YUC in Plant Developmental Processes

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The YUC gene family encodes the rate-limiting enzymes in the TAA/YUC pathway, which stands as the primary endogenous auxin biosynthesis pathway in plants. YUC-medicated local auxin biosynthesis is important for establishing auxin gradient within cells/tissues and precisely regulating various major developmental processes such as root development, leaf morphogenesis, and reproductive development. The spatiotemporal expressions of different YUC genes enable function specialization across different plant species.

auxin local biosynthesis root development leaf morphogenesis

reproductive development

1. Introduction

Auxins play important roles in a wide range of plant development processes, from the promotion of cell elongation, induction of cell division activity of cambia, and initiation of root and leaf architecture to contributions to flower, embryo, and fruit development[1][2][3][4]. Loss of function of multiple *YUC* genes caused severe developmental defects such as failure in flower formation and embryo development in Arabidopsis[5][6]. Although the mechanisms of auxin biosynthesis seem to be generally conserved, the *YUC* gene family is capable of rapid functional divergence with the potential to generate novel plant morphologies[7][8]. Additionally, many essential transcriptional factors that transcriptionally regulate YUC-mediated development processes have been identified in the past decades, such as STYLISH 1 (STY1)[9], LEAFY COTYLEDON 2 (LEC2)[10][11], SPOROCYTELESS[12], REVEILLE 1[13], and PHYTOCHROME INTERACTING FACTOR (PIF)[14][15][16][17], which stitch the changes in environmental clues (such as light) as well as developmental processes together with local auxin biosynthesis in plants.

2. Root Development

The root system of dicotyledonous plants consists of a primary root and lateral roots, which enable the plants to exploit water and nutrient in the soil[18][19][20]. Root apical meristem has a high rate of IAA biosynthesis due to high expression of genes involved in auxin biosynthesis[21][22]. In combination with PAT[23][24], local auxin biosynthesis converges to establish the critical auxin gradient within the root apex, resulting in changes in auxin homeostasis and root architecture[25]. In Arabidopsis, changes in the expression of the *YUC* genes have an impact on local auxin biosynthesis[26][27]. Particularly the quintuple mutants *yuc3 yuc5 yuc7 yuc8 yuc9* have severely disturbed root growth and gravitropism[5]. Notably, auxin derived from the shoot could not fully rescue the root growth at the root tip with auxin deficiency, highlighting that local auxin biosynthesis and long-distance auxin transport could synergistically regulate auxin homeostasis required for root growth[5]. Antisense expression of *YUC1* in rice resulted in a defective root which resembled the root phenotype of auxin-insensitive mutant[28]. The missing *YUC6* caused defects in root formation in woodland strawberry (*Fragaria vesca* L.)[29]. Other evidences suggest that local auxin synthesis might depend upon auxin transport because disruption of the GNOM, which facilitates the cellular trafficking of PIN proteins, led to the decrease of *YUC* gene expression during lateral root emergence[30]. Multiple *YUC* genes including *YUC3*/*5*/*7*/*8*/*9* are required for *HIGH HOMEODOMAIN-LEUCINE ZIPPER* III (*HD-ZIP* III) expression and metaxylem differentiation in the vascular bundle of Arabidopsis primary root[31]. Crown root initiation and elongation in rice was regulated by a YUC-auxin-WOX11 (WUSCHEL-RELATED HOMEOBOX 11) module[32].

Auxin is the master regulator of adventitious root (AR) formation[33], and other signaling pathways also can mount auxin to shape root architecture, such as nitrate[34]. Numerous studies have demonstrated that early auxin accumulation is a critical signal to initiate cell fate transition of the root founder cells, which is essential for vegetative propagation of plants[35][36][37]. This auxin peak was the combined outcome of PAT and increased local synthesis in response to multiple exogenous stimuli such as wounding and depletion of water and nutrient[38][39]. It is demonstrated that YUC gene family orchestrated endogenous auxin biosynthesis required for AR induction, among which *YUC1* and *4* appeared to play the most important role[40][41]. Using transcriptome and genetic approaches, Pan et al. also found that expression of *YUC1*/*4* was critically responsive to the extent of leaf maturation, which in turn largely determined the regeneration capacity of adventitious roots on leaf explant[42]. Several environmental regulators including light[43], sugar availability[44], and circadian rhythms[42] are also involved in the regulation of YUC activity in de novo root development. Furthermore, YUC also participated in regulating plant primary root growth and hypocotyl growth in response to heat stress[14][16]and aluminum (Al)[17], which will be discussed in detail in the later sections.

YUC genes also play a role in the interactions of plant–microbes or plant–plant by regulating auxin levels. Root nodules are a unique type of lateral organ on the roots of most legumes that house nitrogen-fixing bacteria[45]. Although it seems that auxin signaling is crucial for nodulation[46], it was found that rhizobia infection and nodule organogenesis were closely associated with *GmYUC2a*, an ortholog of Arabidopsis *YUC2*, to regulate local auxin biosynthesis in legumes[7]. In line with this, GH3s were also found to play a role in regulating proper nodule maturation in soybean[45]. These results highlight the importance of auxin metabolism, besides auxin transport, in legume nodulation. Moreover, in the root parasitic plant *Phtheirospermum japonicum*, the upregulation of *YUC3* was an early response to parasitic plants in the host epidermis cells[47]. The spatiotemporal expression of *YUC3* at the epidermal cells near the contact site was required for priming haustorium formation, whereas *YUC3* knockdown transgenics formed less haustoria than wildtype plants[47].

3. Leaf Morphogenesis

It is well recognized that removal of multiple *YUC* genes resulted in plants with auxin-deficient phenotypes of narrow leaves[48][6], whereas auxin overproduction resulted in curled leaves[49]. Leaf adaxial-abaxial polarity formed at the primordium stage was vital for succeeding leaf expansion[50][51]. This process was involved in local auxin accumulation in leaf margin cells[52][53] [117,118], which was mediated by several *YUC* genes[50] [115]. Similarly, transgenic Arabidopsis plants harboring soybean (*Glycine max*) *GmYUC5* displayed downward curling of the leaf blade margin[54][55], suggesting the functional conservation of *YUC* genes in both plant species. Mutants of *YUC1*/*2*/*4*/*6* caused a reduced number of leaf vein and vascular strands, and this phenotypic strength was highly dependent on the gene dosage of these four *YUC* genes, suggesting that locally produced auxin is important for vascular strand formation[56]. However, *yuc1 yuc4* double mutants showed no obvious defects in leaf formation with regard to the number and position of the leaves. *yuc1 yuc4 pin1* triple mutants, however, failed to form true leaves, demonstrating that *YUC* and *PIN1* genes synergistically control leaf development[6]. Increased expression of *YUC8*/*9* is important for leaf heteroblastic development in rainforest tree *Gevuina avellane* to adapt to different light environment[57]. Moreover, *YUC* genes have been shown to regulate leaf angle in both monocots and dicots. Arabidopsis *YUC6* homologs in potato and oilseed rape (*Brassica napus* L.) were identified to affect leaf angle modulation[58][59]. Additionally, it is found that a dominant activation mutant *yuc6-1D* and *35S:YUC6* transgenic plants displayed a delayed senescence phenotype, which was closely related to the elevated auxin levels in leaves[60]. Overproduction of auxins repressed the transcription of several known senescence-associated transcription factors including *SENESCENCE ASSOCIATED GENE 12* (*SAG12*), *NAC1*, and *NAC6*[60]. Overexpression of *YUC8* and *YUC9* led to aberrant secondary growth of the stem and narrow leaves in Arabidopsis[61]. Genetic and phenotypic analysis showed that *YUC2* and *YUC6*, two key genes essential for leaf development, may be indirectly repressed by SPOROCYTELESS/NOZZLE (SPL/NZZ) transcription factor to regulate auxin homeostasis in lateral organ morphogenesis, including leaf[12]. Additionally, AP2 PLETHORA transcription factors were also found to regulate lateral organ out-growth via the regulation of localized auxin synthesis controlled by *YUCs*[62].

4. Reproductive Development

One of the earliest assigned functions of *YUC* genes were their expression in reproductive organs in Arabidopsis[56][6]. In floral organs, initiation of flower primordia correlated well with the transcriptional levels of *YUC1* and *YUC4*[56]. It was also found that *SUPER1*, which encoded YUC5, was largely parallel but partially interacted to the ERECTA receptor signaling pathway during elaboration of Arabidopsis inflorescence architecture[63]. Several lines of evidence have confirmed the synergic interaction between auxin biosynthesis and auxin transport, with both being required for plant development[6][8]. It was demonstrated that *spi1*-mediated auxin biosynthesis was required for upregulation of *ZmPIN1a* expression during axillary meristem initiation in maize inflorescence development[8]. In flowering plants, the patterning of female gametophytes depended upon an asymmetric distribution of auxin which is primarily correlated with local accumulation of auxin mediated by *YUC* genes rather than auxin transport[64].

YUC1/*4*/*10*/*11* is required for the establishment of the basal part of the embryo and for the initiation of embryonic organs[6]. Specifically, *YUC1*, *3*, *4*, *8*, and *9* were found to be involved in the control of localized auxin biosynthesis in early initiation of embryos during plant embryogenesis[65]. This process was further transcriptionally mediated by a decreased ethylene biosynthesis and signaling to induce *YUC* expression and to establish the local auxin distribution for somatic embryo initiation[66]. Other studies showed that *YUC* genes were regulated by LEC2 transcription factor in somatic embryogenic induction and that the interaction of LEC2 with the promotor of *YUC4* was evidenced by chromatin immunoprecipitation[10][11].

Auxin plays a critical role in fruit development, beginning with flower formation and patterning of the gynoecium, through fruit set, fruit growth, and ripening[67][68]. Exogenous application of auxin to ovaries can bypass the requirement of pollination producing seedless fruit. A number of studies showed that genes expressions of several *YUC* were high in seed tissue such as maize[8], rice[69], melon[54], and strawberry[70], suggesting that auxin biosynthesis via the TAA/YUC pathway is likely dominant in fruit. Nevertheless, alternative pathways may also be active depending on the species and developmental stage. For example, members of the tomato *YUC* family, particularly *ToFZY6*, showed preferential expression in seed[71]but exhibited low expression in apple fruit[72]. Furthermore, by combining RNA-seq technique and laser capture microdissection, transcription factor PLETHORA, which has been implicated in regulating the expression of *YUC1* and *YUC4*[62], was co-expressed with auxin reporter DR5 activity in funiculus, where auxin accumulated in a tissue-specific manner in tomato fruit[73].

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