Journal of Plant Physiology 182 (2015) 62–78

Contents lists available at ScienceDirect

Journal of Plant Physiology

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

Review article

Plant development regulation: Overview and perspectives

Inmaculada Yruela [a,b,*]

[a] Estación Experimental de Aula Dei, Consejo Superior de Investigaciones Científicas (EEAD-CSIC), Avda. Montañana 1005, 50059 Zaragoza, Spain
[b] Instituto de Biocomputacióon y Física de Sistemas Complejos, Mariano Esquillor, Edificio I+D, 50018 Zaragoza, Spain

ARTICLE INFO

Article history:
Received 7 January 2015
Received in revised form 28 April 2015
Accepted 4 May 2015
Available online 27 May 2015

Keywords:
Plant development
Regulation
Monocots
Eudicots
Disordered/ductile proteins

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 summarize the 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 regulatory 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.

Contents

Abbreviations: ABI, ABA INSENSITIVE; ACR, *Arabidopsis* CRINKLY; AG, AGAMOUS; AGL, MAD-box AGAMOUS-LIKE; AP, APETALA; ARF, auxin response factors; ARR, ARABIDOPSIS RESPONSE REGULATOR; AS, ASYMMETRIC LEAVES; ATC, *Arabidopsis thaliana* CENTRORADIALIS homologue; AUX, AUXIN INFLUX CARRIER PROTEIN; AXR, AUXIN RESISTANT1; BBM, BABY BOOM; BDL, BODENLOS; BFT, BROTHER OF FT; BOP, BLADE-ON-PETIOLE1; BLR, BELLRINGER; BLH, BEL1-like TALE homeodomain; BOP, BLADE ON PETIOLE; BP, BREVIPEDICELLUS; BRX, BRAVIS RADIX; CAL, CAULIFLOWER; CDF, CYCLING DOF FACTOR; CIGR, CHITIN-INDUCIBLE GA-RESPONSIVE; CIN, CINCINNATA; CLEL, CLE-LIKE; CLF, CURLY LEAF; CLV, CLAVATA; CO, CONSTANS; COP, CONSTITUTIVE PHOTOMORPHOGENIC; CRC, CRABS CLAW; CUC, CUP-SHAPED COTYLEDON; CUY, CURVY; CZ, CENTRAL ZONE; DDB, DAMAGED DNA BINDING PROTEIN; DME, DEMETER; EHD, EARLY HEADING DATE; ELF, EARLY FLOWERING; EMF, EMBRYONIC FLOWER; FIL, FILAMENTOUS FLOWER; FKF, FLAVIN-BINDING KELCH REPEAT, F-BOX PROTEIN; FLC, FLOWERING LOCUS C; FLM, FLOWERING LOCUS M; FBP, FLORAL BINDING PROTEIN; FRI, FRIGIDA; FT, FLOWERING LOCUS T; FUL, FRUITFULL; GI, GIGANTEA; GH, AUXIN-INDUCIBLE GRETCHEN HAGEN; GRAS, GIBBERELLIC ACID INSENSITIVE (GAI), REPRESSOR of GAI (RGA) and SCARECROW (SCR); GRF, GROWTH-REGULATING FACTORS; HD, HEADING DATE; HY, ELONGATED HYPOCOTYL; IAA, INDOLE-3-ACETIC ACID, AUXIN; IG, INDETERMINATE GAMETOPHYTE; JLO, JAGGED LATERAL ORGANS; KNAT, knotted in *Arabidopsis thaliana*; KNOX, Class 1 KNOX homeodomain transcription factors; LAS, LATERAL SUPPRESSOR; LAX, LIKE-AUX1; LBD, LATERAL ORGAN BOUNDARY DOMAIN; LFY, LEAFY; LUG, LEUNIG; LUH, LEUNIG-HOMOLOG; MP, MONOPTEROS; MAPK, MITOGEN ACTIVATED PROTEIN KINASES; MAX, MORE AXILLARY GROWTH; MFT, MOTHER OF FT; OC, organizing center; PAT, PHYTOCHROME A SIGNAL TRANSDUCTION; PIN, PIN-FORMED; PI, PISTILLATA; PLT, PLETHORA; PRC, POLYCOMB REPRESSOR COMPLEX; RPK, RECEPTOR-LIKE PROTEIN KINASE; RS, ROUGH SHEATH; RZ, RIB ZONE; SAM, SHOOT APICAL MERISTEM; SCL, SCARECROW-like protein; SCN, stem-cell niche; SEP, SEPALLATA; SHP, SHATTERPROOF; SHR, SHORTROOT; SLR, SLENDER RICE; SMR, SIM-RELATED; SMZ, SCHLAFMÜTZE; SOC, SUPPRESOR OF OVEREXPRESSION OF CONSTANS; SPA, SUPPRESSOR OF PHYA; SPL, SQUAMOSA PROMOTER BINDING LIKE; STK, SEEDSTICK; STM, SHOOT MERISTEMLESS; SVP, SHORT VEGETATIVE PHASE; TCP, TEONSITE BRANCHED 1 CYCLOIDEA; TEM, TEMPRANILLO; TFL, TERMINAL FLOWER; TOAD, TOADSTOOL; TSF, TWIN SISTER OF FT; TSL, TOUSLED; TIR, TRANSPORT INHIBITOR RESPONSE protein; TZ, transition zone; VIN, VERNALIZATION INSENSITIVE; VRN, vernalization proteins; YUCCA/YUC, flavin monooxygenase-like proteins; WOX, WUSCHEL-RELATED HOMEOBOX; WUS, WUSCHEL; ZLL, ZWILLE.

* Corresponding author at: Estación Experimental de Aula Dei, Consejo Superior de Investigaciones Científicas (EEAD-CSIC), Avda. Montañana 1005, 50059 Zaragoza, Spain. Tel.: +34 976716058; fax: +34 976716145.
E-mail address: i.yruela@csic.es

http://dx.doi.org/10.1016/j.jplph.2015.05.006
0176-1617/

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 (Nakajima 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 RZ, which is responsible for the elongation of the stem. Cells in the peripheral zone and the RZ 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. These characteristics will be also discussed.

Embryo, root and shoot apical meristems development

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 involves the regulation of many different genes and protein families. In this section, a briefly information