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One for All and All for One: Cross-Talk of Multiple Signals Controlling the Plant Phenotype

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Abstract

The plant hormone ethylene plays a pivotal role in steering various processes by regulating the biosynthesis, distribution, or signal transduction of other hormones. Ethylene also mediates the effects of other hormones. Similarly, hormones control the ethylene synthesis and signalling pathway. Eventually, integration of this network of signals leads to an appropriate morphological or biochemical response. Consequently, this cross-talk results in the characteristic plasticity associated with plant development. Here, the interplay of ethylene with other hormones is described for germination and seedling growth, stomatal control, and tissue elongation. The mechanisms by which this occurs are discussed in more detail.

Key words: Auxins; Abscissic acid; brassinosteroids; Cross-talk; Ethylene; Gibberellins; Signal transduction

Introduction

Plant development is highly dependent on internal signals coming from hormones. Hormonal interactions—collectively integrated with environmental signals—result in phenotypic alterations. Growth and differentiation is a function of multiple signaling pathways, not only involving numerous growth factors but also governed by external factors. For example, the phenotypic plasticity that occurs during the shade avoidance response is derived from the integration of various hormonal pathways with photomorphogenic and circadian regulatory systems (Vandenbussche and others 2005). In pathogenesis and stress responses, ethylene interacts with jasmonate and salicylic acid, eventually providing the plant with suitable protection (Brodersen and others 2006). In addition, the interplay between ethylene and other hormones occurs at different developmental stages, often in specific tissue and cell types (Vandenbussche and Van Der Straeten 2004). Here we focus on interactions of ethylene with compounds that are determinants for plant growth: auxins, cytokinins, gibberellins (GA), brassinosteroids (BR), abscisic acid (ABA), and glucose.

A prerequisite for signal interactions is a sharing of components between two pathways. This connection can be at the basis (hormone production is turned on

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by another hormone), in the middle (common use of a signaling intermediate), at the end of the pathways (a common target gene or a cooperative activation of a subcellular process), or a combination thereof. Integrators, components functioning in multiple pathways, often are associated with pleiotropic mutations. Probably the best example is the *BIG* gene. *BIG* encodes a protein of over 5000 amino acids, containing several putative Zn finger domains, with significant homology to the *Drosophila* protein Calossin/Pushover, also present in *Caenorhabditis* and humans. A mutation in this gene was first isolated as *tir3-1* in a screen for resistance to an auxin transport inhibitor and proven to be required for normal auxin efflux (Gil and others 2001). In addition, the gene was also retrieved as *asa1* (altered shade avoidance) and as *umb1* (umbrella), which has altered cytokinin sensitivity (Kanyuka and others 2003). All alleles have defects in ethylene and GA responses and are affected in auxin, abscisic acid, and brassinolide responses as well. The analysis of *big* mutants thus indicates that a single gene with functions throughout development can be subject to regulation by different hormonal pathways. Numerous developmental processes are subject to coordination by various plant hormones. Yet, the majority of hormonal interactions do not go beyond three different hormonal inputs on a single mechanism. This article provides an overview of a number of developmental and growth responses in which ethylene signaling has been shown to function in concert with other pathways, and it explores the mechanisms by which ethylene-based hormonal interactions occur or may occur.

Regulation of Germination

Many plant hormones have been shown to regulate germination. Among those, GAs are long known as potent stimulators of germination. Central players are the GA biosynthesis genes *GA3ox1* and *GA3ox2* (Mitchum and others 2006), *GA2ox2*, which is involved in GA breakdown (Yamauchi and others 2004), and the signaling protein RGL2 (Cao and others 2005). *rgl2* knockout mutants can germinate in the absence of gibberellins, indicating a role for the RGL2 DELLA protein as a suppressor of germination (Lee and others 2002; Tyler and others 2004). Besides the prominent role for GAs as stimulators for germination, BRs also stimulate germination and rescue GA-deficient mutants (Steber and McCourt 2001).

In many species ABA counteracts the gibberellin effect and enhances dormancy. Interestingly, ethylene-insensitive mutants are hypersensitive to ABA and the constitutive triple-response mutant *ctr1-1* is ABA insensitive (Beaudoin and others 2000; Ghassemian and others 2000), supporting an antagonistic relationship between both hormones in this phenotypic response. It appears that ethylene acts through the regulation of ABA biosynthesis, conjugation, and signaling for stimulating germination. Seeds of the ethylene-insensitive mutant *etr1-2* contain more ABA and less inactive ABA conjugates than those of the wild type (Chiwocha and others 2005). In particular, the accumulation of ABA glucose ester upon germination was less pronounced in the *etr1-2* mutant compared with that of the wild type, indicating a role for ethylene in stimulating germination by inactivating ABA. Like ABA, glucose itself is, at low concentrations, also an inhibitor of germination (Dekkers and others 2004). Interestingly, ethylene-insensitive mutants are hypersensitive to high concentrations of exogenously applied glucose, whereas ethylene-overproducing and constitutive ethylene-signaling mutants are glucose insensitive (Cheng and others 2002; Zhou and others 1998). The counteracting signals of ethylene and glucose meet at EIN3, an ethylene-signaling component that is degraded through the 26S proteasome machinery in the presence of high glucose concentrations and, conversely, stabilized by ethylene (Yanagisawa and others 2003). Exactly how the ethylene effects on ABA metabolism and sugar signaling are connected remains to be demonstrated. In any case, the control point is probably not the *GIN1/ABA2/SDR1* ABA biosynthesis gene because an ethylene-related phenotype was found only in *gin4* mutants (allelic to *ctr1*) and not in other gin mutants (including *gin1*) (Cheng and others 2002). A model of ethylene interactions with other pathways upon germination is shown in Figure 1.

Control of the Pores

Vital processes such as carbon fixation and transpiration are dependent on the opening and closure of stomata. Several plant hormones regulate the formation and the opening of stomata (Chaerle and others 2005). In *Arabidopsis*, GA is a prime determinant of stomatal development on the hypocotyl. Chemical blocking of GA biosynthesis severely diminishes and addition of exogenous GA increases the number of stomata. Combined with exogenous ACC or auxin, an enhancement of stomatal number is observed (Saibo and others 2003).

The effect of ethylene on stomatal closure is dependent on the species and on the growth conditions (Madhavan and others 1983; Merritt and others 2001). Ethylene induces stomatal closure via

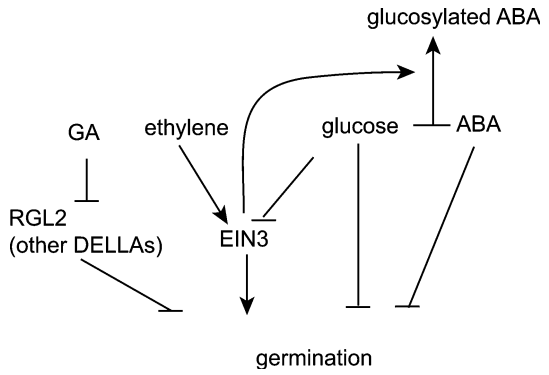

Figure 1. Model of interactions of ethylene with other endogenous plant compounds controlling germination. Gibberellins (GA) are known to stimulate germination by degradation of DELLA proteins, RGL2 being the most important one in this process. GA counteracts the effect of ABA, a promoter of dormancy. The ABA effect is overcome by ethylene, which enhances the sequestration of ABA in an inactive glucosyl ester. The ethylene and glucose pathways compete by respectively stabilizing/destabilizing EIN3, which is necessary for the promotion of seed germination in the presence of sugar.

hydrogen peroxide synthesis in *Arabidopsis* (Desikan and others 2006). However, in combination with ABA, the ethylene precursor ACC inhibits ABA-induced stomatal closure. The ABA effect on closure cannot be reverted by ACC in ethylene-insensitive mutants or tissues treated with the ethylene action inhibitor 1-MCP (Tanaka and others 2005). This indicates that ethylene counteracts ABA-induced stomatal closure. Moreover, ethylene also mediates the reduction of ABA-induced stomatal closure that is regulated by auxins and cytokinins. These hormones therefore are thought to exert their effect by increasing ethylene production (Tanaka and others 2006).

Elongation Processes

Hypocotyl and Stem Elongation

Ethylene is well known for its effects on *Arabidopsis* hypocotyl elongation. Contrasting effects have been noted in the presence and absence of light. In darkness, ethylene inhibits extension growth (Bleecker and others 1988; Knight and others 1910). This effect also occurs when auxins or cytokinins are added exogenously, both of which stimulate ethylene biosynthesis (see below). In the light, the hypocotyl is short and ethylene does not inhibit but rather stimulates elongation growth (Smalle and Van Der Straeten 1997). This ethylene-stimulated hypocotyl extension needs auxin, gibberellin, and brassinosteroid signals (De Grauwe and others 2005; Saibo and others 2003; Vandenbussche and others 2003). Other studies have extended the role of ethylene in stem elongation. In wheat, internode elongation was shown to be stimulated by ethylene (Suge and others 1997). In a shaded environment, stems of ethylene-insensitive tobacco plants show a severely reduced stem elongation, supporting the notion that ethylene can serve as a signal for extension growth in those conditions (Pierik and others 2004; Vandenbussche and others 2005). However, the most conspicuous examples of ethylene stimulating growth were found in semiaquatic rice and *Rumex* species (Jackson and Ram 2003; Voesenek and others 2003; Vriezen and others 2003). In all cases, the ethylene response is dependent on a gibberellin signal (Kende and others 1998; Pierik and others 2004).

Root Elongation

In general, ethylene has a negative effect on the elongation growth of roots (Le and others 2001; Rauser and Horton 1975; Smalle and Van Der Straeten 1997). Low concentrations of exogenous auxins enhance root elongation (Evans and others 1994). Both ethylene and auxin act at least partly through modulation of the stability of DELLA proteins. Auxin appears to decrease the stability of the RGA DELLA-GFP fusion protein, whereas ethylene stabilizes this protein (Achard and others 2003; Fu and Harberd 2003; Vriezen and others 2004).

Drought stress is known to stimulate root growth, including lateral root formation in *Arabidopsis* (Xiong and others 2006). In drought-stressed maize plants, reducing ABA biosynthesis causes an increase in ethylene production (Sharp and LeNoble 2002; Spollen and others 2000). This implies that the higher ABA levels found in water-stressed plants are necessary to prevent excess ethylene production and thus maintain sufficient root growth (Sharp and LeNoble 2002). The molecular mechanism of this regulation of ethylene biosynthesis by ABA remains unknown. Contrasting with the situation in drought-stressed maize, auxin enhances ethylene production, which induces ABA accumulation and consequently results in inhibition of shoot growth of cleavers (*Galium asparine*) (Hansen and Grossmann 2000).

Additional Root Hairs

Root hair development is regulated by ethylene signaling (Dolan and Roberts 1995). Plants treated with the ethylene precursor ACC have ectopic root

hairs that develop on atrichoblasts. Auxins also have a positive effect on root hair growth. Root hairs of the auxin response mutants *aux1* have mild defects in elongation, those of *axr1* have severe defects in elongation, whereas roots are absent in *axr2* and *axr3* (Lincoln and others 1990; Wilson and others 1990; Leyser and others 1996; Pitts and others 1998). Ethylene interacts with auxin to stimulate root hair formation (Pitts and others 1998). Defects in ethylene signaling confer reduced sensitivity to auxin-driven root hair initiation and elongation (Rahman and others 2002). More detailed studies revealed that ethylene promotes auxin-induced microtubule randomization in trichoblasts (Takahashi and others 2003).

Recently it has been demonstrated that methyl jasmonate stimulates the initiation of root hair outgrowth of trichoblast cells (Zhu and others 2006). This process is inhibited in the absence of an ethylene response. Hence, ethylene does not only play a role in generating ectopic root hairs on atrichoblast cells, but it is also required for normal root hair growth on trichoblasts. On the other hand, JA biosynthesis blockers diminish the ethylene response, which illustrates an interdependence of JA and ethylene effect on root hair development (Zhu and others 2006).

Differential Growth: Apical Hooks, Tropisms and Nastic Growth Responses

From the very beginning of its discovery as a plant growth factor, ethylene was shown to be involved in differential growth in plants. Ethylene induces bending of dark-grown pea stems toward the horizontal (Neljubow 1901). Almost a century later a similar phenotype was found in *Arabidopsis* as part of the triple response, consisting of exaggeration of the apical hook (Bleecker and others 1988). Ethylene is thought to be responsible for the establishment of a differential auxin signal across the apical hook, a process in which the *HLS1* gene plays a central role (Lehman and others 1996). In addition, the auxin efflux regulator PIN3 and a pathway involving the auxin response factor NPH4/ARF7 are associated with ethylene-controlled apical hook maintenance (Friml and others 2002; Harper and others 2000). Ethylene may indeed be acting through PIN1/PIN3 or PIN1/PIN3-controlled events because *pin3* loss-of-function mutants and PIN1 overexpressors show a reduced ethylene sensitivity (De Grauwe and others 2005). On the other hand, the partial hookless phenotype of *nph4* mutants can be reverted by application of exogenous ethylene (Harper and others 2000). GAs are also implicated in apical hook development. GA biosynthesis mutants lack an apical hook (Achard and others 2003; Vriezen and others 2004). Ethylene appears to stabilize negative regulators of GA signaling, thus revealing a complex interaction that results in hook formation (Vriezen and others 2004). Finally, BRs are also necessary for correct hook maintenance. Therefore, disruption of BR biosynthesis or exogenous application of BR can lead to attenuation of ethylene-stimulated differential growth in the hook region (De Grauwe and others 2005). An overview of these interactions is given in Figure 2.

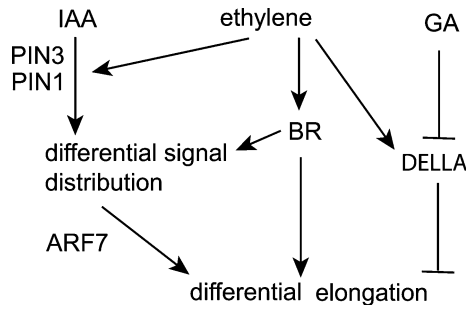

Figure 2. Hormonal interactions during regulation of differential growth as seen in the apical hook. Ethylene plays a central role, determining the differential auxin signal, which leads to unequal growth on both sides, and affecting general elongation regulating GA and BR signals. Of major importance for this auxin-regulated differential growth are the PIN1 and PIN3 auxin efflux regulators and the auxin response factor ARF7. Ethylene inhibits GA signaling by stabilizing DELLA proteins, which are inhibitors of elongation, but needs BRs for exaggeration of the apical hook. All of these interactions lead to a balanced response visible as differential growth. IAA: auxin; GA: gibberellin; BR: brassinosteroid.

The intimate interaction between ethylene and auxin in differential growth is also apparent from phototropism and gravitropism. Similar to apical hook formation, phototropism is mainly dependent on an auxin gradient and PIN3 (Esmon and others 2006; Friml and others 2002) and on the function of the auxin response factor NPH4/ARF7 (Stowe-Evans and others 1998). Furthermore, *nph4* mutants are suppressed in their phototropic defect by application of ethylene (Harper and others 2000). An analogous rescue of hypocotyl gravitropism by ethylene in *nph4* mutants was also observed (Harper and others 2000). The suppression mechanism remains unknown to date, but redundancy of NPH4/ARF7 with other ARFs, induced by ethylene, is a possibility. Indeed, there are indications that an increased copy number of the closest ARF7 homolog, the ethylene inducible ARF19, can rescue phototropism in *nph4/arf7* mutants (Li and others 2006).

Table 1. F-box Proteins involved in Hormone Signaling Pathways

Hormone signaling	F-box protein	aka	Reference
Auxin	TIR1		Kepinski and Leyser 2005
			Dharmasiri and others 2005a
	AFB1		Dharmasiri and others 2005b
	AFB2		Dharmasiri and others 2005b
	AFB3		Dharmasiri and others 2005b
	AFB5		Walsh and others 2006
Jasmonate	COI1		Xu and others 2002
Ethylene	EBF1		Guo and Ecker 2003; Potushak and others 2003; Gagne and others 2004
	EBF2		Guo and Ecker 2003; Potushak and others 2003; Gagne and others 2004
Gibberellin	SLY1	GAR2	McGinnis and others 2003; Dill and others 2004
	SNE		Strader and others 2004

Gravitropic bending in roots is yet another example of differential growth that is mainly controlled by auxins. The auxin import carrier AUX1 (Abas and others 2006; Friml and others 2002; Swarup and others 2005), possibly also AUX1-like proteins LAX1-4 (Swarup and Bennett 2003), and auxin efflux regulators (PIN proteins) are necessary for this process. Interestingly, the *eir1* mutant, which was isolated based on its ethylene-insensitive root phenotype, proved to be an allele of *PIN2*, a major auxin transport regulator (Abas and others 2006; Luschnig and others 1998). At this point, a role for ethylene in directly controlling *PIN2* gene expression or PIN2 stability is lacking. Yet, evidence for a regulatory role of ethylene in gravitropism is accumulating. ACC treatment reduces gravitropic response in the wild type, whereas ethylene-insensitive mutants do not show this response, suggesting a positive role for ethylene signaling in gravitropic bending (Buer and others 2006). Interestingly, mutants in flavonoid biosynthesis do not show this ethylene response, even though they exhibit a wild-type sensitivity to root growth inhibition by ACC. Moreover, in wild type grown in the presence of ACC, instead of a transient flavonoid induction observed upon gravistimulation of untreated seedlings, a delayed but sustained flavonoid accumulation is visible in root tips. Flavonoids are inhibitors of auxin transport and might therefore act as a control point for ethylene in modulating the gravitropic response (Buer and others 2006).

Sex Determination and Fertility: The Longer, the Better

Male fertility in *Arabidopsis* is dependent on several hormones, including gibberellins, brassinosteroids, and ethylene. The GA signal is necessary for production of viable pollen grains (Huang and others 2003). In GA-related dwarf mutants, male sterility is also caused by an impaired outgrowth of stamens. Short stamens limit the chances of proper fertilization on the stigma. *ga1* mutants are male-sterile dwarfs (Koornneef and Van Der Veen 1980; Sun and Kamiya 1994) and can be rescued by mutations in DELLA growth repressor proteins (Tyler and others 2004). Likewise, the loss of fertility of the brassinosteroid biosynthesis mutant *dwf4* was attributed to the reduced length of the stamen filaments relative to the gynoecium, which resulted in mature pollen deposition mainly on the ovary wall rather than on the stigmatic surface, causing small siliques or the absence thereof (Azpiroz and others 1998). Plants with constitutive ethylene signaling also have severe defects in anther elongation due to early growth arrest, which leads to low fertility (Hall and Bleecker 2003; Kieber and others 1993). It is not known whether the ethylene effect depends on brassinosteroids or gibberellins.

In cucumber, the hormonal effect on floral organ growth is even more pronounced. Male or female flowers develop due to an arrest of pistil or stamen primordial, respectively. Plant hormones have a dramatic effect on this sex determination. Ethylene stimulates the formation of female flowers in gynoecious and monoecious cucumber (Yamasaki and others 2003). Auxin has a similar effect, which was suggested to be ethylene-mediated (Shannon and de la Guardia 1969). GA has the opposite effect and stimulates male flower formation (Halevy and Rudich 1967). Similar effects were found in *Cannabis sativa* (Zeevaart 1978). Aspects of stamen growth have not been analyzed in depth at the molecular level, and future research will reveal if there are any parallels with the hormonal interac-

tions occurring at different stages of development, in different elongating organs.

Mechanisms for Interhormonal Connections with the Ethylene Pathway

Regulation of Ethylene Production by Other Hormones

In many of the physiologic effects presented above, the cross-talk of hormone pathways is based on one hormone affecting biosynthesis of the other. This can either be the influence of ethylene on another pathway or that of another hormone on the ethylene pathway. Profound studies were performed on regulation of ethylene production by other hormones (most often exogenously applied) (Burg and Burg 1966; Abeles and others 1992; Joo and others 2006; Vogel and others 1998a, b). Increased ethylene production can be caused by regulation of transcript or protein levels of ethylene biosynthesis genes.

Auxin is known to be a strong stimulator of ethylene production. In all cases studied this is due to an ACC synthase transcript accumulation (Woltering and others 2005; Yoon and others 1999). Except for *ACS1*, *7*, and *9*, all other functional ACC synthases (that is, 7 of 10) of *Arabidopsis* are induced by auxin at the transcript level (Yamagami and others 2003). Auxin induction of ACC oxidase transcripts is usually considered a secondary effect of auxin-stimulated ethylene production resulting from an increase in ACC synthase (Peck and Kende 1995). Hence, ACC oxidase is induced by ethylene in an autostimulatory way.

Cytokinin can induce the typical ethylene-related triple response in dark-grown *Arabidopsis* seedlings. Measurement of ethylene emanation indicated an elevated ethylene production in cytokinin-treated seedlings (Vogel and others 1998a, b). This characteristic was used by Vogel and others (1998b) to isolate cytokinin-insensitive (*cin*) mutants. The *cin5* mutant was found to be allelic to ethylene overproducer 2 (*eto2*), which encodes ACC synthase 5. The analysis of ACS5 protein extracted from seedlings grown in the presence of cytokinin revealed a stabilization of this ACC synthase compared to nontreated plants (Chae and others 2003). Brassinosteroids were shown to elevate ethylene production in mung bean stem segments (Arteca and others 1983). Brassinosteroids induce *ACS4* gene expression in *Arabidopsis* (Joo and others 2006). However, since *axr1-3* and *axr2-1* mutants lack this induction and given that *ACS4* is inducible by IAA, auxin may be a prerequisite for the response that can be enhanced by BR (Joo and others 2006).

Finally, there is a report on GA-mediated reduction of the level of an ACC oxidase mRNA and activity in Azuki bean, but a consequent reduction in ethylene production was not observed (Kaneta and others 1997).

Effect of Ethylene on the Biosynthesis of Other Hormones

Although the effects of other hormones on the synthesis of ethylene are documented more than the reverse, some examples of ethylene influencing biosynthesis of other hormones exist. Analysis of the weakly ethylene insensitive *wei2* and *wei7* mutants added a further level of complexity to the ethylene-auxin interaction (Stepanova and others 2005). The mutants *wei2* and *wei7* have a root elongation phenotype. The *WEI2* and *WEI7* genes encode anthranylate synthase α and β, respectively. These genes are involved in tryptophan biosynthesis, a major route toward auxin synthesis. Both genes are induced by ethylene treatment.

Furthermore, *etr1* and *ein2* mutants produce less ABA and have a lower expression of zeaxanthin epoxidase, the first committed enzyme in ABA biosynthesis (Ghassemian 2000; Hansen and Grossmann 2000; Cheng and others 2002).

Mechanisms Based on Signaling Effects

Competition for the Protein Degradation Machinery?

Over the last few years, the protein degradation machinery has proven to be essential for almost all plant hormone responses (Vandenbussche and Van Der Straeten 2004). Selective protein degradation occurs via labeling of target proteins by ubiquitins. Ubiquitins are linked to the target protein through the sequential activity of E1 (ubiquitin activating enzyme), E2 (ubiquitin conjugating enzyme), and E3 (ubiquitin ligase) enzymes. Several types of E3 ligases exist: HECT (homology to E6AP C-terminus), SCF (composed of SKP1, Cullin, and F-box proteins), RING (real interesting new gene), and APC (anaphase promoting complex) protein complexes. SCF E3s are involved in a number of hormonal signaling cascades. Their specificity is thought to be determined mainly by the F-box component, of which there are 694 in *Arabidopsis* (Lechner and others 2006; Vierstra 2003).

Various E3 complexes, relying on a plethora of F-box proteins, determine the specificity of ubiquitin-mediated degradation of factors involved in different hormonal pathways. F-box proteins specific to gibberellin, jasmonate, auxin, and ethylene signaling exist, each with their specific targets (Table 1).

Currently, a common regulatory mechanism at the E3 level has been suggested only for auxin and jasmonate signaling (Tiryaki and Staswick 2002). Some of the jasmonate mutant phenotypes overlap with those of auxin mutants (that is, apical dominance, inhibition of root elongation). The SGT1b and AXR1 proteins control both auxin and jasmonate responses by regulating the activity of the E3 complexes (through rubylation of CULLIN1) (Lorenzo and others 2005; Xu and others 2002). Moreover, the auxin-binding F-box proteins (AFBs) and COI1 share high homology. Homologous F-box proteins likely use similar SCF components and interfere with each other's pathways. An example of homologous F-box proteins that influence each other's function is seen in GA signaling, where SLEEPY (SLY1) is the F-box protein that directs DELLA proteins for degradation. Overexpression of the SLY1 homolog, SNEEZY (SNE), can suppress the *sly1* mutant phenotype and thus interfere with GA signaling (Strader and others 2004). Analogously, the homologous F-box proteins TIR1 (or other AFBs) and COI could compete for auxin signaling components. The EBF1 and EBF2 proteins seem to be very specific for ethylene signaling, and thus far no other F-box protein has been shown to be involved in regulating ethylene effects (Gagne and others 2004; Guo and Ecker 2003; Potushak and others 2003). The target protein of the EBFs is EIN3, which is stabilized by ethylene treatment. Interestingly, degradation of EIN3 is accelerated by glucose (Yanagisawa and others 2003). However, it is not yet known whether glucose signaling influences the EBFs directly or affects another upstream component of ethylene signaling.

Effects on TranscriptR

A lack of common early targets at the transcriptional level suggests the absence of a common regulatory mechanism for elongation growth by plant hormone action (Nemhauser and others 2006). However, pairwise comparison shows common regulation of ACC (ethylene), GA, BR, auxin, and MeJA target genes. Regulation of different members of a gene family by individual hormones may exist, eventually influencing the same or similar processes. For instance, this is the case for the ACC synthase gene family of *Arabidopsis*, members of which are regulated by auxin, BR, cytokinins, or ethylene itself (Chae and others 2003; Joo and others 2006; Thain and others 2004; Yamagami and others 2003).

Recently, the *EIN5* gene was cloned and shown to be an allele of the 5′-3′ exoribonuclease *XRN4* (Olmedo and others 2006). This enzyme functions in eliminating cleavage products derived from miRNA-mediated degradation of genes such as the auxin response factors ARF10 and ARF17 (Mallory and others 2005; Olmedo and others 2006). This suggests potential ethylene interference in other hormonal pathways, for example, auxin signaling, through regulation of RNA stability.

Concluding Remarks and Perspectives

The ethylene pathway interacts with many other hormonal pathways, eventually codetermining the plant phenotype. The ethylene-auxin interaction is particularly complex, with reciprocal regulation between these hormones at several biochemical levels. Future molecular research on processes that have been very well described in physiologic terms can add great value to our understanding of flower development and the regulation of stomata. Those studies will determine whether similar molecular mechanisms in hormone cross-talk act throughout the lifecycle of a plant and among species.

REFERENCES

Abas L, Benjamins R, Malenica N, Paciorek T, Wirniewska J, Moulinier-Anzola JC, Sieberer T, Friml J, Luschnig C. 2006. Intracellular trafficking and proteolysis of the Arabidopsis auxin-efflux facilitator PIN2 are involved in root gravitropism. Nat Cell Biol 8:249–256.

Abeles S, Morgan PW, Saltveit ME. 1992. Ethylene in Plant Biology. San Diego, CA: Academic Press.

Achard P, Vriezen WH, Van Der Straeten D, Harberd NP. 2003. Ethylene regulates Arabidopsis development via the modulation of DELLA protein growth repressor function. Plant Cell 15:2816–2825.

Arteca RN, Tsai DS, Schlagnhaufer C, Mandava NB. 1983. The effect of brassinosteroid on auxin-induced ethylene production by etiolated mung bean segments. Physiol Plant 59:539–544.

Azpiroz R, Wu YW, LoCascio JC, Feldmann KA. 1998. An Arabidopsis brassinosteroid-dependent mutant is blocked in cell elongation. Plant Cell 10:219–230.

Beaudoin N, Serizet C, Gosti F, Giraudat J. 2000. Interactions between abscisic acid and ethylene signaling cascades. Plant Cell 12:1103–1115.

Bleecker AB, Estelle MA, Somerville C, Kende H. 1988. Insensitivity to ethylene conferred by a dominant mutation in *Arabidopsis thaliana*. Science 241:1086–1089.

Brodersen P, Petersen M, Bjorn Nielsen H, Zhu S, Newman MA, Shokat KM, Rietz S, Parker J, Mundy J. 2006. MAP kinase 4 regulates salicylic acid- and jasmonic acid/ethylene-dependent responses via EDS1 and PAD4. Plant J 47:532–546.

Buer CS, Sukumar P, Muday GK. 2006. Ethylene modulates flavonoid accumulation and gravitropic responses in roots of Arabidopsis. Plant Physiol 140:1384–1396.

Burg SP, Burg EA. 1966. Auxin-induced ethylene formation: its relation to flowering in the pineapple. Science 152:1269 .

Cao DN, Hussain A, Cheng H, Peng JR. 2005. Loss of function of four DELLA genes leads to light- and gibberellin-independent seed germination in Arabidopsis. Planta 223:105–113.

Chae HS, Faure F, Kieber JJ. 2003. The eto1, eto2, and eto3 mutations and cytokinin treatment increase ethylene biosynthesis in Arabidopsis by increasing the stability of ACS protein. Plant Cell 15:545–559.

Chaerle L, Saibo N, Van Der Straeten D. 2005. Tuning the pores: towards engineering plants for improved water use efficiency. Trends Biotechnol 23:308–315.

Cheng WH, et al. 2002. A unique short-chain dehydrogenase/reductase in Arabidopsis glucose signaling and abscisic acid biosynthesis and functions. Plant Cell 14:2723–2743.

Chiwocha SDS, Cutler AJ, Abrams SR, Ambrose SJ, Yang J, Ross ARS, Kermode AR. 2005. The etr1-2 mutation in *Arabidopsis thaliana* affects the abscisic acid, auxin, cytokinin and gibberellin metabolic pathways during maintenance of seed dormancy, moist-chilling and germination. Plant J 42:35–48.

De Grauwe L, Vandenbussche F, Tietz O, Palme K, Van Der Straeten D. 2005. Auxin, ethylene and brassinosteroids: Tripartite control of growth in the Arabidopsis hypocotyl. Plant Cell Physiol 46:827–836.

Dekkers BJ, Schuurmans JA, Smeekens SC. 2004. Glucose delays seed germination in *Arabidopsis thaliana*. Planta 218:579–588.

Desikan R, Last K, Harrett-Williams R, Tagliavia C, Harter K, Hooley R, Hancock JT, Neill SJ. 2006. Ethylene-induced stomatal closure in Arabidopsis occurs via AtrbohF-mediated hydrogen peroxide synthesis. Plant J 47:907–916.

Dharmasiri N, Dharmasiri S, Estelle M. 2005a. The F-box protein TIR1 is an auxin receptor. Nature 435:441–445.

Dharmasiri N, Dharmasiri S, Weijers D, Lechner E, Yamada M, Hobbie L, Ehrismann JS, Jurgens G, Estelle M. 2005b. Plant development is regulated by a family of auxin receptor F box proteins. Dev Cell 9:109–119.

Dill A, Thomas SG, Hu J, Steber CM, Sun TP. 2004. The Arabidopsis F-box protein SLEEPY1 targets gibberellin signaling repressors for gibberellin-induced degradation. Plant Cell 16:1392–1405.

Dolan L, Roberts K. 1995. The development of cell pattern in the root epidermis. Phil Trans R Soc Lond Ser B Biol Sci 350:95–99.

Esmon CA, Tinsley AG, Ljung K, Sandberg G, Hearne LB, Liscum E. 2006. A gradient of auxin and auxin-dependent transcription precedes tropic growth responses. Proc Natl Acad Sci U S A 103:236–241.

Evans ML, Ishikawa H, Estelle MA. 1994. Responses of Arabidopsis roots to auxin studied with high temporal resolution: comparison of wild type and auxin-response mutants. Planta 194:215–222.

Friml J, Wisniewska J, Benkova E, Mendgen K, Palme K. 2002. Lateral relocation of auxin efflux regulator PIN3 mediates tropism in Arabidopsis. Nature 415:806–809.

Fu XD, Harberd NP. 2003. Auxin promotes Arabidopsis root growth by modulating gibberellin response. Nature 421:740–743.

Gagne JM, Smalle J, Gingerich DJ, Walker JM, Yoo SD, Yanagisawa S, Vierstra RD. 2004. Arabidopsis EIN3-binding F-box 1 and 2 form ubiquitin-protein ligases that repress ethylene action and promote growth by directing EIN3 degradation. Proc Natl Acad Sci U S A 101:6803–6808.

Ghassemian M, Nambara E, Cutler S, Kawaide H, Kamiya Y, McCourt P. 2000. Regulation of abscisic acid signaling by the ethylene response pathway in Arabidopsis. Plant Cell 12:1117–1126.

Gil P, Dewey E, Friml J, Zhao Y, Snowden KC, Putterill J, Palme K, Estelle M, Chory J. 2001. BIG: a calossin-like protein required for polar auxin transport in Arabidopsis. Genes Dev 15:1985–1997.

Guo HW, Ecker JR. 2003. Plant responses to ethylene gas are mediated by SCF (EBF1/EBF2)-dependent proteolysis of EIN3 transcription factor. Cell 115:667–677.

Halevy AH, Rudich Y. 1967. Modification of sex expression in muskmelon by treatment with the growth retardant B995. Physiol Plant 20:1052–1058.

Hall AE, Bleecker AB. 2003. Analysis of combinatorial loss-of-function mutants in the Arabidopsis ethylene receptors reveals that the ers1 etr1 double mutant has severe developmental defects that are EIN2 dependent. Plant Cell 15:2032–2041.

Hansen H, Grossmann K. 2000. Auxin-induced ethylene triggers abscisic acid biosynthesis and growth inhibition. Plant Physiol 124:1437–1448.

Harper RM, Stowe-Evans EL, Luesse DR, Muto H, Tatematsu K, Watahiki MK, Yamamoto K, Liscum E. 2000. The NPH4 locus encodes the auxin response factor ARF7, a conditional regulator of differential growth in aerial Arabidopsis tissue. Plant Cell 12:757–770.

Huang S, Cerny RE, Qi YL, Bhat D, Aydt CM, Hanson DD, Malloy KP, Ness LA. 2003. Transgenic studies on the involvement of cytokinin and gibberellin in male development. Plant Physiol 131:1270–1282.

Jackson MB, Ram PC. 2003. Physiological and molecular basis of susceptibility and tolerance of rice plants to complete submergence. Ann Bot 91:227–241.

Joo S, Seo YS, Kim SM, Hong DK, Park KY, Kim WT. 2006. Brassinosteroid induction of AtACS4 encoding an auxin-responsive 1-aminocyclopropane-1-carboxylate synthase 4 in Arabidopsis seedlings. Physiol Plant 126:592–604.

Kaneta T, Kakimoto T, Shibaoka H. 1997. Gibberellin A(3) causes a decrease in the accumulation of mRNA for ACC oxidase and in the activity of the enzyme in azuki bean (*Vigna angularis*) epicotyls. Plant Cell Physiol 38:1135–1141.

Kanyuka K, Praekelt U, Franklin KA, Billingham OE, Hooley R, Whitelam GC, Halliday KJ. 2003. Mutations in the huge Arabidopsis gene BIG affect a range of hormone and light responses. Plant J 35:57–70.

Kende H, van der Knaap E, Cho HT. 1998. Deepwater rice: A model plant to study stem elongation. Plant Physiol 118:1105–1110.

Kepinski S, Leyser O. 2005. The Arabidopsis F-box protein TIR1 is an auxin receptor. Nature 435:446–451.

Kieber JJ, Rothenberg M, Roman G, Feldmann KA, Ecker JR. 1993. CTR1, a negative regulator of the ethylene response pathway in Arabidopsis encodes a member of the Raf family of protein kinases. Cell 72:427–441.

Knight LI, Rose RC, Crocker W. 1910. Effect of various gases and vapors upon etiolated seedlings of the sweet pea. Science 31:635–636.

Koornneef M, Vanderveen JH. 1980. Induction and analysis of gibberellin sensitive mutants in *Arabidopsis thaliana* (L) Heynh. Theoret Appl Genet 58:257–263.

Le J, Vandenbussche F, Van Der Straeten D, Verbelen JP. 2001. In the early response of Arabidopsis roots to ethylene, cell elongation is up- and down-regulated and uncoupled from differentiation. Plant Physiol 125:519–522.

Lechner E, Achard P, Vansiri A, Potuschak T, Genschik P. 2006. F-box proteins everywhere. Curr Opin Plant Biol 9:631–638.

Lee S, Cheng H, King KE, Wang W, He Y, Hussain A, Lo J, Harberd NP, Peng J. 2002. Gibberellin regulates Arabidopsis seed germination via RGL2, a GAI/RGA-like gene whose expression is up-regulated following imbibition. Genes Dev 16:646–658.

Lehman A, Black R, Ecker JR. 1996. HOOKLESS1, an ethylene response gene, is required for differential cell elongation in the Arabidopsis hypocotyl. Cell 85:183–194.

Leyser HMO, Pickett FB, Dharmasiri S, Estelle M. 1996. Mutations in the AXR3 gene of Arabidopsis result in altered auxin response including ectopic expression from the SAUR-AC1 promoter. Plant J 10:403–413.

Li JS, Dai XH, Zhao YD. 2006. A role for auxin response factor 19 in auxin and ethylene signaling in Arabidopsis. Plant Physiol 140:899–908.

Lincoln C, Britton JH, Estelle M. 1990. Growth and development of the axrl mutants of Arabidopsis . Plant Cell 2:1071–1080.

Lorenzo O, Solano R. 2005. Molecular players regulating the jasmonate signalling network. Curr Opin Plant Biol 8:532–540.

Luschnig C, Gaxiola RA, Grisafi P, Fink GR. 1998. EIR1, a root-specific protein involved in auxin transport, is required for gravitropism in *Arabidopsis thaliana*. Genes Dev 12:2175–2187.

Madhavan S, Chrmoinski A, Smith BN. 1983. Effect of ethylene on stomatal opening in tomato and carnation leaves. Plant Cell Physiol 24:569–572.

Mallory AC, Bartel DP, Bartel B. 2005. MicroRNA-directed regulation of Arabidopsis AUXIN RESPONSE FACTOR17 is essential for proper development and modulates expression of early auxin response genes. Plant Cell 17:1360–1375.

McGinnis KM, Thomas SG, Soule JD, Strader LC, Zale JM, Sun TP, Steber CM. 2003. The Arabidopsis SLEEPY1 gene encodes a putative F-box subunit of an SCF E3 ubiquitin ligase. Plant Cell 15:1120–1130.

Merritt F, Kemper A, Tallman G. 2001. Inhibitors of ethylene synthesis inhibit auxin-induced stomatal opening in epidermis detached from leaves of *Vicia faba* L. Plant Cell Physiol 42:223–230.

Mitchum MG, Yamaguchi S, Hanada A, Kuwahara A, Yoshioka Y, Kato T, Tabata S, Kamiya Y, Sun TP. 2006. Distinct and overlapping roles of two gibberellin 3-oxidases in Arabidopsis development. Plant J 45:804–818.

Neljubow D. 1901. Ueber die horizontale Nutation der Stengel von *Pisum sativum* and einiger anderen Pflanzen. Beihefte Botaniaschen centralblatt 10:128–139.

Nemhauser JL, Hong FX, Chory J. 2006. Different plant hormones regulate similar processes through largely nonoverlapping transcriptional responses. Cell 126:467–475.

Olmedo G, Guo HW, Gregory BD, Nourizadeh SD, Aguilar-Henonin L, Li HJ, An FY, Guzman P, Ecker JR. 2006. ETHYLENE-INSENSITIVE5 encodes a 5′ → 3′ exoribonuclease required for regulation of the EIN3-targeting F-box proteins EBF1/2. Proc Natl Acad Sci U S A 103:13286–13293.

Peck SC, Kende H. 1995. Sequential induction of the ethylene biosynthetic-enzymes by indole-3-acetic-acid in etiolated peas. Plant Mol Biol 28:293–301.

Pierik R, Cuppens MLC, Voesenek L, Visser EJW. 2004. Interactions between ethylene and gibberellins in phytochrome-mediated shade avoidance responses in tobacco. Plant Physiology 136:2928–2936.

Pitts RJ, Cernac A, Estelle M. 1998. Auxin and ethylene promote root hair elongation in Arabidopsis. Plant J 16:553–560.

Potuschak T, Lechner E, Parmentier Y, Yanagisawa S, Grava S, Koncz C, Genschik P. 2003. EIN3-dependent regulation of plant ethylene hormone signaling by two Arabidopsis F box proteins: EBF1 and EBF2. Cell 115:679–689.

Rahman A, Hosokawa S, Oono Y, Amakawa T, Goto N, Tsurumi S. 2002. Auxin and ethylene response interactions during Arabidopsis root hair development dissected by auxin influx modulators. Plant Physiol 130:1908–1917.

Rauser WE, Horton RF. 1975. Rapid effects of indoleacetic acid and ethylene on the growth of intact pea roots. Plant Physiol 55:443–447.

Saibo NJM, Vriezen WH, Beemster GTS, Van Der Straeten D. 2003. Growth and stomata development of Arabidopsis hypocotyls are controlled by gibberellins and modulated by ethylene and auxins. Plant J 33:989–1000.

Shannon S, de la Guardia MD. 1969. Sex expression and the production of ethylene induced by auxin in the cucumber (*Cucumis sativum* L.). Nature 223:186 .

Sharp RE, LeNoble ME. 2002. ABA, ethylene and the control of shoot and root growth under water stress. J Exp Bot 53:33–37.

Spollen WG, LeNoble ME, Samuels TD, Bernstein N, Sharp RE. 2000. Abscisic acid accumulation maintains maize primary root elongation at low water potentials by restricting ethylene production. Plant Physiol 122:967–976.

Smalle J, Van Der Straeten D. 1997. Ethylene and vegetative development. Physiol Plant 100:593–605.

Steber CM, McCourt P. 2001. A role for brassinosteroids in germination in Arabidopsis. Plant Physiol 125:763–769.

Stepanova AN, Hoyt JM, Hamilton AA, Alonso JM. 2005. A link between ethylene and auxin uncovered by the characterization of two root-specific ethylene-insensitive mutants in Arabidopsis. Plant Cell 17:2230–2242.

Stowe-Evans EL, Harper RM, Motchoulski AV, Liscum E. 1998. NPH4, a conditional modulator of auxin-dependent differential growth responses in Arabidopsis. Plant Physiol 118:1265–1275.

Strader LC, Ritchie S, Soule JD, McGinnis KM, Steber CM. 2004. Recessive-interfering mutations in the gibberellin signaling gene SLEEPY1 are rescued by overexpression of its homologue, SNEEZY. Proc Natl Acad Sci U S A 101:12771–12776.

Suge H, Nishizawa T, Takahashi H, Takeda K. 1997. Phenotypic plasticity of internode elongation stimulated by deep-seeding and ethylene in wheat seedlings. Plant Cell Environ 20:961–964.

Sun TP, Kamiya Y. 1994. The Arabidopsis Ga1 locus encodes the cyclase ent-kaurene synthetase-a of gibberellin biosynthesis. Plant Cell 6:1509–1518.

Swarup R, Bennett M. 2003. Auxin transport: the fountain of life in plants? Dev Cell 5:824–826.

Swarup R, Kramer EM, Perry P, Knox K, Leyser HMO, Haseloff J, Beemster GTS, Bhalerao R, Bennett MJ. 2005. Root gravitropism requires lateral root cap and epidermal cells for transport and response to a mobile auxin signal. Nat Cell Biol 7:1057–1065.

Takahashi H, Kawahara A, Inoue Y. 2003. Ethylene promotes the induction by auxin of the cortical microtubule randomization required for low-pH-induced root hair initiation in lettuce (*Lactuca sativa* L.) seedlings. Plant Cell Physiol 44:932–940.

Tanaka Y, Sano T, Tamaoki M, Nakajima N, Kondo N, Hasezawa S. 2005. Ethylene inhibits abscisic acid-induced stomatal closure in Arabidopsis. Plant Physiol 138:2337–2343.

Tanaka Y, Sano T, Tamaoki M, Nakajima N, Kondo N, Hasezawa S. 2006. Cytokinin and auxin inhibit abscisic acid-induced stornatal closure by enhancing ethylene production in Arabidopsis. J Exp Bot 57:2259–2266.

Thain SC, Vandenbussche F, Laarhoven LJ, Dowson-Day MJ, Wang ZY, Tobin EM, Harren FJ, Millar AJ, Van Der Straeten D. 2004. Circadian rhythms of ethylene emission in *Arabidopsis*. Plant Physiol 136:3751–3761.

Tiryaki I, Staswick PE. 2002. An Arabidopsis mutant defective in jasmonate response is allelic to the auxin-signaling mutant axr1. Plant Physiol 130:887–894.

Tyler L, Thomas SG, Hu JH, Dill A, Alonso JM, Ecker JR, Sun TP. 2004. DELLA proteins and gibberellin-regulated seed germination and floral development in Arabidopsis. Plant Physiol 135:1008–1019.

Vandenbussche F, Van Der Straeten D. 2004. Shaping the shoot: a circuitry that integrates multiple signals. Trends Plant Sci 9:499–506.

Vandenbussche F, Vriezen W, Smalle J, Laarhoven LJ, Harren F, Van Der Straeten D. 2003. The Arabidopsis mutant alh1 illustrates a cross talk between ethylene and auxin. Plant Physiol 131:1228–1238.

Vandenbussche F, Pierik R, Millenaar FF, Voesenek LA, Van Der Straeten D. 2005. Reaching out of the shade. Curr Opin Plant Biol 8:462–468.

Vierstra RD. 2003. The ubiquitin/26S proteasome pathway, the complex last chapter in the life of many plant proteins. Trends Plant Sci 8:135–142.

Voesenek L, Benschop JJ, Bou J, Cox MCH, Groeneveld HW, Millenaar FF, Vreeburg RAM, Peeters AJM. 2003. Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot Rumex palustris. Ann Bot 91:205–211.

Vogel JP, Woeste KE, Theologis A, Kieber JJ. 1998a. Recessive and dominant mutations in the ethylene biosynthetic gene ACS5 of Arabidopsis confer cytokinin insensitivity and ethylene overproduction, respectively. Proc Natl Acad Sci U S A 95:4766–4771.

Vogel JP, Schuerman P, Woeste K, Brandstatter I, Kieber JJ. 1998b. Isolation and characterization of Arabidopsis mutants defective in the induction of ethylene biosynthesis by cytokinin. Genetics 149:417–427.

Vriezen WH, Zhou ZY, Van Der Straeten D. 2003. Regulation of submergence-induced enhanced shoot elongation in *Oryza sativa* L. Ann Bot 91:263–270.

Vriezen WH, Achard P, Harberd NP, Van Der Straeten D. 2004. Ethylene-mediated enhancement of apical hook formation in etiolated *Arabidopsis thaliana* seedlings is gibberellin dependent. Plant J 37:505–516.

Walsh TA, Neal R, Merlo AO, Honma M, Hicks GR, Wolff K, Matsumura W, Davies JP. 2006. Mutations in an auxin receptor homolog AFB5 and in SGT1b confer resistance to synthetic picolinate auxins and not to 2,4-dichlorophenoxyacetic acid or indole-3-acetic acid in Arabidopsis. Plant Physiol 142:542–552.

Wilson AK, Pickett FB, Turner JC, Estelle M. 1990. A dominant mutation in Arabidopsis confers resistance to auxin, ethylene and abscisic acid. Mol General Genet 222:377–383.

Woltering EJ, Balk PA, Nijenhuis-de Vries MA, Faivre M, Ruys G, Somhorst D, Philosoph-Hadas S, Friedman H. 2005. An auxin-responsive 1-aminocyclopropane-1-carboxylate synthase is responsible for differential ethylene production in gravistimulated *Antirrhinum majus* L. flower stems. Planta 220:403–413.

Xiong L, Wang RG, Mao G, Koczan JM. 2006. Identification of drought tolerance determinants by genetic analysis of root response to drought stress and abscisic acid. Plant Physiol 42:1065–1074.

Xu L, Liu F, Lechner E, Genschik P, Crosby WL, Ma H, Peng W, Huang D, Xie D. 2002. The SCF(COI1) ubiquitin-ligase complexes are required for jasmonate response in Arabidopsis. Plant Cell 14:1919–1935.

Yamagami T, Tsuchisaka A, Yamada K, Haddon WF, Harden LA, Theologis A. 2003. Biochemical diversity among the 1-aminocyclopropane-1-carboxylate synthase isozymes encoded by the Arabidopsis gene family. J Biol Chem 278:49102–49112.

Yamasaki S, Fujii N, Takahashi H. 2003. Characterization of ethylene effects on sex determination in cucumber plants. Sex Plant Reprod 16:103–111.

Yamauchi Y, Ogawa M, Kuwahara A, Hanada A, Kamiya Y, Yamaguchi S. 2004. Activation of gibberellin biosynthesis and response pathways by low temperature during imbibition of *Arabidopsis thaliana* seeds. Plant Cell 16:367–378.

Yanagisawa S, Yoo SD, Sheen J. 2003. Differential regulation of EIN3 stability by glucose and ethylene signalling in plants. Nature 425:521–525.

Yoon IS, Park DH, Mori H, Imaseki H, Kang BG. 1999. Characterization of an auxin-inducible 1-aminocyclopropane-1-carboxylate synthase gene, VR-ACS6, of mungbean (*Vigna radiata* (L.) Wilczek) and hormonal interactions on the promoter activity in transgenic tobacco. Plant Cell Physiol 40:431–438.

Zeevaart JAD. 1978. Phytohormones and Flower Formation. In: Phytohormones and related compounds: a comprehensive treatise volume II – Phytohormones and the Development of higer plants, Letham DS, Goodwin PB, Higgins TJV, eds. City:Amsterdam. Elsevier Publisher, pp 291–324.

Zhou L, Jang JC, Jones TL, Sheen J. 1998. Glucose and ethylene signal transduction crosstalk revealed by an Arabidopsis glucose-insensitive mutant. Proc Natl Acad Sci USA 95:10294–10299.

Zhu CH, Gan LJ, Shen ZG, Xia K. 2006. Interactions between jasmonates and ethylene in the regulation of root hair development in Arabidopsis. J Exp Bot 57:1299–1308.