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Mini Review

# Insights into the mechanism of plant development: Interactions of miRNAs pathway with phytohormone response

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ABSTRACT

MicroRNAs (miRNAs) are small non-coding regulatory RNAs that regulate gene expression in plants by targeting mRNAs for cleavage or translational repression. Over the past years, miRNAs have been validated to play crucial roles in plant growth and development. Recent researches have witnessed the identification of intersection between miRNAs pathways and phytohormone responses, which improves our understanding of miRNAs and hormone action in developmental control. In this review, we highlight the progress on the current known relationship of miRNAs with phytohormone signaling, and the potential roles of some specific miRNAs in hormone signaling were also discussed.



## Introduction

The life of multicellular organisms depends on complex networks of gene regulatory pathways. MicroRNA (miRNA), an endogenous small non-coding RNA, which was found recently, have been validated to be the key components of these networks [1]. They not only control patterning of plant, but also play a role in environmental responses, including hormonal response. Plant hormones are recognized as key regulators of plant growth and development. Almost every aspect of plant growth and development is under hormonal control to some degree [2]. Recent researches have witnessed the great progress in the area of identification of intersection between miRNAs pathways and phytohormone responses, which improves our understanding of mechanism of plant development controlled by miRNAs and hormone action to a large extent. Manipulation of miRNA guided gene regulation in hormone response might represent a novel and feasible approach to disclose the complex networks of plant development. In this review we summarize the interactions of miRNAs pathway with phytohormone response in an effort to provide new insights into the mechanism of plant development.

## miRNA regulation of abscisic acid (ABA) signaling

Abscisic acid (ABA) is a plant hormone involved in bud and seed dormancy, root growth, leaf senescence and abscission, stomata opening, and protection plant from a variety of environmental stress [3]. At present, many miRNAs have been confirmed experimentally to be involved in a variety of abiotic stress responses and several miRNAs have already been verified to be involved in ABA signaling (see Fig. 1).

Sunkar and Zhu reported that the expression of miR393 is strongly up-regulated by ABA, and miR397b and miR402 are slightly up-regulated, while miR389a and miR319 appear to be down-regulated by ABA treatments [4]. What is more, in germinating *Arabidopsis thaliana* seeds, the expression level of miR159 increased in ABA-treated seedlings. MiR159 mediates cleavage of *MYB101* and *MYB33* transcripts. Over-expression of miR159 suppresses *MYB33* and *MYB101* mRNAs levels and renders plants hyposensitive to ABA whereas transgenic plants over-expressing cleavage-resistant forms of *MYB33* and *MYB101* are hypersensitive to ABA treatment [5]. This suggests that miR159 plays a key role in resetting ABA responses by directing *MYB33* and *MYB101* mRNAs degradation during seed germination [5].

More recently, it was shown that miR167 and miR413 were also regulated by ABA in *Oryza sativa* (rice), suggesting that they may be involved in stress-responsive gene expression and stress adaptation [6]. MiR167 was obviously down-regulated by ABA while miR413 was up-regulated by ABA. The ABA down-regulation of miR167, which was validated to target *auxin response factor 8* (*ARF8*) mRNA, suggests that ABA may cause increased *ARF8* mRNA accumulation or translational promotion. Because ARF8 is a positive regulator of both female and male reproduction [7,8], the accumulation of ARF8 by miR167 would accelerate female and male reproduction and plant maturation. Thus, the down-regulation of miR167 may contribute to plant prematurity under stress

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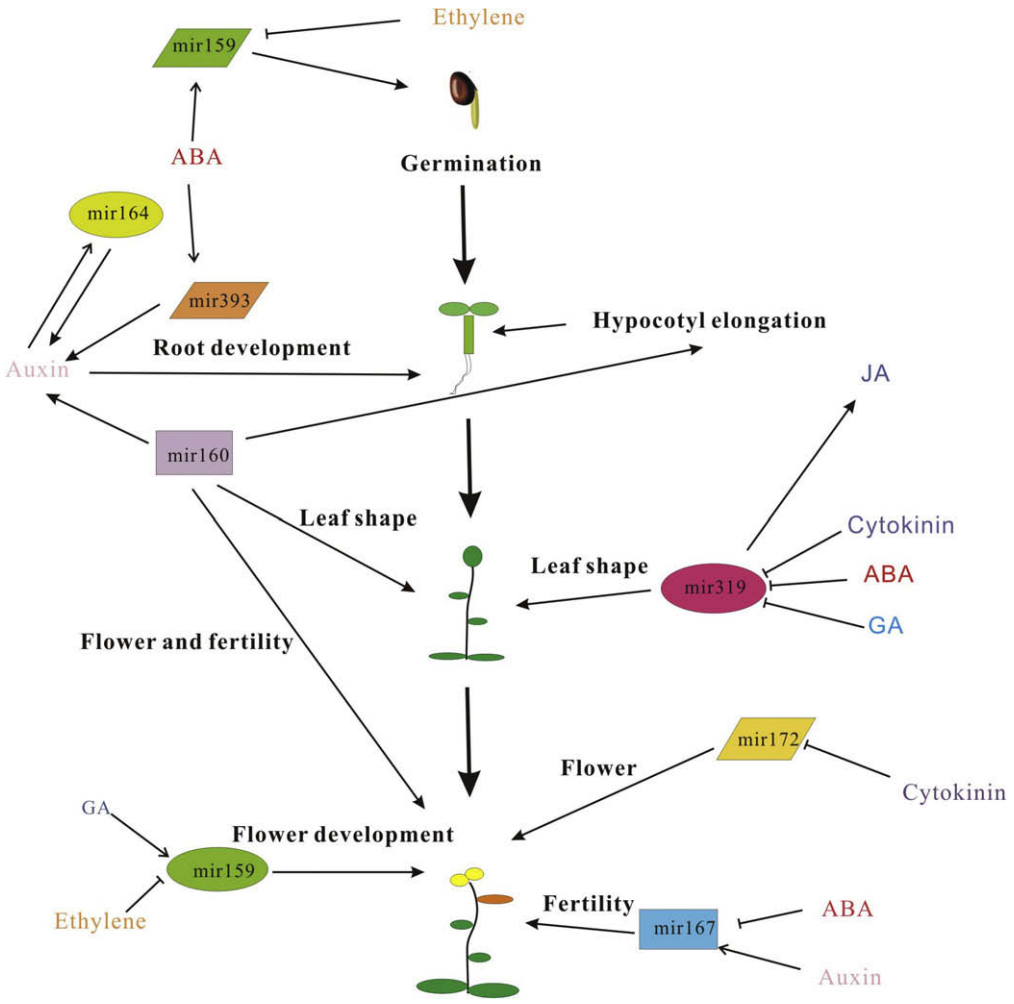


**Fig. 1.** A diagrammatic representation of the interaction between miRNAs and phytohormone in plant development. Bold arrows show the involvement movements; Slim arrows show simultaneous effect in the pathway; Nail shape represents repression. ABA, abscisic Acid; GA, gibberellin; JA, jasmonate acid.

conditions. Additionally, since ARF8 is an auxin response factor and the down-regulation of miR167 by ABA implies that there is likely to be an intersection between ABA and auxin signaling through altering miR167 expression level [7,8].

## MiRNAs in auxin signaling

Auxin regulates a host of plant developmental and physiological processes, including embryogenesis, vascular differentiation, organogenesis, and root and shoot architecture [9]. In the plant life cycle, few developmental processes occur without the involvement of the phytohormone auxin [9]. Auxin controls many aspects of plant growth and development by influencing *AUXIN RESPONSE FACTORS* (*ARFs*) transcriptional levels [10]. At present, many ARFs have been conformed to be regulated by miRNAs. In *Arabidopsis thaliana*, miR167 controls patterns of *ARF6* and *ARF8* expression, and regulates both female and male reproduction [8]. MiR167 was also induced by auxin (2,4-D) in cultured rice cells, and led to decrease of both *ARF8* mRNA and *OsGH3-2* mRNA, an rice AA-conjugating enzyme which was positively regulated by ARF8 [11]. This proposed auxin signal transduction pathway, auxin-miR167-*ARF8*-*OsGH3-2*, could be an important regulator for determining the cellular free auxin level which guides appropriate auxin responses [11]. Furthermore, miR160 cleavages *ARF10, ARF16* and *ARF17* to affect many aspects of plant development (Fig. 1) and freeing ARF17 or ARF16 from miR160 regulation results in dramatic morphological changes and alters basal levels of auxin-induced transcripts [1,12,13].

Intriguingly, not only the ARFs, but also auxin receptors are subject to miRNA-mediated regulation. MiR393 targets *TIR1* and three other closely related F-box proteins (*AFB1, AFB2* and *AFB3*) [14]. These F-box proteins are all auxin receptors which target short-lived repressors of ARF transcriptional activators for ubiquitin-mediated degradation in response to auxin [1,15,16]. This implies that miRNA can also target F-box proteins and affect the ubiquitin (Ub) proteasome pathway.

In addition to these, miR164 is induced by auxin to clear NAC1 mRNA to reset auxin signals [17]. NAC1 is a transcriptional activator in the auxin signaling pathway for lateral root initiation by regulating *transport inhibitor response 1* (*TIR1*) [18]. Loss-of-function miR164 mutants blocked the auxin signaling pathway, resulting in increased *NAC1* mRNA levels and more lateral root production [17]. The induction of miR164 by auxin suggests an autoregulatory loop by which the miRNA mediates the clearance of *NAC1* mRNA to attenuate and terminate auxin signaling in order to reduce lateral root production [17].

Recent researches have also indicated the involvement of miR168 and miR169 in auxin signaling [6,19]. In soybean roots, increasing levels of miR168 and ARF17 were observed in response to *Bradyrhizobium japonicum*. MiR168 targets *ARGONAUTE1* (*AGO1*) and AGO1 then targets ARF17 [19], hence we indicated that miR168 regulates the expression of ARF17 probably through

AGO1. Moreover, miR168 as well as miR169 were found to be firstly down-regulated in the earlier treatment and then up-regulated at 48 h by auxin in rice [6]. MiRNA-guided gene regulation requires that miRNA form a complex with RISC and AGO1 protein is a core component of RISC. Decreasing the complementarity of *AGO1* mRNA with miR168 resulted in increased accumulation of *AGO1* mRNA and developmental defects similar to *dcl1* or *hen1* mutants, illustrating the importance of feedback control by miR168 through regulation of *AGO1* mRNA [20]. Such feedback regulation is analogous to that proposed for *DCL1* mRNA by miR162. Post-transcriptional AGO1-mediated stabilization of miR168 works in concert with miR168-programmed, AGO1-catalyzed cleavage of *AGO1* mRNA to maintain AGO1 homeostasis, proper miRNA pathway functioning, and normal plant development [21]. As a result, the regulation of miR168 by auxin may contribute to keep normal development when exogenous auxin levels changed.

MiR169 is a big miRNA family containing 17 several members representing different mature sequences. In *Medicago truncatula*, miR169 was found to target *MtHAP2-1*, a key transcriptional regulator, to regulate symbiotic nodule development [22]. In addition, miR169 has been verified to be involved in abiotic stress responses [23]. These together with recent results of auxin-regulation of miR169 suggest that miR169 family play a fundamental role in plant development. The regulation of the interaction between miR169 and Auxin signaling, however, has not been elucidated yet. Future analysis of *HAP2* mRNA and protein levels with altered miR169 expression, or expressing miR169-resistant forms of *HAP2* mRNA, will help to illustrate its key roles and reveal the connections between miR169 and phytohormone signaling.

## The involvement of miRNAs in GA signaling

The plant hormone gibberellin (GA) has long been known to modulate development throughout the plant life cycle, from seed germination to the development of flowers and fruits [24]. Up to know, three miRNAs were proved to function in regulation GA signaling. Earlier research has indicated the role of miR159 in regulation GA signaling in the aspect of flower development [25]. MiR159 directs the cleavage of mRNA encoding GAMYB-related proteins which are transcription factors that are thought to be involved in the GA-promoted activation of the floral meristem identity gene *LEAFY* and in the regulation of anther development. Elevated level of miR159 by GA resulted in the reduction of GAMYB level which then reduced *LEAFY* activity and that the reduction in *LEAFY* activity delayed flowering and perturbed anther development [25]. This suggests that miR159 is a phytohormonally regulated homeostatic modulator of GAMYB activity, and hence of GAMYB-dependent developmental processes [25].

Another two miRNAs, miR319 and miR166, were found to be down-regulated by GA recently. MiR166 mediated the cleavage of class III homeodomain-leucine zipper (*HD-ZIP*) transcription factors which involved in the regulation of shoot meristem initiation, vascular development and others [26]. Down-regulation of miR166 by GA leading to increased level of class III HD-ZIP protein might cause abnormal plant development such as meristem defects. Further examination of the regulatory interactions between the various miR166 family members and their *HD-ZIP III* target genes will reveal insights into the complex interplay between GA signaling and miR166 in regulating plant development.

## Two miRNAs were found to be regulated by ethylene

Of the numerous hormones that govern plant development, the gaseous alkene ethylene plays important roles during all stages of the plant life cycle, functioning through seed germination to maturation [27]. Ethylene also protects plants from various abiotic stress conditions [27]. To date, no studies report miRNA involved in ethylene signaling except the latest one, wherein the author identified that miR159 and miR394 expression levels decreased when subjected to ethylene treatment in rice [6]. Just as miR393, miR394 also targets F-box family proteins, which are involved in different signaling pathways through their ability to target specific proteins for degradation [28]. The F-box protein is an important component of the E3 ubiquitin ligase Skp1-Cullin-F-box protein complex, involved in plant hormone response as receptors or important medial components, indicating that the ubiquitin (Ub) proteasome pathway is a central regulatory mechanism in the signal transduction pathways of different plant hormones [29]. This provided further evidence for the conclusion that the regulation networks of miRNA are involved in ubiquitin (Ub) proteasome pathway.

Except for regulated by GA and ABA, miR159 was also found to be down-regulated by ethylene [6], down-regulation of miR159 by ethylene may led to the accumulation of mRNA encoding GAMYB-related proteins and as a result, promote flowering time through reducing *LEAFY* mRNAs expression level. This is accordant with previous results that ethylene can promote flowing time and flower senescence and overexpression of miR159 resulted in delayed flowering time [30]. In addition, ethylene has been shown to inhibit growth in a GA-antagonistic manner [31]. These suggest that the antagonistic interaction between ethylene and GA mediates the timing of the decision to flower at least in part miR159-dependent. The intrinsic mechanism of antagonistic interaction between GA and ethylene and miR159 deserves to be further studied.

## MiRNAs and cytokinin signaling

The cytokinin class of plant hormones regulates numerous growth and developmental processes. They have since been shown to play a role in diverse aspects of plant growth and development, including cell division, shoots initiation and apical meristem function [32]. Lu and Fedoroff showed that the *hyl1* mutant shows decreased sensitivity to cytokinin [33]. These implied the relationship between miRNAs and cytokinin.

MiR172 and miR319 were discovered to be down-regulated when subjected to 6-BA treatment [6]. MiR172 regulates flowering time and floral organ identity by down-regulating *APETALA2*-like target genes [34] and down-regulates *glossy15* to promote vegetative phase change in maize [35]. *APETALA2*-like genes which contain putative miR172 target sites are conserved in eudicots and monocots [34]. The down-regulation of miR172 by cytokinin which resulted in increased AP2 protein level would lead to floral patterning defects that included proliferation of numerous petals, stamens and carpels indicating loss of floral determinacy [34]. Thus far, little is known about the roles of cytokinin in flower development issue and the miRNA pathway might be a useful tool to reveal new functions for cytokinin.

## MiRNAs and other phytohormone signaling

For a long time, we refer to phytohormone as the five classic classes. However, more recently, other classes were also found such as JA and BR [2]. All of them reveal a broad role in regulating plant development [2]. Schommer et al. reported the involvement of miR319 in control of jasmonate biosynthesis and senescence, which extended the relationship between miRNAs and plant hormone signaling [36]. MiR319 targets the *TCP* (*TEOSINTE BRANCHED/CYCLOIDEA/PCF*) transcription factor genes, already well known for their effects on leaf growth. In contrast to other miRNA targets, most of which modulate hormone responses, TCPs control

biosynthesis and senescence of the hormone jasmonic acid [36]. TCP transcription factors function throughout leaf development to coordinate the balance between leaf growth, which they negatively regulate, and leaf senescence, which they positively regulate, by affecting JA levels. According to these, we present that miR319-controlled TCP transcription factors coordinate two sequential processes between leaf growth and leaf senescence [36]. Presently, though many conserved miRNAs influence transcription factor genes with pivotal roles in plant development, the targets that mediate the effects of these transcription factors are still largely unknown [36]. The identification of targets of miR319-regulated TCPs provides us a significant advance in understanding of regulatory networks controlled by small RNAs. Besides, it confirms that the function of miRNA-targeted transcription factors is not limited to the modulation of downstream hormonal responses, but that miRNAs could also regulate development through effects on hormone biosynthesis [36].

## MiRNAs regulated by multiply phytohormones

Long ago, plant physiologists had already noted the apparent antagonistic interactions between some of the phytohormones, such as between auxin and cytokinin in the regulation of root–shoot differentiation [2]. Generally developmental processes are synergistically regulated by multiple hormones. Though it has long been obvious that hormones do not function in discrete pathways, but rather exhibit extensive cross-talk and signal integration with each other, the molecular mechanism of such coordinated regulation has been unclear [2]. Manipulation of miRNA guided gene regulation in hormone response might represent a novel and feasible approach to resolve this problem, as several miRNAs appear to response to multiply plant hormones.

As indicated above, there are four miRNAs (miR319, miR159, miR393 and miR167) validated to be regulated by more than one class of plant hormones (Fig. 1). Among them, miR159 responses to GA, ABA and ethylene while miR319 responses to GA, ABA and 6-BA. In addition, both of miR393 and miR167 were involved in ABA and auxin signaling. The regulatory pathways of these miRNAs might help to elucidate the molecular details of some of the signal integration events between these hormones.

## Conclusion

Great progress has been made in the past few years in the area of plant hormones and miRNAs pathways. However, the field is relatively nascent in terms of identifying and characterizing the intersection between miRNAs and hormone response as well as their regulatory roles in plant development. The extent of miRNAs involvement in phytohormone response should become clear in the next several years with the progression of research techniques and direction of sufficient effort to these studies.

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