* / *LBD6* is not only involved in leaf adaxial–abaxial polarity but also in flower development (Majer and Hochholdinger, 2011). In cooperation with *ASL1* and *JAGGED* (*JAG*) it restricts the boundary cells in the floral organs. The closest homolog of *ASL2* / *LBD6*,

the *LBD* gene *ASL1 / LBD36*, shows a partially redundant function, by repressing *BP* when over-expressed.

In *Z. mays*, the *INDETERMINATE GAMETOPHYTE1 (IG1)* restricts the proliferative phase of the female gametophyte development (Evans, 2007). *IG1* interacts with *ROUGH SHEATH2 (RS2)*, which is ortholog of *AtAS1*. Another *LBD* genes involved in floral development are *RAMOSA2 (RA2)* from *Z. mays*, which is expressed at the sites of axillary meristem initiation at the inflorescences; *DEGENERATED HULL1 (DH1)* from *O. sativa*, which is involved in flower development (Li et al., 2008); and *LjLOB4* from *L. japonicus* which is expressed in the boundaries between the whorls of the floral bud could indicate a role in flowering.

5.5 Other floral response regulators

The SUPPRESSOR OF PHYA-105 1 (*SPA1*) – CONSTITUTIVE PHOTOMORPHOGENIC 1 (*COP1*) complex promotes the polyubiquitination of the *CO* protein and its subsequent degradation in the dark, where light dependent modifications that stabilize the *CO* protein are absent. Consistent with a negative role for *COP1* in flowering control, mutations in this gene cause extreme early flowering under SD. *COP1* and *CO* proteins interact both in vivo and in vitro and *COP1* contributes to daylength perception by reducing the abundance of the *CO* protein during the night (Jang et al., 2008). The Arabidopsis CULLIN4 E3 RING ligase bound to DAMAGED DNA BINDING PROTEIN 1 (*DDB1*) interacts with the *SPA1* – *COP1* complex and regulates flowering time (Chen et al., 2010). On the contrary, in the morning *CO* degradation occurs independently of the *SPA1*–*COP1* complex (Jang et al., 2008). Other proteins such as DAY NEUTRAL FLOWERING (*DNF*), LONG VEGETATIVE PHASE 1 (*LOV1*), RED AND FAR-RED INSENSITIVE 2 (*RFI2*) or SENSITIVE TO FREEZING 6 (*SFR6*) act as negative regulators of Arabidopsis *CO* expression being potential floral repressors (Chen and Ni, 2006;

Yoo et al., 2007; Knight et al., 2008; Morris et al., 2010).

TEMPRANILLO 1 (TEM1) and TEM2 are proteins involved in direct repression of FT in Arabidopsis (Castillejo and Pelaz, 2008). No clear orthologues of TEM1 or TEM2 have been found in O. sativa and B. distachyon suggesting that TEM1 and TEM2 may have originated by gene duplication after the monocot/dicot divergence (Higgins et al., 2010). Arabidopsis TEM1 and TEM2 genes are partially redundant, and only simultaneous knockdown of both induces early flowering, while overexpression of either gene results in delayed flowering under LD.

VERNALIZATION INSENSITIVE 3 (VIN3) or its homologs VERNALIZATION 1 (VRN1), VRN2, VRN5 / VIN3-LIKE 1 (VIL1) regulate the expression of the related floral repressors FLC and FLM (Michaels, 2009). VRN proteins belong to Polycomb group (PcG) proteins, which act by forming multiprotein complexes required to maintain the transcriptionally repressive state of homeotic genes throughout development. VIN3, and VRN2 participate in a Polycomb Repressor Complex 2 (PRC2)-like complex with other chromatin-remodeling proteins such as CURLY LEAF (CLF), SWINGER (SWN), and FERTILIZATION INDEPENDENT ENDOSPERM (FIE) that are involved in histone H3K27 methylation (Wood et al., 2006; Adrian et al., 2009), a chromatin mark associated with gene silencing necessary for the maintenance of FLC repression. The achievement of this repressed state requires the participation of LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) / TERMINAL FLOWER 2 (TFL2) (Mylne et al., 2006), a protein that binds H3K27me3 and maintains stable gene repression, similarly to the function of the PRC1 in animals. EMBRYONIC FLOWER 2 (EMF2) is also a component of Arabidopsis PRC2 (Yoshida et al., 2001). EMF1 and EMF2 participate in the same regulatory mechanism, and both proteins cooperate in the silencing of AGAMOUS (AG) during vegetative growth (Calonge et al., 2008). In O. sativa, some components of the PcG complex have been characterized such as FERTILIZATION-INDEPENDENT ENDOSPERM 2 (OsFIE2), which is

crucial for reproduction and endosperm formation (Li et al., 2014).

In O. sativa, OsGHD7 protein presents similarity to VRN2 (Yan et al., 2004). In cereals VRN2 functions in the repression of VRN3, an FT homologue. Another key component of the vernalization pathway in cereals is VRN1, but encodes a protein functionally distinct from AtVRN1. In temperate cereals, VRN1 is responsible for the repression of VRN2 after prolonged exposure to cold (Preston and Kellog, 2008). In cereals, an interaction between VRN3 (FT) and FD-LIKE2 (FDL2), a wheat homologue of AtFD, takes place (Li and Dubovsky, 2008). In general, vernalization response of temperate cereals show certain difference compared with Arabidopsis (Greenup et al., 2010).

Additional floral repressors in O. sativa include the 14-3-3 protein GF14c that interacts with OsHD3A (Purwestri et al., 2009). Members of this family also interact with FT proteins in S. lycopersicum and Arabidopsis. In addition, the DAYS TO HEADING on chromosome 8 from O. sativa (OsDTH8) is an important element in the regulation of photoperiodic flowering. OsDTH8 down-regulates the expression of OsEHD1 and OsHD3A in LD, similarly to OsGHD7 and OsHD1 (Wei et al., 2010). Other SD plants such as Pharbitis nil and G. max regulate FT expression similarly, but they have additional regulatory networks that operate together with the GI-CO-FT module (Hayama et al., 2007).

SQUAMOSA PROMOTER BINDING LIKE (SPL) factors in Arabidopsis promotes phase change and, subsequently, flowering. These transcription factors activate the transcription in the SAM of floral integrator genes, such as SOC1, LFY, AP1 and FUL (Wang et al., 2009a). In particular, Arabidopsis SPL9 and SPL10 act as positive regulators of miR172 which targets APETALA2 (AP2) and several AP2-like transcription factors such as TARGET OF EAT 1-3 (TOE1-3), SCHLAFMÜTZE (SMZ) and SCHNARCHZAPFEN (SNZ), involved in the repression of the floral integrator FT in the leaf vasculature (Yant et al., 2009). SMZ is also

involved in the repression of *SOC1* and *AP1* which is dependent on *FLM*, suggesting a direct connection between AP2- and MADS-domain proteins (Mathieu et al., 2009).

CRABS CLAW (*CRC*) and *TOUSLED* (*TSL*) control important aspects of carpel development. Orthologues of *CRC* and *TSL* from the basal angiosperm species *Amborella trichopoda* and *Cabomba aquatica* have been identified. The expression patterns of these genes in carpels were very highly conserved, both spatially and temporally, with those of their Arabidopsis orthologues. *CRC* orthologue in *O. sativa*, *DROOPING LEAF* (*DL*), presents a divergent role which probably arose specifically in the monocot lineage (Fourquin et al., 2005).

5.6 Chromatin remodeling factors

In addition to the repression of *FLC* by vernalization, chromatin remodelling has also been implicated in the positive regulation of *FLC* (Jarillo and Piñeiro, 2011). Chromatin remodelling processes are pivotal in the regulation of a number of developmental transitions in plants, and particularly in the control of flowering time (Jarillo and Piñeiro 2011). Beside the epigenetic switch mediated by the activation/repression of the floral repressor *FLC*, chromatin remodeling processes are also involved in the regulation of other flowering time genes. Other proteins involved in chromatin remodelling processes for instance are *ELF6* and *JUMONJI 4* (*AtJMJ4*) (Jeong et al., 2009), and *EARLY BOLTING IN SHORT DAYS* (*EBS*), required for the repression of *FT* (Piñeiro et al., 2003; Champagne and Kutateladze, 2009).

6. PERSPECTIVES

The role of most actors involved in plant development is well established in Arabidopsis and data from other plant species is emerging, which point out some differences among species. Most of the current investigations have been focused on gene expression and regulatory mechanisms but

more information at a structural/functional level is necessary. Further biochemical and structural investigations including molecular interactions and recognition are necessary to know the molecular basis of these regulatory networks. The discovery of intrinsically disordered/ductile proteins (IDPs) has attracted the attention of many researchers during the last decade. These IDPs proteins are involved in key biological processes especially those associated with signalling, transcription regulation, DNA condensation, cell division, and cellular differentiation (He et al., 2009; Dunker et al., 2014). In eukaryotes, protein families involved in developmental processes are enriched in IDPs (Habchi et al., 2014). In *A. thaliana* and *O. sativa* is estimated that ca. 85% of proteins acting in developmental processes are IDPs (Fig. 2). These values are much higher than that predicted (53% and 49%) for the whole proteomes, respectively (Yruela and Contreras-Moreira, 2012; 2013). In plants, the available information about intrinsic disorder in proteins is rather limited compared to other eukaryotic organisms, however, in the last years some protein families involved in development have been investigated containing IDPs members. For instance, LATE EMBRYOGENESIS ABUNDANT (LEA) proteins, basic domain/leucine zippers (bZIPs), NAC transcription factors, GRAS family members, cryptochromes (CRY) contain IDP regions and play critical roles in plant development and signalling. The ductility and flexibility feature of these proteins make them to have a degree of binding plasticity that confers advantages for their functional versatility (Sun et al., 2011; Sun et al., 2012). A link between disorder/ductility and phosphorylation has been postulated. This mechanism is crucial for the stability and activity of different developmental proteins. Phosphorylation and dephosphorylation states of the DELLA subfamily are correlated with their plant growth repressive activity, and gibberellic acid (GA)-induced degradation; in *O. sativa* CIGR1 and CIGR2 are induced by GA signals, depending on both phosphorylation and dephosphorylation events; the light-dependent phosphorylation of the disordered C-terminal

domains of cryptochromes (CRYs) plays a key role in their regulatory mechanisms (Sun et al., 2013). Further studies are necessary to understand the molecular mechanisms undergoing plant development processes in different plant species. The analysis of disordered/ductile regions in plant developmental proteins and their implications in the molecular mechanisms, among other structural features, could contribute to elucidate the keys of these regulatory pathways.

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ABBREVIATIONS

1531	ABI, ABA INSENSITIVE
1532	ACR, <i>Arabidopsis</i> CRINKLY
1533	AG, AGAMOUS
1534	AGL, MAD-box AGAMOUS-LIKE
1535	AGP, ARABINOGLACTAN PROTEIN
1536	AP, APETALA
1537	APL, ALTERED PHLOEM DEVELOPMENT
1538	ARF, AUXIN RESPONSE FACTORS
1539	ARR, ARABIDOPSIS RESPONSE REGULATOR
1540	AS, ASYMMETRIC LEAVES
1541	ATC, <i>Arabidopsis thaliana</i> CENTRORADIALIS homologue
1542	ATX, ARABIDOPSIS TRITHORAX
1543	AUX, AUXIN INFLUX CARRIER PROTEIN
1544	AXR, AUXIN RESISTANT1
1545	BBM, BABY BOOM
1546	BDL, BODENLOS
1547	BFT, BROTHER OF FT
1548	BOP, BLADE-ON-PETIOLE1
1549	BLR, BELLRINGER
1550	BLH, BEL1-LIKE TALE HOMEODOMAIN
1551	BOP, BLADE ON PETIOLE
1552	BP, BREVIPEDICELLUS
1553	BRI, BRASSINOSTEROID-INSENSITIVE
1554	BRX, BRAVIS RADIX
1555	CAL, CAULIFLOWER
1556	CDF, CYCLING DOF FACTOR
1557	CESA, CELLULOSE SYNTHASE
1558	CIGR, CHITIN-INDUCIBLE GA-RESPONSIVE
1559	CIN, CINCINNATA
1560	CLEL, CLE-LIKE
1561	CLF, CURLY LEAF
1562	CLV, CLAVATA
1563	CO, CONSTANS
1564	COB, COBRA
1565	COP, CONSTITUTIVE PHOTOMORPHOGENIC
1566	CRC, CRABS CLAW
1567	CRN, CORYNE
1568	CSL, CELLULOSE SYNTHASE-LIKE
1569	CUC, CUP-SHAPED COTYLEDON
1570	CUY, CURVY
1571	CZ, CENTRAL ZONE
1572	DDB, DAMAGED DNA BINDING PROTEIN
1573	DH, DEGENERATED HULL
1574	DL, DROOPING LEAF
1575	DME, DEMETER
1576	DNF, DAY NEUTRAL FLOWERING

1577

DTH, DAYS TO HEADING

1578

EBS, EARLY BOLTING IN SHORT DAYS

1579

EDE, ENDOSPERM DEFECTIVE

1580

EFS, EARLY FLOWERING IN SHORT DAYS

1581

EHD, EARLY HEADING DATE

1582

1583

ELF, EARLY FLOWERING

1584

EMF, EMBRYONIC FLOWER

1585

EMK, EMBRYOMAKER

1586

ER, ERECTA

1587

ERL, ERECTA-LIKE

1588

ESD, EARLY IN SHORT DAYSES, ENHANCER OF SHOOT
REGENERATION

1589

1590

ESR, ENHANCER OF SHOOT REGENERATION

1591

FCP, FON2-LIKE CLE PROTEIN

1592

FIE, FERTILIZATION INDEPENDENT ENDOSPERM

1593

FIL, FILAMENTOUS FLOWER

1594

FKF, FLAVIN-BINDING KELCH REPEAT, F-BOX PROTEIN

1595

FLC, FLOWERING LOCUS C

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FLD, FLOWERING LOCUS DFLK, FLOWERING LOCUS K

1597

FLM, FLOWERING LOCUS M

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FBP, FLORAL BINDING PROTEIN

1599

FRA, FRAGILE FIBER

1600

FRI, FRIGIDA

1601

FT, FLOWERING LOCUS T

1602

FUL, FRUITFUL

1603

FUS, FUSCA

1604

GI, GIGANTEA

1605

GH, AUXIN-INDUCIBLE GRETCHEN HAGEN

1606

GLV, GOLVEN

1607

GRAS, GIBBERELLIC ACID INSENSITIVE (GAI),
REPRESSOR of GAI (RGA) and SCARECROW (SCR)

1608

1609

GRF, GROWTH-REGULATING FACTORS

1610

GT, GLYCOSYLTRANSFERASE

1611

HAM, LATERAL SUPPRESSOR, HAIRY MERISTEM

1612

HD, HEADING DATE

1613

HD-ZIP III, CLASS III HOMEODOMAIN-LEUCINE

1614

ZIPPER

1615

HER, HERCULES RECEPTOR KINASE

1616

HRGP, HYDROXYPROLINE-RICH GLYCOPROTEIN

1617

HTL, HYPOSENSITIVE TO LIGHT

1618

HY, ELONGATED HYPOCOTYL

1619

IAA, INDOLE-3-ACETIC ACID, AUXIN

1620

ICU, INCURVATA

1621

IDD, INDETERMINATE DOMAIN

1622

IG, INDETERMINATE GAMETOPHYTE

1623

INO, INNER NO OUTER

1624

IPA, INDOLE-3-PYRUVIC ACID

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1625	IRX, IRREGULAR XYLEM	1673	REV, REVOLUTA
1626	JAG, JAGGED	1674	RFI, RED AND FAR-RED INSENSITIVE
1627	JLO, JAGGED LATERAL ORGANS	1675	RGF, ROOT GROWTH FACTOR
1628	KNAT, Knotted in Arabidopsis thaliana	1676	RGI, RHAMNOGALACTURONAN-I
1629	KNOX, Class 1 KNOX homeodomain transcription factors	1677	RIC, CRIB MOTIF-CONTAINING PROTEIN
1630	KNU, KNUCKLES	1678	RLK, RECEPTOR-LIKE KINASES
1631	KOR, KORRIGAN	1679	RPK, RECEPTOR-LIKE PROTEIN KINASE
1632	KRP, KIP-RELATED PROTEIN	1680	ROS, REPRESSOR OF SILENCING
1633	LAS, LATERAL SUPPRESSOR	1681	ROX, REGULATOR OF AXILLARY MERISTEM
1634	LAX, LIKE-AUX1	1682	FORMATION
1635	LBD, LATERAL ORGAN BOUNDARY DOMAIN	1683	RS, ROUGH SHEATH
1636	LD, LUMINEDEPENDES	1684	RZ, RIB ZONE
1637	LEC, LEAFY COTYLEDON	1685	SAM, SHOOT APICAL MERISTEM
1638	LFY, LEAFY	1686	SCL, SCARECROW-LIKE PROTEIN
1639	LHL, LONESOME HIGHWAY LIKE	1687	SCN, STEM-CELL NICHE
1640	LHP, LIKE HETEROCHROMATIN PROTEIN	1688	SCR, SCARECROW
1641	LHW, LONESOME HIGHWAY	1689	SEP, SEPALLATA
1642	LOV, LONG VEGETATIVE PHASE	1690	SERK, SOMATIC EMBRYOGENESIS RECEPTOR-LIKE
1643	LRR, LEUCINE-RICH REPEAT	1691	KINASE
1644	LRX, LRR-extensin	1692	SEU, SEUSS
1645	LUG, LEUNIG	1693	SFR, SENSITIVE TO FREEZING
1646	LUH, LEUNIG-HOMOLOG	1694	SGL, SINGLE LEAF LET
1647	LZF, LIGHT-REGULATED ZINC FINGER PROTEIN	1695	SHP, SHATTERPROOF
1648	MP, MONOPTEROS	1696	SHR, SHORTROOT
1649	MAPK, MITOGEN ACTIVATED PROTEIN KINASES	1697	SLK, SEUSS-LIKE
1650	MAX, MORE AXILLARY GROWTH	1698	SLR, SLENDER RICE
1651	MFT, MOTHER OF FT	1699	SMR, SIM-RELATED
1652	MOC, MONOCULM	1700	SMZ, SCHLAFMÜTZE
1653	NAM, NO APICAL MERISTEM	1701	SND, SECONDARY WALL ASSOCIATED NAC DOMAIN
1654	NST, NAC SECONDARY WALL THICKENING	1702	PROTEIN
1655	PROMOTING FACTOR	1703	SNZ, SCHNARCHZAPFEN
1656	OC, ORGANIZING CENTER	1704	SOC, SUPPRESSOR OF OVEREXPRESSION OF CONSTANS
1657	PAT, PHYTOCHROME A SIGNAL TRANSDUCTION	1705	SP, SPARSE INFLORESCENCE
1658	PGP, P-GLYCOPROTEIN (PGP) AUXIN ABC-TYPE	1706	SPA, SUPPRESSOR OF PHA
1659	TRANSPORTERS	1707	SPL, SQUAMOSA PROMOTER BINDING LIKE
1660	PIN, PIN-FORMED	1708	SPT, SPATULA
1661	PID, PINOID kinase	1709	SQN, SQUINT
1662	PI, PISTILLATA	1710	SQUA, SQUAMOSA
1663	PKL, PICKLE	1711	SRF, STRUBBELIG-RECEPTOR
1664	PKR, PICKLE-RELATED	1712	STK, SEEDSTICK
1665	PLT, PLETHORA	1713	STM, SHOOT-MERISTEMLESS
1666	PLL, PLOTERGEIST	1714	SUB, STRUBBELIG
1667	PP2A, PROTEIN PHOSPHATASE 2A	1715	SVP, SHORT VEGETATIVE PHASE
1668	PRC, POLYCOMB REPRESSOR COMPLEX	1716	SWN, SWINGER
1669	QC, QUIESCENT CENTRE	1717	TAA/TAR, TRYPTOPHAN AMINOTRANSFERASE OF
1670	RAMOSA	1718	ARABIDOPSIS
1671	RAX, REGULATOR OF AXILLARY MERISTEMS 1	1719	TCP, TEONITE BRANCHED 1 CYCLOIDEA
1672	RBL, REBELOTE	1720	TEM, TEMPRANILLO

1721	TFL, TERMINAL FLOWER
1722	THE, THESEUS
1723	TOAD, TOADSTOOL
1724	TOE, TARGET OF EAT
1725	TOM, TARGET OF MONOPTEROS
1726	TOR, TARGET OF RAPAMYCIN
1727	TPR, TOPLESS-RELATED
1728	TSE, TWIN SISTER OF FT
1729	TSL, TOUSELD
1730	TIR, TRANSPORT INHIBITOR RESPONSE protein
1731	TSL, TOUSLED
1732	TZ, TRANSITION ZONE
1733	UFO, UNUSUAL FLORAL ORGANS
1734	ULT, ULTRAPETALA
1735	UNI, UNIFOLIATA
1736	VDD, VERDANDI
1737	VIN, VERNALIZATION INSENSITIVE
1738	VND, VASCULAR-RELATED NAC-DOMAIN
1739	VRN, VERNALIZATION
1740	XEG, XYLOGLUCOTRANSFERASE
1741	XND, XYLEM NAC DOMAIN
1742	XTH,XYLOGLUCAN
1743	ENDOTRANSGLUCOSYLASE/HYDROLASE
1744	YUCCA /YUC, FLAVIN MONOOXYGENASE-LIKE
1745	PROTEINS
1746	WAK, WALL-ASSOCIATED KINASES
1747	WAT, WALLS ARE THIN
1748	WOX, WUSCHEL-RELATED HOMEBOX
1749	WUS, WUSCHEL
1750	ZLL, ZWILLE
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1753 **TABLE 1.-** Main family proteins involved in plant development regulation.

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Protein family	Plant	References
Embryo and root meristem		
Auxin response regulators Aux/IAA	<i>A. thaliana</i> <i>O. sativa</i> <i>P. trichocarpa</i> <i>S. bicolor</i> <i>V. vinifera</i> <i>Z. mays</i>	Reinhardt <i>et al.</i> , 2000; Friml <i>et al.</i> , 2003; Ludvig <i>et al.</i> , 2013 Shen <i>et al.</i> , 2010; Zhu <i>et al.</i> , 2012; Kalluri <i>et al.</i> , 2007 Balzan <i>et al.</i> , 2014 Kohn <i>et al.</i> , 2012 Ludwig <i>et al.</i> , 2013; Zhang <i>et al.</i> , 2014a; Balzan <i>et al.</i> , 2014
MAPK	<i>A. thaliana</i> , <i>B. distachyon</i> , <i>P. trichocarpa</i> <i>O. sativa</i> <i>Z. mays</i>	Zhang <i>et al.</i> , 2008; Rodríguez <i>et al.</i> , 2010 Agrawal <i>et al.</i> , 2003 Kong <i>et al.</i> , 2013
MAX	<i>O. sativa</i> <i>P. hybrida</i> <i>P. sativum</i> <i>P. trichocarpa</i>	De Saint Germain <i>et al.</i> , 2013 <i>idem</i> <i>idem</i> Czarnecki <i>et al.</i> , 2014
PIN	<i>A. thaliana</i> <i>O. sativa</i>	Ongaro and Leyser, 2008; Swarup <i>et al.</i> , 2008; Kleine-Vehn <i>et al.</i> , 2010; del Bianco and Kepinski, 2011; Garay-Arroyo <i>et al.</i> , 2013; Saini <i>et al.</i> , 2013; Tian <i>et al.</i> , 2014 Yamamoto <i>et al.</i> , 2007; Wang <i>et al.</i> , 2014
SOC	<i>C. sinensis</i> <i>H. vulgare</i> <i>Dendrobium</i> Chao Parya <i>Smile</i> <i>O. sativa</i> <i>T. aestivum</i>	Tan and Swain, 2007 Papaefthimiou <i>et al.</i> , 2012 Ding <i>et al.</i> , 2013 Lee <i>et al.</i> , 2004 Shitsukawa <i>et al.</i> , 2007
YUCCA	<i>A. thaliana</i> <i>O. sativa</i> <i>T. aestivum</i> <i>V. vinifera</i> <i>Z. mays</i>	Cheng <i>et al.</i> , 2006; Yamamoto <i>et al.</i> , 2007 Li <i>et al.</i> , 2014a Böttcher <i>et al.</i> , 2013 Gallavotti <i>et al.</i> , 2008
Cytokinin response regulators ARR	<i>A. thaliana</i> <i>O. sativa</i>	Müller and Sheen, 2008; Moubayidin <i>et al.</i> , 2010 Tsai <i>et al.</i> , 2012;
Gibberellins response regulators DELLA	<i>A. thaliana</i>	Lee <i>et al.</i> , 2002; Weng and Chang, 2002; Heo <i>et al.</i> , 2011; Claeys <i>et al.</i> ,

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	<i>O. sativa</i>	2013; Fukuzawa <i>et al.</i> , 2014 Fu <i>et al.</i> , 2001; Itoh <i>et al.</i> , 2002; 2005; Ueguchi-Tanaka <i>et al.</i> , 2007 Chitnis <i>et al.</i> , 2014
	<i>T. aestivum</i>	
Class I KNOX	<i>A. thaliana</i>	Scofield and Murray, 2006; .Hay and Tsiantis, 2010; Kuijt <i>et al.</i> , 2014
	<i>H. vulgare</i>	Kuijt <i>et al.</i> , 2014
	<i>L. japonicus</i>	Luo <i>et al.</i> 2005
	<i>M. truncatula</i>	Di Giacomo <i>et al.</i> 2008; Zhou <i>et al.</i> 2014
	<i>P. sativum</i>	Tattersall <i>et al.</i> 2005
	<i>O. sativa</i>	Kim <i>et al.</i> 2003; Kuijt <i>et al.</i> , 2014
BLH	<i>A. thaliana</i>	Mizumoto <i>et al.</i> , 2011; Arnaud and Pautot, 2014
	<i>S. tuberosum</i>	Sharma <i>et al.</i> 2014
CUC	<i>A. majus</i>	Zimmermann and Werr, 2005
	<i>A. thaliana</i>	Vroemen <i>et al.</i> 2003; Ikeda <i>et al.</i> , 2006
	<i>C. colocynthis</i>	Wang <i>et al.</i> 2014
	<i>M. truncatula</i>	Cheng <i>et al.</i> , 2012
	<i>P. hybrida</i>	Zimmermann and Werr, 2005
	<i>P. abis</i>	Larsson <i>et al.</i> , 2012
	<i>Z. mays</i>	Zimmermann and Werr, 2005; Fan <i>et al.</i> 2014
LBD /LOB containing domain	<i>A. thaliana</i>	Majer and Hochholdinger, 2011
	<i>O. sativa</i>	Inukai <i>et al.</i> , 2005; Liu <i>et al.</i> , 2005; Coudert <i>et al.</i> , 2014
	<i>Z. mays</i>	Taramino <i>et al.</i> , 2007
WUSCHEL	<i>A. thaliana</i>	Ikeda <i>et al.</i> , 2009; Stahl and Simon, 2010; Yue <i>et al.</i> , 2014
	<i>O. sativa</i>	Zhao <i>et al.</i> , 2009; Chen <i>et al.</i> , 2014
	<i>P. tomentosa</i>	Liu <i>et al.</i> , 2104
	<i>P. avis</i>	Zhu <i>et al.</i> , 2014
	<i>P. sativum</i>	Zhuang <i>et al.</i> , 2012
	<i>R. canina</i>	Gao <i>et al.</i> , 2014b
	<i>S. lycopersicum</i>	Ji <i>et al.</i> , 2010
	<i>T. aestivum</i>	Zhao <i>et al.</i> , 2014
bHLH	<i>A. thaliana</i>	Schlereth <i>et al.</i> , 2010
Leaf		
Class I KNOX	<i>A. thaliana</i>	Zhou <i>et al.</i> , 2014
	<i>C. hirsute</i>	Zhou <i>et al.</i> , 2014
	<i>M. truncatula</i>	Zhou <i>et al.</i> 2014; Ge <i>et al.</i> , 2014
	<i>P. sativum</i>	Zhou <i>et al.</i> 2014
	<i>S. lycopersicum</i>	Zhou <i>et al.</i> 2014
LBD /LOB containing domain	<i>A. thaliana</i>	Majer and Hochholdinger, 2011
	<i>C. cristata</i>	Majer and Hochholdinger, 2011

	<i>O. sativa</i> <i>Z. mays</i>	Yang <i>et al.</i> , 2006 Zhang <i>et al.</i> , 2014
FIL/YABBY	<i>A. thaliana</i> <i>C. caroliniana</i> <i>L. longiflorum</i> <i>O. poppy</i> <i>O. sativa</i> <i>V. pseudoreticulata</i>	Stahle <i>et al.</i> 2009; Lugassi <i>et al.</i> , 2010; Bonaccorso <i>et al.</i> , 2012 Yamada <i>et al.</i> , 2011 Wang <i>et al.</i> , 2009c Vosnakis <i>et al.</i> , 2012 Toriba <i>et al.</i> , 2007; Dai <i>et al.</i> , 2007 Xiang <i>et al.</i> , 2013
Seed MADS-box	<i>A. thaliana</i> <i>Conifers</i> <i>H. vulgare</i> <i>O. sativa</i> <i>P. hybrida</i>	Matías-Hernández <i>et al.</i> , 2010; Kapazoglou <i>et al.</i> , 2012 Gramzow <i>et al.</i> , 2014 Kapazoglou <i>et al.</i> , 2012 Kapazoglou <i>et al.</i> , 2012; Ishikawa <i>et al.</i> , 2011 Kapazoglou <i>et al.</i> , 2012
YUCCA	<i>Z. mays</i>	LeClere <i>et al.</i> , 2010
Flower CONSTANS	<i>A. thaliana</i> <i>H. vulgare</i> <i>G. max</i> <i>O. sativa</i> <i>S. bicolor</i> <i>Z. mays</i>	Michaels <i>et al.</i> , 2009; Fornara <i>et al.</i> , 2009; Bu <i>et al.</i> , 2014; Yang <i>et al.</i> , 2014 Griffiths <i>et al.</i> , 2003 Wu <i>et al.</i> , 2014 Griffiths <i>et al.</i> , 2003; Tsuji <i>et al.</i> , 2011 Yang <i>et al.</i> , 2014 Miller <i>et al.</i> , 2008
FT	<i>A. thaliana</i> <i>B. distachyon</i> <i>B. vulgaris</i> <i>H. vulgare</i> <i>G. max</i> <i>O. sativa</i> <i>P. sativum</i> <i>S. tuberosum</i> <i>T. aestivum</i>	Takada and Goto, 2003 Lv <i>et al.</i> , 2014 Pin <i>et al.</i> , 2010 Faure <i>et al.</i> , 2007 Nan <i>et al.</i> , 2014 Komiya <i>et al.</i> , 2008; 2009; Lee <i>et al.</i> , 2010 Hecht <i>et al.</i> , 2011 Navarro <i>et al.</i> , 2011 Lv <i>et al.</i> , 2014
MADS-box	<i>A. thaliana</i> <i>A. comosus</i> <i>B. distachyon</i> <i>G. max</i> <i>H. vulgare</i> <i>O. sativa</i> <i>P. hybrida</i> <i>P. somniferum</i>	Ng and Yanofsky, 2001; Dorca-Fornell <i>et al.</i> , 2011; Liu <i>et al.</i> , 2013 Moyle <i>et al.</i> , 2014 Schmitz <i>et al.</i> , 2000; Wei <i>et al.</i> , 2014 Huang <i>et al.</i> , 2014 Schmitz <i>et al.</i> , 2000; Wei <i>et al.</i> , 2014 Liu <i>et al.</i> , 2013 Parenicová <i>et al.</i> , 2003 Singh <i>et al.</i> , 2014

	<i>S. lycopersicum</i>	Quinet <i>et al.</i> , 2014; Wang <i>et al.</i> , 2014
	<i>V. vinífera</i>	Fernández <i>et al.</i> , 2013
	<i>Z. mays</i>	Fornara <i>et al.</i> , 2004
LBD /LOB containing domain	<i>A. thaliana</i>	Majer and Hochholdinger, 2011
	<i>O. sativa</i>	Li <i>et al.</i> 2008
	<i>Z. mays</i>	Evans, 2007; Li <i>et al.</i> 2008
VRN	<i>A. thaliana</i>	Michaels <i>et al.</i> , 2009
	<i>O. sativa</i>	Yan <i>et al.</i> , 2004
	<i>Z. mays</i>	Li and Dubovsky, 2008

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FIGURE LEGENDS

Figure 1. Scheme of main regulatory proteins involved in plant development. AGL, MAD-box AGAMOUS-LIKE; ASL, ASymmetric Leaves; ARF, auxin response factors; ARR, Arabidopsis response regulator; BLH, bel1-like tale homeodomain; CUC, cup-shaped cotyledon; FIL, Filamentous flower; KNOX, Class 1 KNOX homeodomain transcription factors; LBD, Lateral Organ Boundary domain; MAPK, Mitogen Activated Protein Kinases; MAX, more axillary growth; NAC, NAC-domain transcriptional regulators ; PIN, PIN-formed; SOC, suppressor of overexpression of constans; VRN, vernalization; WOX, Wuschel-related homeobox ; WUS, Wuschel.

Figure 2. Distribution of predicted disordered/ductile proteins from *A. thaliana* and *O. sativa*. The whole proteomes and two sets of proteins including those encoded by nuclear genome with a chloroplastic origin (Yruela and Contreras-Moreira, 2012) and those involved in plant development reviewed in this work were analysed with DISOPRED3 (<http://bioinfadmin.cs.ucl.ac.uk/>)

FIGURE 1

Figure 2