Ethylene regulates auxin-mediated root gravitropic machinery and controls root angle in cereal crops

Xiuzhen Kong[1,2,#], Yali Xiong[1,#], Xiaoyun Song[1,#], Samuel Wadey[3], Suhang Yu[1], Jinliang Rao[1], Aneesh Lale[3], Marco Lombardi[3], Riccardo Fusi[3], Rahul Bhosale[3,4,*], and Guoqiang Huang[1,*]

[1] *Joint International Research Laboratory of Metabolic & Developmental Sciences, State Key Laboratory of Hybrid Rice, SJTU-University of Adelaide Joint Centre for Agriculture and Health, School of Life Sciences and Biotechnology, Shanghai Jiao Tong University, Shanghai, China*

[2] *Shanghai Collaborative Innovation Center of Agri-Seeds/School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai, China*

[3] *Future Food Beacon and School of Biosciences, University of Nottingham, LE12 5RD, UK*

[4] *International Crops Research Institute for the Semi Arid Tropics, Patancheru, Hyderabad, India*

[#] These authors contribute equally

*Corresponding authors: huang19880901@sjtu.edu.cn (G.H.) or rahul.bhosale@nottingham.ac.uk (R.B.)

Short Title: Ethylene-auxin cascade regulates root angle

The authors responsible for distribution of materials integral to the findings presented in the article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/General-Instructions) are Guoqiang Huang (huang19880901@sjtu.edu.cn) and Rahul Bhosale (rahul.bhosale@nottingham.ac.uk).

One-sentence summary: Ethylene regulates root angle in rice and maize by modulating auxin biosynthesis.

Abstract

Root angle is a critical factor in optimising the acquisition of essential resources from different soil depths. The regulation of root angle relies on the auxin-mediated root gravitropism machinery. While the influence of ethylene on auxin levels is known, its specific role in governing root gravitropism and angle remains uncertain, particularly when Arabidopsis (*Arabidopsis thaliana*) core ethylene signaling mutants show no gravitropic defects. Our research, focusing on rice (*Oryza sativa* L.) and maize (*Zea mays*), clearly reveals the involvement of ethylene in root angle regulation in cereal crops through the modulation of auxin biosynthesis and the root gravitropism machinery. We elucidated the molecular components by which ethylene exerts its regulatory effect on auxin biosynthesis to control root gravitropism machinery. The ethylene-insensitive mutants *ethylene insensitive2* (*osein2*) and *ethylene insensitive like1* (*oseil1*)*,* exhibited substantially shallower crown root angle compared to the wild type. Gravitropism assays revealed reduced root gravitropic response in these mutants. Hormone profiling analysis confirmed decreased auxin levels in the root tips of the *osein2* mutant, and exogenous auxin (NAA) application rescued root gravitropism in both ethylene-insensitive mutants. Additionally, the auxin-biosynthetic mutant *mao hu zi10* (*mhz10*)/*tryptophan aminotransferase2* (*ostar2*) showed impaired gravitropic response and shallow crown root angle phenotypes. Similarly, maize ethylene-insensitive mutants (*zmein2*) exhibited defective gravitropism and root angle phenotypes. In conclusion, our study highlights that ethylene controls the auxin-dependent root gravitropism machinery to regulate root angle in rice and maize, revealing a functional divergence in ethylene signaling between *Arabidopsis* and cereal crops. These findings contribute to a better understanding of root angle regulation and have implications for improving resource acquisition in agricultural systems.

Keywords: root angle; gravitropism, ethylene; auxin; cereal crops

Introduction

Root angle, also known as gravitropic setpoint angle (GSA), refers to the angle at which a root emerges relative to the gravity vector while growing away from the vertical primary root (Roychoudhry et al., 2013). This is a crucial root architectural trait that plays a key role in enabling plants to adapt to various soil environments, such as phosphate deprivation, water scarcity, and salinity (Osmont et al., 2007; Rogers and Benfey, 2015). A steep root angle can enhance drought tolerance by promoting water uptake from deep soils (Uga et al., 2013), whereas a shallow root angle can increase phosphate uptake from topsoils (Liao et al., 2001; Peret et al., 2014; Huang et al., 2018) and mitigate yield loss by staying away from salt accumulated in deep soils (Kitomi et al., 2020). Thus, a better understanding of the underlying mechanisms that control root angle can pave the way for breeding crop cultivars better adapted to abiotic stressors associated with global climate change.

To date, a multitude of genes accountable for regulating root angle have been identified in cereal crops. In rice, Rice Morphology Determinant (RMD), a type II formin (OsFH5), localizes on the surface of statoliths in root cap cells and regulates crown root angle by dampening statolith sedimentation in gravity-sensing process (Zhang et al., 2011; Huang et al., 2018); DEEPER ROOTING1 (DRO1), a plasma membrane-localized protein, appears not to affect early auxin response genes of gravitropic signaling in root meristem zone (Uga et al., 2013); AUXIN RESISTANT 1 (OsAUX1), an auxin influx carrier, affects root angle by influencing basal auxin transport in gravitropic process (Bennett et al., 1996; Giri et al., 2018); Soil-surface rooting 1 (SOR1)/MHZ2 is a RING finger E3 ubiquitin ligase, and its knockout mutants show reduced gravitropic response and soil-surface rooting phenotype (Hanzawa et al., 2013; Chen et al., 2018). In barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*), ENHANCED GRAVITROPISM1 (EGT1), an F-box and Tubby domain-containing protein, appears to control root angle by regulating cell wall stiffness (Fusi et al., 2022); *EGT2* encoding a STERILE ALPHA MOTIF (SAM) domain–containing protein is likely involved in gravitropic response by counteracting the auxin-mediated positive gravitropic signaling pathway (Kirschner et al., 2021). In maize, CBL-interacting serine/threonine-protein kinase 15 (ZmCIPK15) modulates root angle in response to external nitrogen (Schneider et al., 2022); Maize Root System Architecture3.1 (ZmRSA3.1), a member of the AUX/IAA protein family, and ZmRSA3.2, an ortholog of Arabidopsis Formin Homology (AtFH1), were found to contribute to the regulation of root angle and root depth (Ren et al., 2022). Overall, some of these genes are suggested to alter auxin transport or signaling to modulate root gravitropic response machinery, thus controlling root angle. However, in contrast to the well-established understanding of the role of auxin in model plant *Arabidopsis*, the involvement of other hormones and their interplay with auxin in regulating gravitropism in crop species remains inadequately understood, thereby impeding the advancement of dissecting the underlying mechanisms governing root angle in crops.

Ethylene, a gaseous hormone, plays crucial roles in plant growth and stress responses. Through studies conducted in the dicot model plant species *Arabidopsis*, a linear ethylene signaling pathway has been established. In order to trigger the ethylene response, ethylene needs to be perceived by five ethylene receptors, namely ETHYLENE RESPONSE 1 (ETR1), ETHYLENE RESPONSE SENSOR 1 (ERS1), ETR2, ERS2, and EIN4 (Ju and Chang, 2015). Subsequently, the signal is transduced by CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1) and EIN2 to activate transcriptional reprogramming (Zhao et al., 2021). Afterward, EIN3/ EIL1 family of transcription factors receive signals from upstream sources and proceed to activate downstream genes in response to external cues (Dolgikh et al., 2019). In rice, several regulators have been found, despite the primary ethylene signaling components being conserved compared to *Arabidopsis*. One such regulator is MHZ1, a rice histidine kinase (OsHK1) that physically interacts with the GAF domain of OsERS2 and in conjugation with the OsEIN2-mediated pathway to regulate ethylene-regulated root growth (Zhao et al., 2020). Another regulator, MHZ3, is an uncharacterized membrane protein localized to the endoplasmic reticulum (ER) and interacts with the Nramp-like domain of OsEIN2, which is required for the proper accumulation of OsEIN2 protein (Ma B, 2018). The protein MHZ9, consisting of a glycine-tyrosine-phenylalanine domain protein, is localized in RNA processing bodies (Huang et al., 2023). The C-terminal domain of MHZ9 interacts with OsEIN2, and the N-terminal domain directly binds to the *EIN3 BINDING F-BOX 1/2* (*OsEBF1/2)* mRNAs to inhibit translation. This inhibition allows for the accumulation of transcription factor OsEIL1, which then activates the downstream signaling (Huang et al., 2023). MHZ11 is localized to the membrane of ER and harbors acyl-hydrolyzing activity (Zhao et al., 2020). MHZ11 may decrease sterol levels, thereby interfering with receptor-OsCTR2 interactions and OsCTR2 phosphorylation for triggering ethylene signaling (Zhao et al., 2020). These discoveries are now enabling us to explore the involvement of ethylene in regulating various biological processes under both developmental and environmental contexts.

The phytohormones ethylene and auxin are key regulators of plant growth and development and their intricate interplay has been extensively studied (Muday et al., 2012). In *Arabidopsis* and rice, ethylene has been found to act upstream of auxin biosynthesis, transport and response pathways (Stepanova et al., 2005; Ruzicka et al., 2007; Stepanova et al., 2007; Swarup et al., 2007). For example, ETHYLENE RESPONSE FACTOR1 (AtERF1) directly activates the expression of *WEAK ETHYLENE INSENSITIVE2*/*ANTHRA NILATE SYNTHASE α1* (*AtWEI2*/*AtASA1*), which encodes a rate-limiting enzyme in tryptophan (Trp) biosynthesis and affects primary root elongation (Mao et al., 2016). Additionally, OsEIL1 has been shown to bind to the promoters of *MHZ10*/*OsTAR2* and *OsYUCCA8* (*OsYUC8*) to regulate ethylene response in primary roots (Qin et al., 2017; Zhou et al., 2022). In the tryptophan-dependent pathways for auxin biosynthesis, the TAA/YUC pathway dependent on indole-3-pyruvic acid (IPyA) is considered as the major route for auxin production in plants (Zhao, 2018). In this pathway, TAA converts tryptophan into IPyA (Stepanova et al., 2008), which is then converted to the final product, indole-3-acetic acid (IAA), by the rate-limiting step catalyzed by YUCs (Mashiguchi et al., 2011). Knockout mutants of genes involved in this auxin biosynthesis pathway (i.e., *AtASA1*, *AtTAA1*, *OsTAR2*, and *OsYUC8*) exhibit ethylene-insensitive phenotypes in primary root growth, and soil compaction response (Stepanova et al., 2005; Stepanova et al., 2008; Huang et al., 2022; Zhou et al., 2022). Thus, the inhibition of primary root growth by ethylene appears to be largely dependent on auxin signaling (Swarup et al., 2007; Giri et al., 2018). Therefore, it seems reasonable to assume that ethylene could also influence the auxin signaling-mediated root gravitropic machinery. However, previous studies on core ethylene-signaling mutants in *Arabidopsis* have provided distinct evidence, demonstrating that these mutants do not display any defects in gravitropism (Buer et al., 2006). Consequently, the prevailing consensus is that ethylene signaling likely does not play an important role in determining root angle in *Arabidopsis*, as well as in crop plants.

Our study has uncovered noteworthy positive function of ethylene in regulating root gravitropism and root angle, particularly in crop plants, which contradicts prevailing assumption. By investigating several rice ethylene-signaling mutants, we have observed a shallow root angle resulting from reduced auxin levels and responses in the root tips, and a consequent decrease in root gravitropism. Moreover, we found that mutants defective in auxin-biosynthesis in the root tip exhibited phenotypic defects similar to those observed in ethylene mutants, affecting both root gravitropism and angle. Notably, exogenous auxin treatment rescued these defects in both ethylene and auxin mutants, validating an interplay between the two hormones in controlling root gravitropism and root angle. The present study provides evidence that the mechanism of ethylene-mediated auxin biosynthesis in the root tip, which controls root gravitropism and root angle is conserved in maize and potentially other cereal crops. Consequently, these results highlight the functional divergence of ethylene signaling between the model plant *Arabidopsis* and cereal crops, especially in regulating root angle.

Results

Ethylene-insensitive mutants exhibit shallow root system in rice

Auxin is a crucial factor in determining root angle in *Arabidopsis* and rice (Bennett et al., 1996; Abas et al., 2006; Giri et al., 2018; Huang et al., 2018), as auxin signaling mutants show reduced root angle (Bennett et al., 1996; Okushima et al., 2005; Giri et al., 2018). Ethylene acts upstream of auxin, the precise role of ethylene in determining root angle, particularly in cereal crops such as rice, remains unknown. This lack of understanding is partly due to the fact that ethylene mutants in the model plant *Arabidopsis* have been demonstrated to exhibit no gravitropism defects (Buer et al., 2006). Our research has now confirmed these observations and further revealed that ethylene mutants do not display any primary root gravitropism defects (Supplemental Figs. S1 and S2). Additionally, the treatment with 100 nM ACC (1-aminocyclopropane-l-carboxylic acid) did not significantly affect the lateral root angle phenotype in either the wild type (WT) or any mutants (Fig. 1, A-K). To investigate whether ethylene plays any role in root angle determinant in rice, we characterized root system architecture (RSA) of ethylene-insensitive mutants (*osein2*/*mhz7* and *oseil1*/*mhz6*) and WT plants. Our findings revealed that 7-day-old seedlings of *osein2* and *oseil1* exhibited a shallow crown root angle than WT plants (Fig. 1, L-O). To further validate the phenotypic observations of the seedlings in the paper column, we analyzed the RSA of ethylene-insensitive mutants and WT using the soil monolith sampling method (Uga et al., 2013). Consistently, mature plants of *oseil1* and *osein2* revealed a larger crown root angle than WT (Supplemental Fig. S3), mimicking the results from the paper-column conditions. These observations indicate that ethylene plays distinct roles in regulating RSA in *Arabidopsis* and rice.

Ethylene-insensitive mutants exhibit impaired root gravitropism

Different root classes, such as primary, lateral and crown roots, emerge at a specific angle to build a radiating system (Roychoudhry et al., 2013). The competition between gravitropic and anti-gravitropic (AGO) mechanisms controls the GSA (Roychoudhry et al., 2013; Huang et al., 2018). To investigate whether ethylene plays a role in either of these mechanisms, we conducted gravitropic bending response assays by turning the plate 90°. We found that *osein2* and *oseil1* mutants had reduced primary and crown root gravitropism and did not respond to external ACC treatment (Fig. 2; Supplemental Fig. S4), indicating that the gravitropic response machinery of these ethylene mutants was impaired. Normal root elongation was observed in ethylene-insensitive mutants that displayed less response to external ACC treatment (Fig. 2). Notably, we observed that treatment with ethylene precursor ACC and 1-MCP (1-methylcyclopropene) enhanced and reduced crown root gravitropism in WT, respectively (Fig. 2; Supplemental Fig. S5A) . This corresponded with the development of deeper and shallower root system in ACC-treated and 1-MCP-treated plants, respectively (Supplemental Fig. S5B). These results suggest that ethylene affects the gravitropic machinery in roots and alters crown root angle, and this process necessitates operative ethylene signaling.

Auxin biosynthesis is affected in the ethylene-insensitive mutants

In numerous growth and developmental processes, ethylene exerts its effects through crosstalk with other phytohormones. Studies on rice roots have shown that auxin and abscisic acid (ABA) act downstream of ethylene (Ma et al., 2014; Yin et al., 2015; Huang et al., 2022). To investigate the involvement of auxin and/or ABA in ethylene-mediated root gravitropism and root angle phenotypes, we measured their basal levels in WT and *osein2* root tips. Our hormone profiling analysis revealed that *osein2* roots had decreased levels of auxin, but maintained normal levels of ABA compared to WT roots (Supplemental Fig. S6). This finding suggests that auxin, not ABA, plays an important role in ethylene-mediated root gravitropism under normal conditions. In support of this notion, we found that external auxin treatment fully restored the gravitropic defects observed in *osein2* and *oseil1* mutants, as well as in *osers2^d*, an ethylene-insensitive mutant (Yin et al., 2015) (Fig. 3, A and B; Supplemental Fig. S7). Furthermore, normal root growth length was observed in these ethylene-insensitive mutants (Fig. 3C; Supplemental Fig. S7). These results demonstrate that ethylene regulates auxin accumulation to modulate root gravitropic response.

When roots are exposed to gravity, auxin is redistributed to the lower side of the root tip, leading to an enhanced response that impedes cell elongation and results in root bending during gravitropism (Band et al., 2012; Yang et al., 2017). To investigate whether auxin response is affected in ethylene mutants during root gravitropism, we employed a widely used rice auxin reporter DR5-VENUS to monitor auxin gradient ratio of the lower to upper side, and also auxin distribution on the lower side of roots. Confocal imaging showed reduced auxin response in *osein2* roots compared to WT roots following a 4-hour gravity stimulation (Fig. 3, D-F), suggesting reduced auxin accumulation and thus auxin response in *osein2*. Additionally, we found that reduced auxin of *osein2* roots could be partially restored by exogenous treatment with NAA (Fig. 3, D-F), providing evidence that auxin biosynthesis is impaired in rice ethylene mutants.

Functional *MHZ10* is required for ethylene-mediated auxin biosynthesis

The ethylene signaling component *OsEIL1* has been shown to directly activate *OsYUC8* and *MHZ10* genes involved in auxin biosynthesis during ethylene-mediated inhibition of root elongation (Qin et al., 2017; Zhou et al., 2022). The transgenic lines Pro*MHZ10*::VENUS-N7 and Pro*OsYUC8*::GUS provided evidence that *MHZ10* exhibited predominant expression in cortex, quiescent centre, columella, and stele of the root, and while *OsYUC8* was mainly expressed in root apex (Supplemental Fig. S8). In order to determine the potential involvement of OsYUC8 and/or MHZ10 in the ethylene-mediated gravitropic response in roots, the expression level of *OsYUC8* and *MHZ10* in ethylene mutants were monitored. Interestingly, the expression of *MHZ10* (rather than *OsYUC8*) was reduced in ethylene-insensitive mutants (Supplemental Fig. S9), implying that MHZ10-mediated auxin biosynthesis involved in ethylene-mediated gravitropism in normal conditions. To verify this assumption, experiments were conducted using *osyuc8-2* and *mhz10-1* mutants under both control and gravistimulated conditions. The *osyuc8-2* mutant lacks any transcripts due to the T-DNA insertion (Woo et al., 2007), while *mhz10-1* harbors an A-to-G base substitution at a 41-bp position upstream of the start codon, which disrupts its binding affinity to OsEIL1 (Zhou et al., 2022). Consistently, *mhz10-1* rather than *osyuc8-2* exhibited reduced root gravitropism, phenocopying that of ethylene-insensitive mutants (Fig. 4, A-C; Supplemental Fig. S10). Additionally, auxin response during gravitropic bending response was attenuated in *mhz10-1* roots, which were crossed with DR5 reporter, compared to the WT DR5 reporter (Supplemental Fig. S11). These findings suggest that MHZ10-dependent auxin biosynthesis is required for ethylene-mediated root gravitropism under normal conditions. It is plausible that OsYUC8 may not be involved in ethylene-mediated local auxin biosynthesis during gravitropism, or other OsYUCs could have overlapping roles with OsYUC8, given there are 14 OsYUCs present in rice.

To confirm the role of MHZ10 in ethylene-mediated auxin biosynthesis, we tested the responsiveness of *mhz10-1* to exogenous auxin and ethylene treatments. Consistent with our initial hypothesis, exogenous NAA treatment rescued the gravitropic defects of *mhz10-1* (Fig. 4, D-H). Additionally, *mhz10-1* did not show any response to exogenous ACC treatment (Fig. 4, D-H), suggesting that ethylene regulates root gravitropism in a MHZ10-dependent manner. We also examined whether MHZ10 regulates RSA as like ethylene signaling mutants. Remarkably, *mhz10-1* exhibited shallow RSA in the paddy field at a mature stage, similar to that of ethylene-insensitive mutants (Supplemental Figs. S3 and S12). These results underscore the importance of ethylene-mediated auxin biosynthesis in the root tip for the formation of steep root system by modulating root gravitropism.

Conserved ethylene-auxin biosynthesis mechanism regulates root angle in maize

We investigated whether the ethylene-auxin regulatory mechanism regulating root angle in rice is also conserved in other cereal crops, such as maize. To disrupt ethylene signaling transduction in maize, we selected *ZmEIN2* as the target gene as there was no known functionally redundant gene for this gene (Gallie and Young, 2004; Zhou et al., 2019). As no mutant was available for *ZmEIN2* in public maize transposon insertion collections, we used CRISPR-Cas9 technology (Dong et al., 2018) to knockout *ZmEIN2*. We obtained three CRISPR edits leading to frameshifts in the CDS of *ZmEIN2* gene, resulting in three allelic mutants: *zmein2-1*, *zmein2-2* and *zmein2-3* with 569 bp, and 21 bp deletion, respectively (Supplemental Fig. S13A). All three allelic mutants of *ZmEIN2* exhibited reduced gravitropism (Supplemental Fig. S13, B-D), similar to what was observed in the above-mentioned rice studies. Furthermore, the gravitropic defects of *zmein2* mutants could be rescued by exogenous NAA treatment (Supplemental Fig. S13, B-D). Consistently, *zmein2-1* formed a shallow root system with less response to ACC treatment (Fig. 5), while it shaped a deep root system after auxin treatment (Fig. 5). These results suggest that the ethylene-auxin biosynthesis mediated root gravitropism pathway, which controls root angle, is conserved in rice and maize, and possibly other cereal crops.

Discussion

The orientation of roots is a key determinant of a plant's capacity to obtain nutrients and water from various layers of soil. Consequently, it is considered as a desirable trait for crop improvement and breeding. Deviations in root angle can affect the spatial distribution of roots in the soil layers, thereby influencing stress tolerance. For instance, a shallow root system can efficiently capture phosphate from the topsoil (Huang et al., 2018), whereas a steep root system facilitates access to mobile water and nitrate from deeper soil layers (Uga et al., 2013). Therefore, modifying RSA by fine-tuning root angle is an important objective for enhancing the resilience and sustainability of crops (de Dorlodot et al., 2007; Rogers and Benfey, 2015). However, the understanding of molecular mechanisms governing root angle in major crops such as rice and maize is currently limited. Our study has shown that ethylene-mediated auxin biosynthesis plays a critical role in the development of deep root systems in rice and maize (Fig. 6). Specially, our findings indicate that ethylene positively influences root gravitropism via stimulating MHZ10-mediated auxin biosynthesis (Fig. 6). Notably, our results revealed that ethylene-insensitive mutants shaped shallow RSA with diminished MHZ10-mediated auxin biosynthesis, in contrast, ethylene-sensitive mutants display deep RSA with upregulated MHZ10-mediated auxin biosynthesis (Fig. 6). This interplay between ethylene and auxin signaling pathways in regulating root angle is also conserved in maize (Fig. 5). Taken together, our findings suggest that ethylene-mediated auxin biosynthesis is essential for the appropriate root angle in rice and maize, as well as potentially other cereal crops.

Auxin plays a critical role in regulating root angle, as it operates in both gravitropic and anti-gravitropic mechanisms (Giri et al., 2018; Huang et al., 2018). While ethylene is known to act upstream of auxin, particularly in regulating root hair expansion and primary root elongation (Rahman et al., 2002; Ruzicka et al., 2007; Swarup et al., 2007), its role in controlling root angle remains unclear. In *Arabidopsis thaliana,* the role of ethylene in these mechanisms is not fully explored, possibly due to the observation that ethylene-insensitive mutants (*Atein2* and *Atetr1*) have similar or slightly better gravitropic curvature than the control plants (Buer et al., 2006). However, the utilization of ACC was shown to attenuate the gravitropic response of WT roots (Buer et al., 2006), suggesting a negative role in root gravitropism. Our research also confirmed that ethylene signaling mutants in *Arabidopsis* do not exhibit gravitropism defects as evidenced by the absence of lateral and primary root angle defects (Fig. 1, A-K; Supplemental Fig. S2). Interestingly, we observed that ACC treatment enhanced root gravitropism in rice, and ethylene-signaling mutants showed reduced gravitropism (Fig. 2; Supplemental Figs. S4 and S7). These findings suggest that the divergence of the regulatory mechanisms controlling root angle may be attributed to morphological differences between the tap-root and fibrous-root systems.

As a multifunctional hormone, the interplay of ethylene and other hormones has been extensively studied in rice (Ruzicka et al., 2007; Swarup et al., 2007; Qin et al., 2017; Huang et al., 2022). For instance, OsEIL1, an essential component of ethylene signaling, has been shown to bind to the promotors of *OsYUC8* and *MHZ10* in an ethylene-mediated response (Qin et al., 2017; Zhou et al., 2022). OsEIL1-OsYUC8 cascade was recently found to modulate root compaction response (Huang et al., 2022). In this work, mutant of *MHZ10* (rather than *OsYUC8*) showed reduced gravitropism (Fig. 4, A-C; Supplemental Fig. S10), suggesting existence of specific ethylene-auxin regulatory modules for particular growth responses. MHZ10/OsTAR2 has three homologs in rice, namely OsTAR1, OsTARL1 and OsTARL2 (Guo et al., 2020). OsTAR1 has been found to regulate grain development, and no aminotransferase activity was detected for OsTARL1 and OsTARL2 (Yoshikawa et al., 2014). Thus, it's possible that MHZ10 plays a major role in root development including root gravitropism. While, there are 14 functional YUCs, and at least 3 OsYUCs (OsYUC5, OsYUC8 and OsYUC11) were induced by ethylene in root (Qin et al., 2017). Presumably, with other OsYUCs playing redundant roles, OsYUC8 alone may not have a clear or primary role in regulating ethylene-mediated root gravitropism.

What is the relevance of ethylene in regulating root angle? The biosynthesis of ethylene is a highly regulated process that can be activated by diverse abiotic and biotic stresses (Frankowski et al., 2007; Savada et al., 2017). The interactions between ethylene and stress signals are pivotal in determining root system plasticity. It is widely accepted that steep RSA is beneficial in absorbing water from deep soil profiles (de Dorlodot et al., 2007). Considering that water deficiency induces ethylene production in rice (Apelbaum and Yang, 1981), and our research show that ethylene can enhance crown root gravitropism and root angle (Fig. 2), we can speculate that the regulation of root angle by ethylene may enable plants to develop steep root system during water stress, helping them escape drying topsoils or access water in sub-soil profiles.

ABA is suggested to act downstream of ethylene in root-ethylene response in rice (Yin et al., 2015). Its accumulation is crucial for mitigating drought stress and promoting root gravitropism in maize (Feng et al., 2022). The strong induction of *ZmDRO1* by external ABA or drought leads to a larger downward root angle and a deeper RSA (Feng et al., 2022). Consistently, our findings demonstrate that ethylene has a favorable effect on root gravitropism in both rice and maize through the stimulation of auxin biosynthesis (Fig. 3; Supplemental Fig. 6). However, in *Arabidopsis*, ABA appears to have antagonistic effects or no effects on root gravitropism, particularly in the context of hydrotropism (Dietrich et al., 2017; Miao et al., 2021). Similarly, mutants with impaired ABA signaling do not exhibit any defects in root gravitropism (Dietrich et al., 2017; Miao et al., 2021). These observations suggest that ABA assumes different functions in dicot (*Arabidopsis*) and monocot (rice and maize) plants. Therefore, it is possible that, consistent with the observation for ABA, ethylene also has different functions in regulating root gravitropism and root angle in *Arabidopsis* and rice.

In summary, our study has yielded valuable insights into the functions of the ethylene-auxin cascade that ethylene regulates auxin biosynthesis in the root tip of rice and maize. This regulation ultimately affects root gravitropism, leading to alterations in root angle, phenomenon that differs from *Arabidopsis*. These findings have the potential to contribute to the optimization of deep RSA in response to changing environmental conditions.

Materials and Methods

Plant materials and growth condition

All rice (*Oryza sativa*) and maize (*Zea mays*) plants for seed generation were cultured in paddy field of Shanghai (30°N, 121°E) and Sanya (18°N, 109°E), China, in summer and winter, respectively. The backgrounds of *osein2*/*mhz7-1* , *oseil1*/*mhz6-1*, *osers2*^{d} and *ostar2*/*mhz10-1* were in Nipponbare (Nip) (Ma et al., 2013), and *osyuc8-2* was in Hwayoung (HWY) (Qin et al., 2017). Seeds were germinated on moist sterilized filter paper for 4 days in dark at 28°C in a growth chamber with 70% relative humidity. Seeds of Arabidopsis (*Arabidopsis thaliana*) ecotype Col-0 (wildtype) and ethylene signaling mutants (*eto1-1*, *ctr1-1*, *ein2-1* and *ein3-1*) were surface sterilized with 70% (v/v) ethanol for 1 min, and 20% (v/v) bleach with 0.01% (v/v) triton X-100 for 8 min, followed by five washes with sterile water and stratified at 4 °C for 48 h in dark. Germinated seeds were grown on 0.5 MS (Murashige and Skoog) plates supplemented with 1% phytagel, at pH 5.8 in growth room (22 ºC, 16h day/8h night, 100-120 μmol/m^{2}/s).

Maize mutant generation

The knockout target was chosen based on its high specificity in relation to the KN5585 genome (http://crispr.hzau.edu.cn/CRISPR2/). The knockout vector was designed and its sequence verified using the *Pcxb053* backbone (Liu et al., 2020). Subsequently, the plasmid was introduced into *Agrobacterium tumefaciens* strain EHA105 through electroporation. The transformation experiments were carried out by Wimi Biotechnology (http://www.wimibio.com/). The process of Agrobacterium-mediated maize transformation has been previously described (Liu et al., 2020). Maize immature embryos measuring 1.5-1.8 mm were extracted from ears collected 10 days after pollination and placed in 2.0-mL tubes containing 1.8 mL of inoculation medium. These embryos were then exposed to an Agrobacterium suspension (consisting of inoculation medium with 200 mM of acetosyringone and Agrobacterium cells) for a duration of 5 minutes, after which they were transferred onto cocultivation medium. Excess liquid was eliminated using pipettes. The immature embryos were positioned with the scutellum side facing upwards on the medium and incubated in darkness at a temperature of 23°C for a period of 48 to 72 h for cocultivation. Following cocultivation, immature embryos were subsequently transferred to a resting medium and cultured for a period of 5-7 days. The resulting calluses were then transferred to a selection medium containing glufosinate-ammonium at a concentration of 10 mg/L. These calluses were incubated in darkness at a temperature of 28 °C for a duration of 2 weeks, after which they were transferred to fresh selection medium for an additional 2 weeks. The calluses that exhibited resistance were then placed on a regeneration medium and incubated under a light intensity of 5000 lux at a temperature of 25°C for a period of 14 to 21 days. The regenerated shoots were subsequently transferred to a rooting medium and exposed to a light intensity of 5000 lux at a temperature of 25 °C for a duration of 14 days. Prior to planting the plantlets in a greenhouse, leaves were sampled for PCR analysis.

Root System Observation

To observe root system of Nip, *osein2*, *oseil1* and *mhz10-1* in the soil, we used a modified trench method (Uga et al., 2013). Plants were grown in paddy field with well irrigation in Shanghai, China, in the summer of 2020 and 2021. After 100 days of planting, the whole soil monolith (20 cm x 20 cm x 5 cm) was picked up from the soil. Then, the soil monolith was carefully fixed on a board (with 10-cm nails). Finally, the root systems were gently washed out with flowing water. The GSA was measured at the emergence site of crown roots. For root system observation on a paper column, the seeds were germinated in darkness for 4 days, and then the germinated seeds were transferred to a paper column wrapped in aluminum foil for an additional 7 days. The GSA was measured at the emergence site of crown root.

NAA and ACC treatments

The rice seeds were germinated under constant darkness at 28 °C for 3 days and then transferred into 96-well plates without bottom floating on water with 18-h lightness and 6-h darkness at 28 °C. For ACC treatment, germinated seedlings were transferred onto the surface of 1% agar with or without addition of 100 μM ACC for 2 h at vertical conditions, and then were placed horizontally for 24 h. Photographs were taken automatically every 1 h with a digital camera (Canon) under the control of ZoomBrower EX software (Canon). The primary root curvature was defined as the angle formed between the growing direction of the apex and the horizontal base line and was measured on the digital images using ImageJ (http://rsb.info.nih.gov/ij/). The maize seeds were germinated for 2 days under darkness at 30 °C, and the germinated seeds were transferred into a paper column containing 100 μM ACC or 100 nM NAA. After 4-day growth, the root system was imaged and analyzed. GSA of crown roots was measured at the insertion site between the crown root and primary root with reference to the gravity vector. Arabidopsis wildtype and ethylene signaling mutants were grown on 0.5 MS 1% agar plates initially for 3 days, during which no lateral roots were visible. Equally germinated seedlings were transferred to fresh 0.5 MS 1% agar plates supplemented with 0 and 100 nM ACC and grown for 6 days. Plates were imaged using Nikon D5100 camera and the lateral root angle (measured at the insertion site between lateral root and primary root) was quantified using the angle tool in ImageJ. For Arabidopsis gravitropic assay, the seeds were grown on 0.5 MS 1% phytagel plates for 3 days in darkness, kept at 4 °C, then the germinated seeds were cultured vertically for 4 days with 12-h lightness/12-h darkness prior to 8-h gravistimulation. The plates were imaged by camera, and then analyzed by ImgaeJ.

Hormone measurements

Rice seeds were germinated for 4 days in darkness kept at 28 °C, and then the germinated seeds were transferred on plates at 28 °C in 16-h lightness/8-h darkness period. After 7-days of growth, the seedlings were transferrd on new 1% agar plates for 24 hours. The seedlings were oriented horizontally by rotating the plates counterclockwise at a 90-degree angle for a duration of 6 h, and 1-cm crown root tips were harvested and stored in the liquid nitrogen. Hormone measurements were performed and analyzed at MetWare Company (https://www.metware.cn/).

Gravitropism Analysis

The rice/maize seeds were germinated under constant dark at 28 °C for 3 days and then transferred into 96-well plates without bottom floating on water with 18-h light and 6-h dark at 28 °C. The 3-day-old seedlings were placed on 1% agar in normal condition for 1 h, and then were placed horizontally by rotating the plates counterclockwise. Photographs were taken automatically every 20 min by a digital camera (Canon) under the control of ZoomBrower EX software (Canon). The primary root curvature was defined as the angle formed between the growing direction of the apex and the horizontal base line and was measured on the digital images using ImageJ (http://rsb.info.nih.gov/ij/).

Confocal Imaging

DR5-VENUS reporter seeds were germinated in dark for 4 days and then transferred onto agar surface to grow for another 5 days under 28 °C. The roots were observed via Leica Laser Scan Microscope (SP5) using an excitation wavelength of 488 nm, intensity less than 10, and collection bandwidth of 500-550 nm, and gain around 800. Confocal images were analysed via ImageJ (https://imagej.nih.gov/ij/).

Accession Numbers

Sequence data from this article can be found in the GenBank/EMBL data libraries under the following accession numbers: *OsYUC8* (Os03g0162000); *OsEIN2*/*MHZ7* (Os07g0155600); *OsEIL1*/*MZH6* (Os03g0324200); *OsERS2* (LOC_Os05g06320); *OsTAR2*/*MHZ10* (Os01g0169800). *AtCTR1* (AT5G03730); *AtEIN2* (AT5G03280); *AtEIN3* (AT3G20770); *AtETO1* (AT3G51770); and *ZmEIN2* (GRMZM2G068217).

Supplemental Data

Supplemental Figure S1. Genotyping verification of the mutants used in this study.

Supplemental Figure S2. Ethylene insensitive mutants exhibit no obvious changes in primary root (PR) angle in altered gravitropic conditions in *Arabidopsis thaliana*.

Supplemental Figure S3. Ethylene insensitive mutants exhibit shallow root system.

Supplemental Figure S4. Ethylene insensitive mutants exhibit reduced gravitropism.

Supplemental Figure S5. Roots impaired in ethylene signaling show reduce gravitropism and shallow RSA.

Supplemental Figure S6. Auxin accumulation is reduced in *osein2.*

Supplemental Figure S7. Auxin treatment restores the gravitropic responses of ethylene receptor mutant (*osers2^{d}*).

Supplemental Figure S8. Expression pattern of *MHZ10* and *OsYUC8* in primary root.

Supplemental Figure S9. *MHZ10* expression is reduced in ethylene-insensitive mutants.

Supplemental Figure S10. Auxin biosynthesis mutant (*osyuc8-2*) shows similar gravitropic responses to WT with/without ACC treatment.

Supplemental Figure S11. Auxin response is disrupted in the *mhz10-1* mutant.

Supplemental Figure S12. *mhz10-1* mutant exhibits shallow root system.

Supplemental Figure S13. Knockout mutants of *ZmEIN2* exhibit reduced gravitropism.

Supplemental Table S1. Primers used in this study

Funding information

This work was supported by the National Natural Science Foundation of China (32101651 and 32130006), and Shanghai Rising Star Program (22QA1404200), and the China Innovative Research Team, Ministry of Education, the Programme of Introducing Talents of Discipline to Universities (111 Project, B14016). R. Bhosale acknowledges support from the Future Food Beacon Nottingham Research and BBSRC Discovery (BB/S011102/1) Fellowships and the BBSRC New Investigator Research Grant (BB/X014843/1). S. Wadey acknowledges BBSRC DTP studentship. A. Lale acknowledges the Nottingham Future Food Beacon and Puri Fellowship.

Acknowledgments

We thank Prof. Jinsong Zhang for kindly providing *mhz10-1/ostar2* and *osers2^{d}* seeds. Especially, we appreciate respected Prof. Dabing Zhang for his helpful comments in manuscript, who passed away on June 22, 2023.

Author contributions

X.K., R.B., and G.H. designed the project; X.K., Y.X., X.S., S.Y., S.W., and J.R. performed all the assays; X.K., Y.X., X.S., S.Y., S.W., A.L., M.L., R.F., and J.R. analyzed and discussed the data; G.H., R.B., and X.K. wrote the manuscript.

Figure 1. Ethylene-insensitive mutants exhibit shallow root system in rice. (**A**-**E**) Representative images of root systems of wildtype (Col-0), *ein2-1*, *ein3-1*, *eto1-1*, and *ctr1-1* (from left to right) without 100 nM ACC treatment after 8 days of growth. Scale bars = 1 cm. (**F**-**J**) Representative images of root systems of wildtype (Col-0), *ein2-1*, *ein3-1*, *eto1-1*, and *ctr1-1* (from left to right) with 100 nM ACC treatment after 8 days of growth. Scale bars = 1 cm. (**K**) GSA analysis (absolute angle of emergence) of Col-0, *eto1-1*, *ctr1-1*, *ein2-1*, and *ein3-1* with/without 100 nM ACC treatment. *n* = 11. The horizontal bar within box represents median. The top and bottom of the box

represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots. (**L**-**N**) Representative root systems of Nip (wild type) (**L**), *oseil1* (**M**) and *osein2* (**N**) after 8-day growth. Scale bars = 1 cm. (**O**) GSA analysis of Nip, *oseil1* and *osein2* after 8-day growth. $^{**}P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 10$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots.

Figure 2. Ethylene insensitive mutants exhibit reduced gravitropism. (**A**-**B**) Representative images showing the root gravitropic bending responses of crown roots of Nip and *oseil1* and *osein2* mutants without (A) and with (B) 100 µM ACC treatment. Scale bars = 1 cm. (**C**) Measured root tip angle of crown roots of Nip (wild type) and *oseil1* and *osein2* mutants with/without ACC treatment after 8-h gravistimulation. Different letters in the box plot indicate significant differences, $P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 10$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots. (**D**) Measured elongation length of crown roots of Nip and *oseil1* and *osein2* mutants with/without ACC treatment after 8-h gravistimulation. $^{**}P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 10$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots.

Figure 3. Auxin acts downstream of ethylene in regulating root gravitropism. (**A**) Representative images of Nip (WT) and *oseil1* and *osein2* mutants after 8-h gravistimulations without and with 10 nM NAA treatment. Scale bars = 1 cm. (**B**) Measured tip angles of 7-day-old primary roots of Nip and *oseil1* and *osein2* mutants after 8-h gravistimulation. $n = 11$. $^{**}P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots. (**C**) Measured elongation length of primary roots of Nip and *oseil1* and *osein2* mutants with/without NAA treatment after 8-h gravistimulation. $n = 11$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots. (**D**) Representative confocal images showing DR5-VENUS i.e., auxin response gradient after 4-h gravistimulation in the 7-day growth seedlings of Nip and *osein2* with/without 10 nM NAA treatment. Scale bars = 100 µm. White arrows represent the direction of gravity. (**E**) Box plot showing the quantitative intensity of fluorescence signals in the region of interest (ROI) of the lower side of early elongation zone. Different letters indicate significant differences, $P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 11$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots. (**F**) Box plot showing the fluorescence intensity ratio of lower side to upper side in the region of interest (ROI) of early elongation zone. Different letters indicate significant differences, $P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 11$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots.

Figure 4. MHZ10-mediated auxin biosynthesis acts downstream of ethylene in regulating root gravitropism. (**A**-**B**) Representative images of gravitropic responses of primary roots in Nip (wild type) (A) and *mhz10-1* (B). Scale bars = 1 cm. (**C**) Tip angle analysis of 7-day growth primary

root of Nip and *mhz10-1*. Error bars are ± SD, $n = 11$. **indicates significant differences, $P < 0.01$ from students' *t*-test. (**D-G**) Representative root images of 7-day growth seedlings after 8-h gravistimulation of Nip under control treatment and *mhz10-1* mutant under control, 100 µM ACC, and 10 nM NAA treatments. Scale bars = 1 cm. (**H**) Measured tip angles of D-G. Different letters indicate significant differences, $P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 10$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots.

Figure 5. Maize ethylene insensitive mutant also exhibits shallow root system. (**A**) Representative images of 7-day growth root systems of WT and *zmein2-1* under control treatment (DMSO, Dimethyl sulfoxide) and *zmein2-1* under 100 µM ACC and 100 nM NAA treatments. Scale bars = 1 cm. (**B**) Measured GSA of WT and *zmein2-1* grown under control treatment and *zmein2-1* with 100 µM ACC and 100 nM NAA treatments after 7-day growth. Different letters indicate significant differences, $P < 0.01$ from one-way analysis of variance (ANOVA) with Tukey's multiple comparison test, $n = 10$. The horizontal bar within box represents median. The top and bottom of the box represent the 0.75 and 0.25 percentiles, respectively. The upper and lower whiskers extend to 1.5 times the interquartile range, with outliers shown as black dots.

Figure 6. A proposed model for how endogenous ethylene regulates RSA. During the developmental process of root system, endogenous ethylene was perceived by ethylene receptors, and which fail to activate CTR2, reducing its repression on OsEIN2. OsEIL1 is directly responsible for activating the expression of *MHZ10*, an auxin-biosynthesis gene, which is necessary for the formation of deep RSA via enhancing gravitropism. Ethylene-insensitive mutants exhibit shallow root system ascribed to reduced gravitropism.

References

Abas L, Benjamins R, Malenica N, Paciorek T, Wisniewska 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

Apelbaum A, Yang SF (1981) Biosynthesis of stress ethylene induced by water deficit. Plant Physiol **68:** 594-596

Band LR, Wells DM, Larrieu A, Sun JY, Middleton AM, French AP, Brunoud G, Sato EM, Wilson MH, Peret B, Oliva M, Swarup R, Sairanen I, Parry G, Ljung K, Beeckman T, Garibaldi JM, Estelle M, Owen MR, Vissenberg K, Hodgman TC, Pridmore TP, King JR, Vernoux T, Bennett MJ (2012) Root gravitropism is regulated by a transient lateral auxin gradient controlled by a tipping-point mechanism. Proc Natl Acad Sci U S A **109:** 4668-4673

Bennett MJ, Marchant A, Green HG, May ST, Ward SP, Millner PA, Walker AR, Schulz B, Feldmann KA (1996) Arabidopsis AUX1 gene: a permease-like regulator of root gravitropism. Science **273:** 948-950

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

Chen H, Ma B, Zhou Y, He SJ, Tang SY, Lu X, Xie Q, Chen SY, Zhang JS (2018) E3 ubiquitin ligase SOR1 regulates ethylene response in rice root by modulating stability of Aux/IAA protein. Proc Natl Acad Sci U S A **115:** 4513-4518

de Dorlodot S, Forster B, Pages L, Price A, Tuberosa R, Draye X (2007) Root system architecture: opportunities and constraints for genetic improvement of crops. Trends Plant Sci **12:** 474-481

Dietrich D, Pang L, Kobayashi A, Fozard JA, Boudolf V, Bhosale R, Antoni R, Nguyen T, Hiratsuka S, Fujii N, Miyazawa Y, Bae TW, Wells DM, Owen MR, Band LR, Dyson RJ, Jensen OE, King JR, Tracy SR, Sturrock CJ, Mooney SJ, Roberts JA, Bhalerao RP, Dinneny JR, Rodriguez PL, Nagatani A, Hosokawa Y, Baskin TI, Pridmore TP, De Veylder L, Takahashi H, Bennett MJ (2017) Root hydrotropism is controlled via a cortex-specific growth mechanism. Nat Plants **3:** 1-8

Dolgikh VA, Pukhovaya EM, Zemlyanskaya EV (2019) Shaping Ethylene Response: The Role of EIN3/EIL1 Transcription Factors. Front Plant Sci **10:** 1030

Dong L, Li L, Liu C, Liu C, Geng S, Li X, Huang C, Mao L, Chen S, Xie C (2018) Genome Editing and Double-Fluorescence Proteins Enable Robust Maternal Haploid Induction and Identification in Maize. Mol Plant **11:** 1214-1217

Feng XJ, Jia L, Cai YT, Guan HR, Zheng D, Zhang WX, Xiong H, Zhou HM, Wen Y, Hu Y, Zhang XM, Wang QJ, Wu FK, Xu J, Lu YL (2022) ABA-inducible improves adaptation of maize to water deficiency. Plant Biotechnol J **20:** 2077-2088

Frankowski K, Kesy J, Kopcewicz J (2007) Regulation of ethylene biosynthesis in plants. Postepy Biochem **53:** 66-73

Fusi R, Rosignoli S, Lou H, Sangiorgi G, Bovina R, Pattem JK, Borkar AN, Lombardi M, Forestan C, Milner SG, Davis JL, Lale A, Kirschner GK, Swarup R, Tassinari A, Pandey BK, York LM, Atkinson BS, Sturrock CJ, Mooney SJ, Hochholdinger F, Tucker MR, Himmelbach A, Stein N, Mascher M, Nagel KA, De Gara L, Simmonds J, Uauy C, Tuberosa R, Lynch JP, Yakubov GE, Bennett MJ, Bhosale R, Salvi S (2022) Root angle is controlled by EGT1 in cereal crops employing an antigravitropic mechanism. Proc Natl Acad Sci U S A **119:** e2201350119

Gallie DR, Young TE (2004) The ethylene biosynthetic and perception machinery is differentially expressed during endosperm and embryo development in maize. Mol Genet Genomics **271:** 267-281

Giri J, Bhosale R, Huang G, Pandey BK, Parker H, Zappala S, Yang J, Dievart A, Bureau C, Ljung K, Price A, Rose T, Larrieu A, Mairhofer S, Sturrock CJ, White P, Dupuy L, Hawkesford M, Perin C, Liang W, Peret B, Hodgman CT, Lynch J, Wissuwa M, Zhang D, Pridmore T, Mooney SJ, Guiderdoni E, Swarup R, Bennett MJ (2018) Rice auxin influx carrier OsAUX1 facilitates root hair elongation in response to low external phosphate. Nat Commun **9:** 1408

Guo T, Chen K, Dong NQ, Ye WW, Shan JX, Lin HX (2020) Tillering and small grain 1 dominates the tryptophan aminotransferase family required for local auxin biosynthesis in rice. J Integr Plant Biol **62:** 581-600

Hanzawa E, Sasaki K, Nagai S, Obara M, Fukuta Y, Uga Y, Miyao A, Hirochika H, Higashitani A, Maekawa M, Sato T (2013) Isolation of a novel mutant gene for soil-surface rooting in rice (Oryza sativa L.). Rice (N Y) **6:** 30

Huang G, Kilic A, Karady M, Zhang J, Mehra P, Song X, Sturrock CJ, Zhu W, Qin H, Hartman S, Schneider HM, Bhosale R, Dodd IC, Sharp RE, Huang R, Mooney SJ, Liang W, Bennett MJ, Zhang D, Pandey BK (2022) Ethylene inhibits rice root elongation in compacted soil via ABA- and auxin-mediated mechanisms. Proc Natl Acad Sci U S A **119:** e2201072119

Huang G, Liang W, Sturrock CJ, Pandey BK, Giri J, Mairhofer S, Wang D, Muller L, Tan H, York LM, Yang J, Song Y, Kim YJ, Qiao Y, Xu J, Kepinski S, Bennett MJ, Zhang D (2018) Rice actin binding protein RMD controls crown root angle in response to external phosphate. Nat Commun **9:** 2346

Huang YH, Han JQ, Ma B, Cao WQ, Li XK, Xiong Q, Zhao H, Zhao R, Zhang X, Zhou Y, Wei W, Tao JJ, Zhang WK, Qian WF, Chen SY, Yang C, Yin CC, Zhang JS (2023) A translational regulator MHZ9 modulates ethylene signaling in rice. Nat Commun **14:** 4674

Ju C, Chang C (2015) Mechanistic Insights in Ethylene Perception and Signal Transduction. Plant Physiol **169:** 85-95

Kirschner GK, Rosignoli S, Guo L, Vardanega I, Imani J, Altmuller J, Milner SG, Balzano R, Nagel KA, Pflugfelder D, Forestan C, Bovina R, Koller R, Stocker TG, Mascher M, Simmonds J, Uauy C, Schoof H, Tuberosa R, Salvi S, Hochholdinger F (2021) ENHANCED GRAVITROPISM 2 encodes a STERILE ALPHA MOTIF-containing protein that controls root growth angle in barley and wheat. Proc Natl Acad Sci U S A **118:** e2101526118

Kitomi Y, Hanzawa E, Kuya N, Inoue H, Hara N, Kawai S, Kanno N, Endo M, Sugimoto K, Yamazaki T, Sakamoto S, Sentoku N, Wu J, Kanno H, Mitsuda N, Toriyama K, Sato T, Uga Y (2020) Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields. Proc Natl Acad Sci U S A **117:** 21242-21250

Liao H, Rubio G, Yan X, Cao A, Brown KM, Lynch JP (2001) Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil **232:** 69-79

Liu HJ, Jian L, Xu J, Zhang Q, Zhang M, Jin M, Peng Y, Yan J, Han B, Liu J (2020) High-Throughput CRISPR/Cas9 Mutagenesis Streamlines Trait Gene Identification in Maize. Plant Cell **32:** 1397-1413

Ma B, He SJ, Duan KX, Yin CC, Chen H, Yang C, Xiong Q, Song QX, Lu X, Chen HW, Zhang WK, Lu TG, Chen SY, Zhang JS (2013) Identification of Rice Ethylene-Response Mutants and Characterization of in Distinct Ethylene Response and Yield Trait Regulation. Mol Plant **6:** 1830-1848

Ma B, Yin CC, He SJ, Lu X, Zhang WK, Lu TG, Chen SY, Zhang JS (2014) Ethylene-induced inhibition of root growth requires abscisic acid function in rice (Oryza sativa L.) seedlings. PLoS Genet **10:** e1004701

Ma B ZY, Chen H, He SJ, Huang YH, Zhao H, Lu X, Zhang WK, Pang JH, Chen SY, Zhang JS (2018) Membrane protein MHZ3 stabilizes OsEIN2 in rice by interacting with its Nramp-dlike domain. Proc Natl Acad Sci U S A **115:** 2520-2525

Mao JL, Miao ZQ, Wang Z, Yu LH, Cai XT, Xiang CB (2016) Arabidopsis ERF1 Mediates Cross-Talk between Ethylene and Auxin Biosynthesis during Primary Root Elongation by Regulating ASA1 Expression. Plos Genet **12:** e1005760

Mashiguchi K, Tanaka K, Sakai T, Sugawara S, Kawaide H, Natsume M, Hanada A, Yaeno T, Shirasu K, Yao H, McSteen P, Zhao Y, Hayashi K, Kamiya Y, Kasahara H (2011) The main auxin biosynthesis pathway in Arabidopsis. Proc Natl Acad Sci U S A **108:** 18512-18517

Miao R, Yuan W, Wang Y, Garcia-Maquilon I, Dang XL, Li Y, Zhang JH, Zhu YY, Rodriguez PL, Xu WF (2021) Low ABA concentration promotes root growth and hydrotropism through relief of ABA INSENSITIVE 1-mediated inhibition of plasma membrane H-ATPase 2. Sci Adv **7:** eabd4113

Muday GK, Rahman A, Binder BM (2012) Auxin and ethylene: collaborators or competitors? Trends Plant Sci **17:** 181-195

Okushima Y, Overvoorde PJ, Arima K, Alonso JM, Chan A, Chang C, Ecker JR, Hughes B, Lui A, Nguyen D, Onodera C, Quach H, Smith A, Yu G, Theologis A (2005) Functional genomic analysis of the AUXIN RESPONSE FACTOR gene family members in Arabidopsis thaliana: unique and overlapping functions of ARF7 and ARF19. Plant Cell **17:** 444-463

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol **58:** 93-113

Peret B, Desnos T, Jost R, Kanno S, Berkowitz O, Nussaume L (2014) Root architecture responses: in search of phosphate. Plant Physiol **166:** 1713-1723

Qin H, Zhang Z, Wang J, Chen X, Wei P, Huang R (2017) The activation of OsEIL1 on YUC8 transcription and auxin biosynthesis is required for ethylene-inhibited root elongation in rice early seedling development. PLoS Genet **13:** e1006955

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

Ren W, Zhao L, Liang J, Wang L, Chen L, Li P, Liu Z, Li X, Zhang Z, Li J, He K, Zhao Z, Ali F, Mi G, Yan J, Zhang F, Chen F, Yuan L, Pan Q (2022) Genome-wide dissection of changes in maize root system architecture during modern breeding. Nat Plants **8:** 1408-1422

Rogers ED, Benfey PN (2015) Regulation of plant root system architecture: implications for crop advancement. Curr Opin Biotechnol **32:** 93-98

Roychoudhry S, Del Bianco M, Kieffer M, Kepinski S (2013) Auxin controls gravitropic setpoint angle in higher plant lateral branches. Curr Biol **23:** 1497-1504

Ruzicka K, Ljung K, Vanneste S, Podhorska R, Beeckman T, Friml J, Benkova E (2007) Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. Plant Cell **19:** 2197-2212

Savada RP, Ozga JA, Jayasinghege CPA, Waduthanthri KD, Reinecke DM (2017) Heat stress differentially modifies ethylene biosynthesis and signaling in pea floral and fruit tissues. Plant Mol Biol **95:** 313-331

Schneider HM, Lor VSN, Hanlon MT, Perkins A, Kaeppler SM, Borkar AN, Bhosale R, Zhang X, Rodriguez J, Bucksch A, Bennett MJ, Brown KM, Lynch JP (2022) Root angle in maize influences nitrogen capture and is regulated by calcineurin B-like protein (CBL)-interacting serine/threonine-protein kinase 15 (ZmCIPK15). Plant Cell Environ **45:** 837-853

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

Stepanova AN, Robertson-Hoyt J, Yun J, Benavente LM, Xie DY, DoleZal K, Schlereth A, Jurgens G, Alonso JM (2008) TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. Cell **133:** 177-191

Stepanova AN, Yun J, Likhacheva AV, Alonso JM (2007) Multilevel interactions between ethylene and auxin in Arabidopsis roots. Plant Cell **19:** 2169-2185

Swarup R, Perry P, Hagenbeek D, Van Der Straeten D, Beemster GT, Sandberg G, Bhalerao R, Ljung K, Bennett MJ (2007) Ethylene upregulates auxin biosynthesis in Arabidopsis seedlings to enhance inhibition of root cell elongation. Plant Cell **19:** 2186-2196

Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K, Kanno N, Inoue H, Takehisa H, Motoyama R, Nagamura Y, Wu J, Matsumoto T, Takai T, Okuno K, Yano M (2013) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat Genet **45:** 1097-1102

Woo YM, Park HJ, Su'udi M, Yang JI, Park JJ, Back K, Park YM, An G (2007) Constitutively wilted 1, a member of the rice YUCCA gene family, is required for maintaining water homeostasis and an appropriate root to shoot ratio. Plant Mol Biol **65:** 125-136

Yang J, Yuan Z, Meng Q, Huang G, Perin C, Bureau C, Meunier AC, Ingouff M, Bennett MJ, Liang W, Zhang D (2017) Dynamic Regulation of Auxin Response during Rice Development Revealed by Newly Established Hormone Biosensor Markers. Front Plant Sci **8:** 256

Yin CC, Ma B, Collinge DP, Pogson BJ, He SJ, Xiong Q, Duan KX, Chen H, Yang C, Lu X, Wang YQ, Zhang WK, Chu CC, Sun XH, Fang S, Chu JF, Lu TG, Chen SY, Zhang JS (2015) Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-mediated abscisic acid pathway. Plant Cell **27:** 1061-1081

Yoshikawa T, Ito M, Sumikura T, Nakayama A, Nishimura T, Kitano H, Yamaguchi I, Koshiba T, Hibara KI, Nagato Y, Itoh JI (2014) The rice FISH BONE gene encodes a tryptophan aminotransferase, which affects pleiotropic auxin-related processes. Plant J **78:** 927-936

Zhang Z, Zhang Y, Tan H, Wang Y, Li G, Liang W, Yuan Z, Hu J, Ren H, Zhang D (2011) RICE MORPHOLOGY DETERMINANT encodes the type II formin FH5 and regulates rice morphogenesis. Plant Cell **23:** 681-700

Zhao H, Duan KX, Ma B, Yin CC, Zhang JS (2020) Histidine kinase MHZ1/OsHK1 interacts with ethylene receptors to regulate root growth in rice. Nature Communications **11**

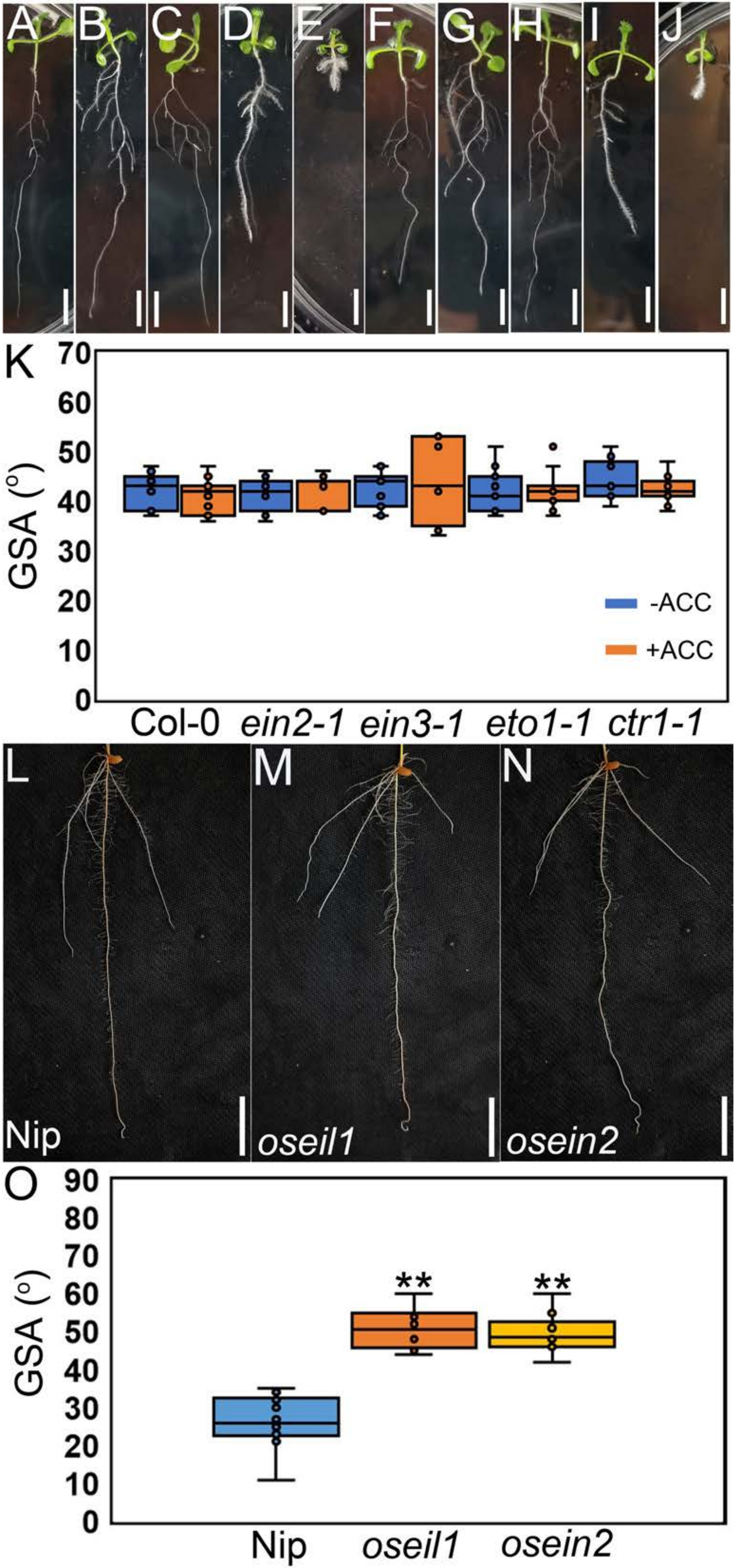
Zhao H, Ma B, Duan KX, Li XK, Zhang JS (2020) The GDSL Lipase MHZ11 Modulates Ethylene Signaling in Rice Roots. The Plant Cell **32:** tpc.00840.02019

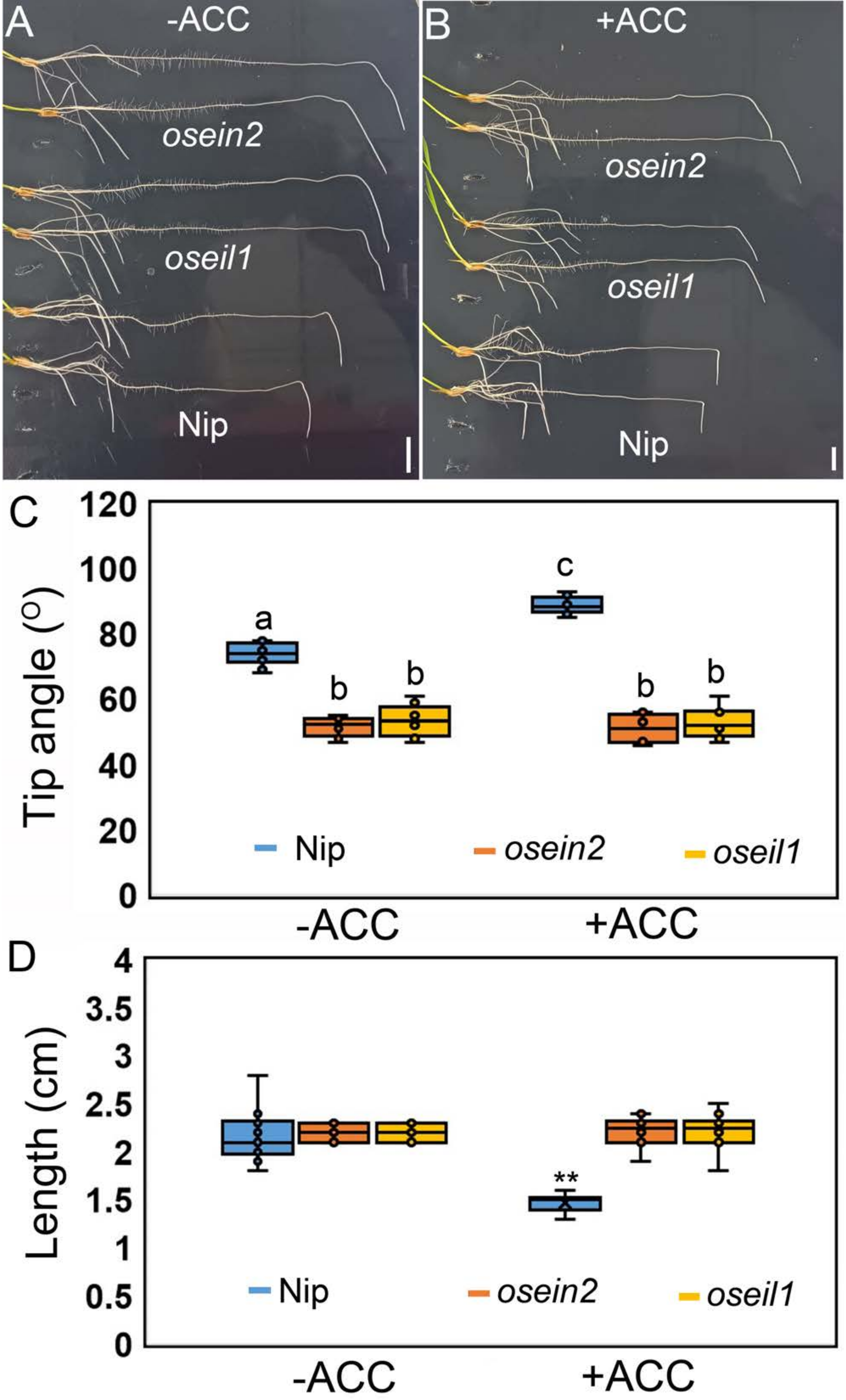
Zhao H, Yin CC, Ma B, Chen SY, Zhang JS (2021) Ethylene signaling in rice and Arabidopsis: New regulators and mechanisms. J Integr Plant Biol **63:** 102-125

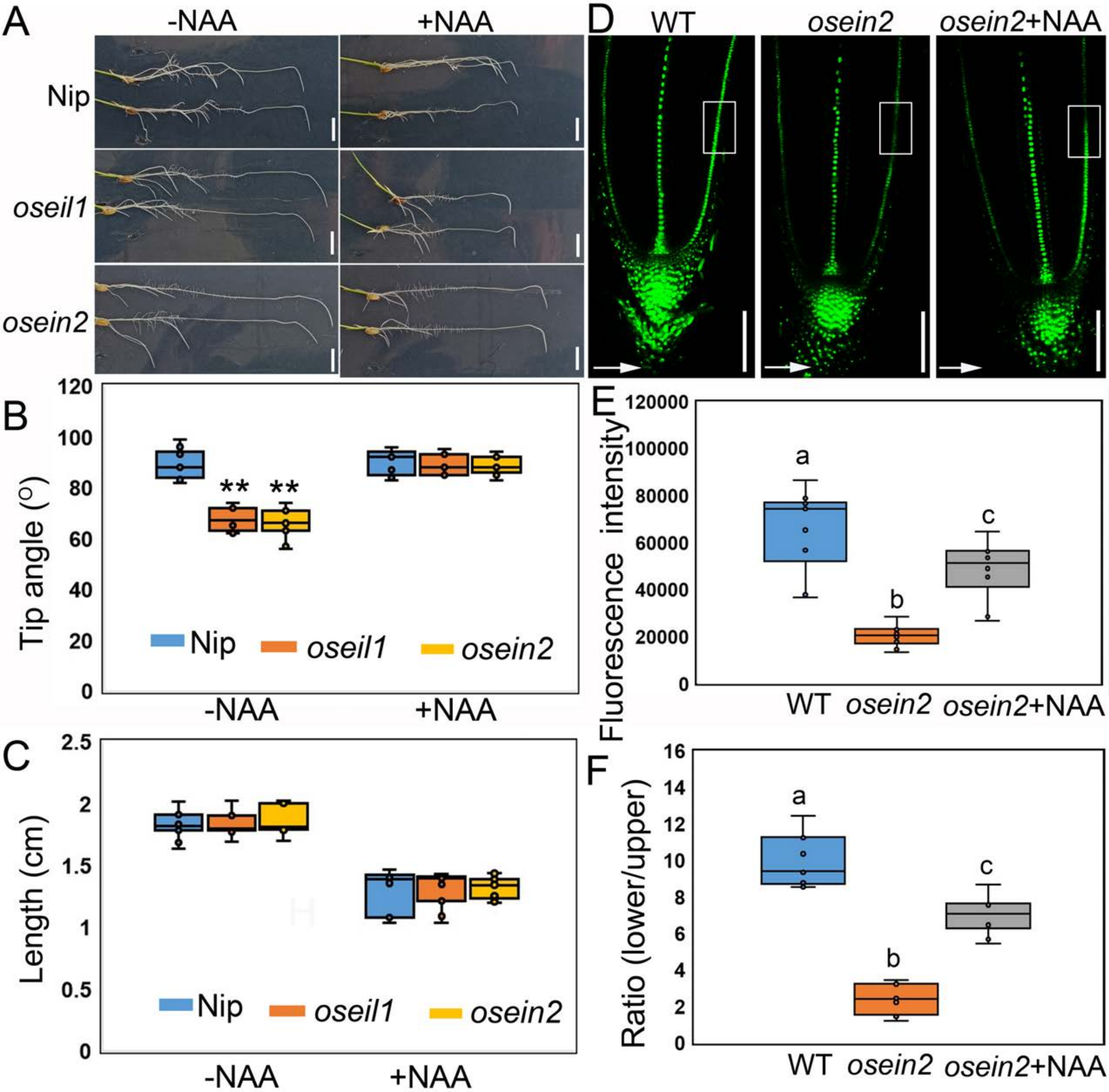
Zhao Y (2018) Essential Roles of Local Auxin Biosynthesis in Plant Development and in Adaptation to Environmental Changes. Annu Rev Plant Biol **69:** 417-435

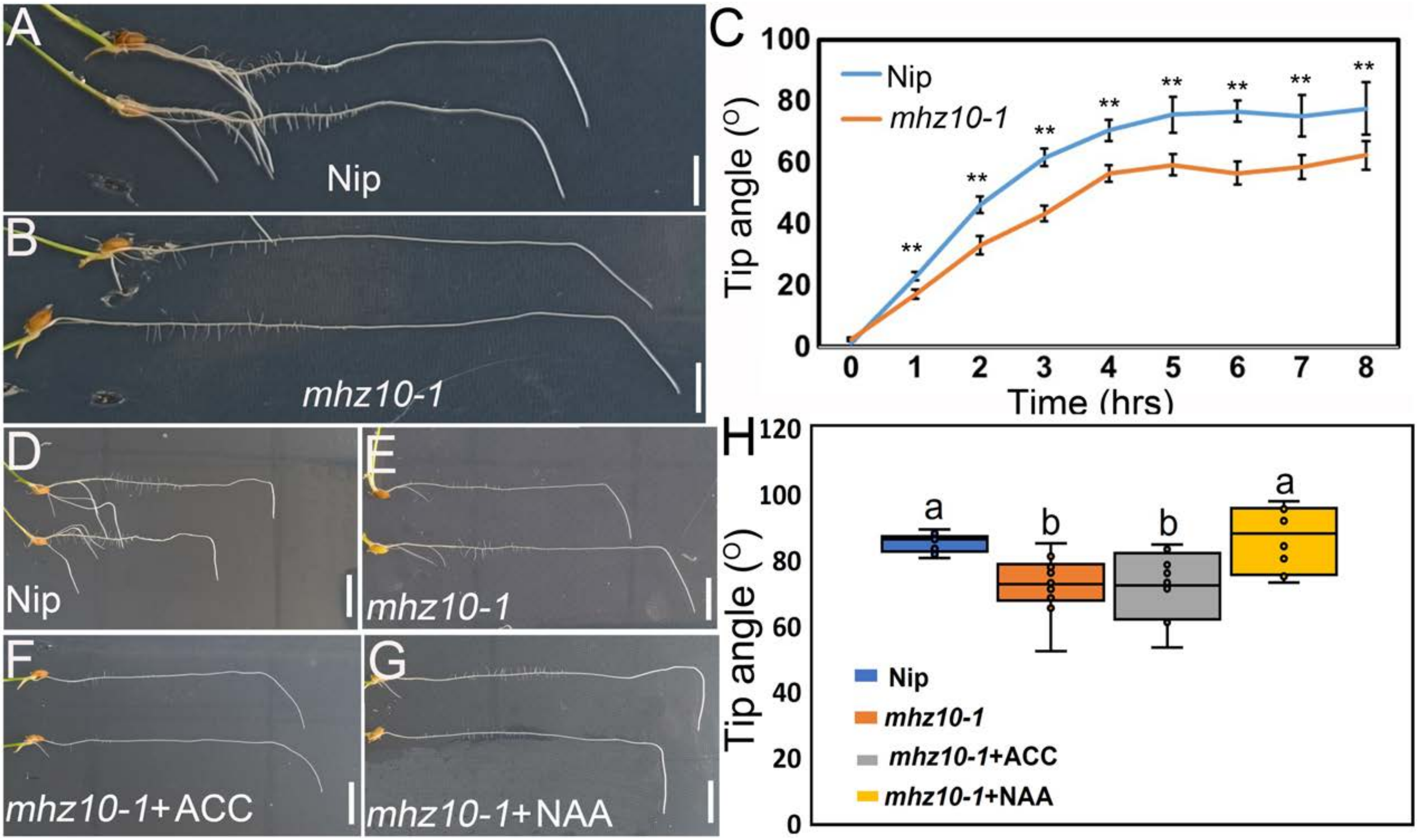
Zhou SQ, Zhang YK, Kremling KA, Ding YZ, Bennett JS, Bae JS, Kim DK, Ackerman HH, Kolomiets MV, Schmelz EA, Schroeder FC, Buckler ES, Jander G (2019) Ethylene signaling regulates natural variation in the abundance of antifungal acetylated diferuloylsucroses and Fusarium graminearum resistance in maize seedling roots. New Phytol **221:** 2096-2111

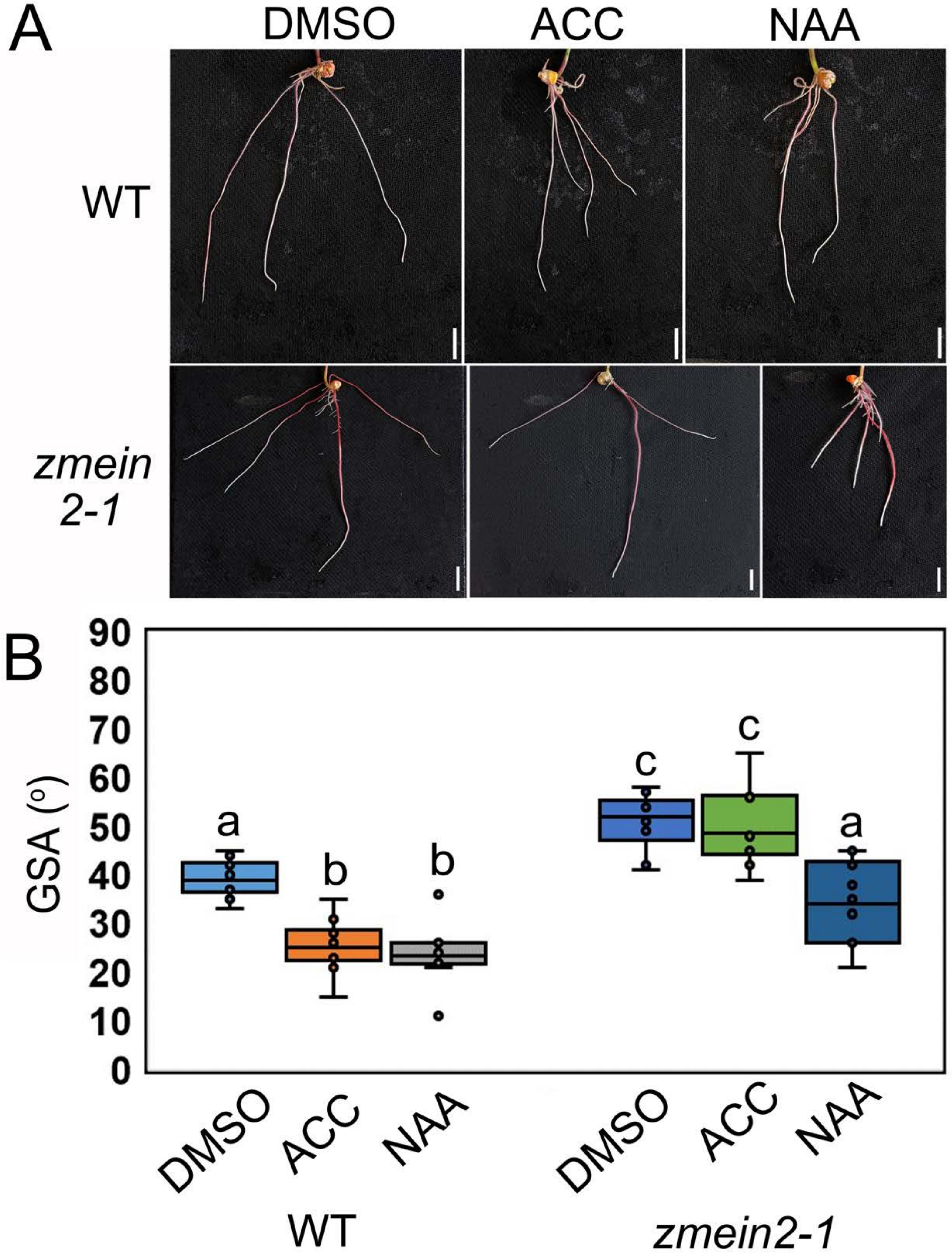
Zhou Y, Ma B, Tao JJ, Yin CC, Hu Y, Huang YH, Wei W, Xin PY, Chu JF, Zhang WK, Chen SY, Zhang JS (2022) Rice EIL1 interacts with OsIAAs to regulate auxin biosynthesis mediated by the tryptophan aminotransferase MHZ10/OsTAR2 during root ethylene responses. Plant Cell **34:** 4366-4387

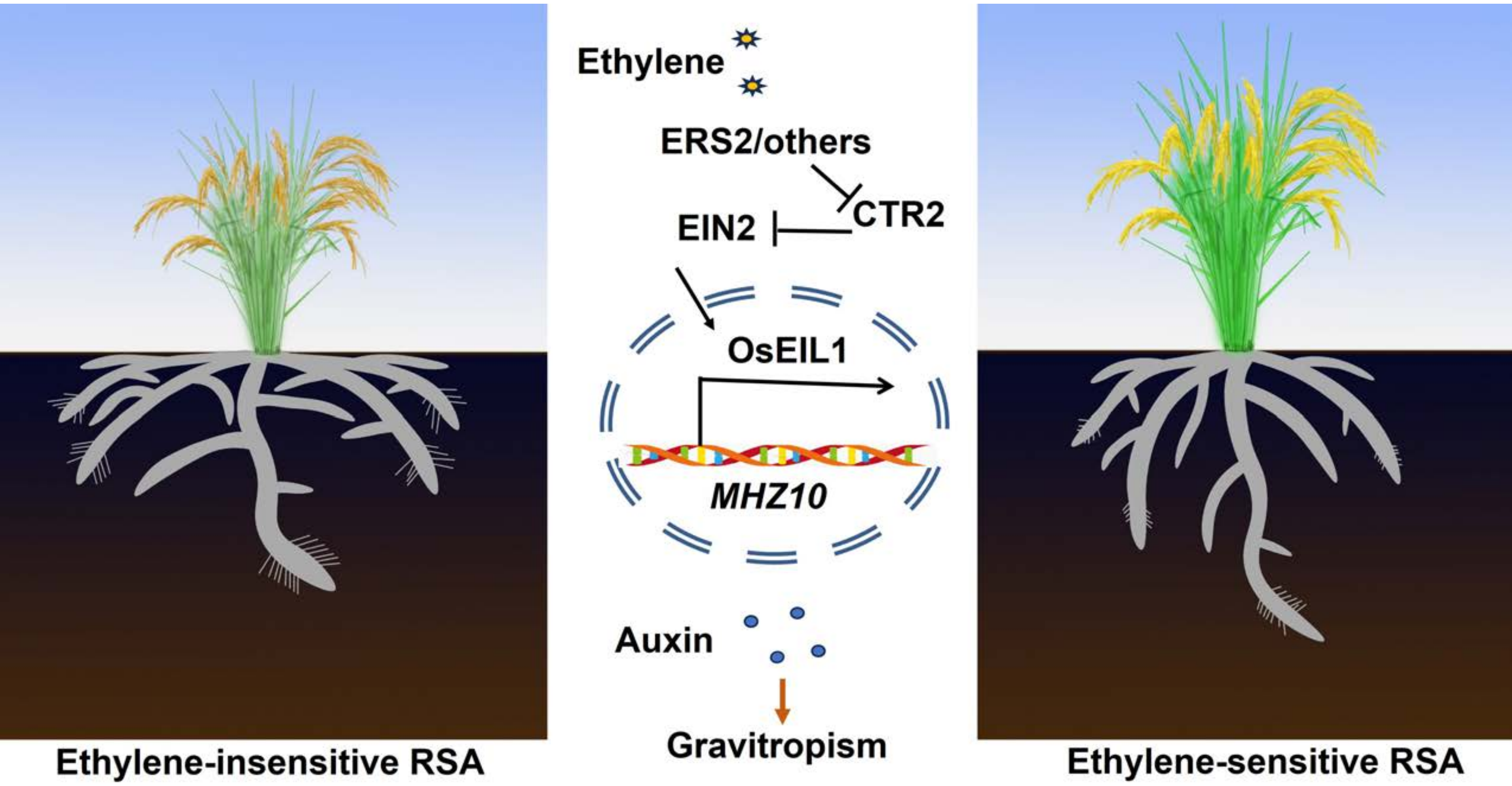

A
B
C
D
E
F
G
H
I
J
K
GSA (°)
70
60
50
40
30
20
10
0
-ACC
+ACC
Col-0
ein2-1
ein3-1
eto1-1
ctr1-1
L
M
N
Nip
oseil1
osein2
O
GSA (°)
90
80
70
60
50
40
30
20
10
0
**
**
Nip
oseil1
osein2


A
-ACC
osein2
oseil1
Nip
B
+ACC
osein2
oseil1
Nip
C
120
100
80
60
40
20
0
Tip angle (°)
a
b
b
c
b
b
Nip
osein2
oseil1
-ACC
+ACC
D
4
3.5
3
2.5
2
1.5
1
0.5
0
Length (cm)
**
Nip
osein2
oseil1
-ACC
+ACC


A
-NAA
+NAA
Nip
oseil1
osein2
D
WT
osein2
osein2+NAA
B
Tip angle (°)
0
20
40
60
80
100
120
**
**
Nip
oseil1
osein2
-NAA
+NAA
C
Length (cm)
0
0.5
1
1.5
2
2.5
Nip
oseil1
osein2
-NAA
+NAA
E
Fluorescence intensity
0
20000
40000
60000
80000
100000
120000
a
b
c
WT
osein2
osein2+NAA
F
Ratio (lower/upper)
0
2
4
6
8
10
12
14
16
a
b
c
WT
osein2
osein2+NAA


A
Nip
B
mhz10-1
C
Tip angle (°)
Time (hrs)
0
20
40
60
80
100
0
1
2
3
4
5
6
7
8
Nip
mhz10-1
**
D
Nip
E
mhz10-1
F
mhz10-1+ACC
G
mhz10-1+NAA
H
Tip angle (°)
0
20
40
60
80
100
120
a
b
b
a
Nip
mhz10-1
mhz10-1+ACC
mhz10-1+NAA


A
DMSO
ACC
NAA
WT
zmein 2-1
B
90
80
70
60
50
40
30
20
10
0
GSA (°)
a
b
b
c
c
a
DMSO
ACC
NAA
DMSO
ACC
NAA
WT
zmein2-1


Ethylene
ERS2/others
CTR2
EIN2
OsEIL1
MHZ10
Auxin
Gravitropism
Ethylene-insensitive RSA
Ethylene-sensitive RSA

Parsed Citations

Abas L, Benjamins R, Malenica N, Paciorek T, Wisniewska 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
Google Scholar: Author Only Title Only Author and Title

Apelbaum A, Yang SF (1981) Biosynthesis of stress ethylene induced by water deficit. Plant Physiol 68: 594-596
Google Scholar: Author Only Title Only Author and Title

Band LR, Wells DM, Larrieu A, Sun JY, Middleton AM, French AP, Brunoud G, Sato EM, Wilson MH, Peret B, Oliva M, Swarup R, Sairanen I, Parry G, Ljung K, Beeckman T, Garibaldi JM, Estelle M, Owen MR, Vissenberg K, Hodgman TC, Pridmore TP, King JR, Vernoux T, Bennett MJ (2012) Root gravitropism is regulated by a transient lateral auxin gradient controlled by a tipping-point mechanism. Proc Natl Acad Sci U S A 109: 4668-4673
Google Scholar: Author Only Title Only Author and Title

Bennett MJ, Marchant A, Green HG, May ST, Ward SP, Millner PA, Walker AR, Schulz B, Feldmann KA (1996) Arabidopsis AUX1 gene: a permease-like regulator of root gravitropism. Science 273: 948-950
Google Scholar: Author Only Title Only Author and Title

Buer CS, Sukumar P, Muday GK (2006) Ethylene modulates flavonoid accumulation and gravitropic responses in roots of Arabidopsis. Plant Physiol 140: 1384-1396
Google Scholar: Author Only Title Only Author and Title

Chen H, Ma B, Zhou Y, He SJ, Tang SY, Lu X, Xie Q, Chen SY, Zhang JS (2018) E3 ubiquitin ligase SOR1 regulates ethylene response in rice root by modulating stability of Aux/IAA protein. Proc Natl Acad Sci U S A 115: 4513-4518
Google Scholar: Author Only Title Only Author and Title

de Dorlodot S, Forster B, Pages L, Price A, Tuberosa R, Draye X (2007) Root system architecture: opportunities and constraints for genetic improvement of crops. Trends Plant Sci 12: 474-481
Google Scholar: Author Only Title Only Author and Title

Dietrich D, Pang L, Kobayashi A, Fozard JA, Boudolf V, Bhosale R, Antoni R, Nguyen T, Hiratsuka S, Fujii N, Miyazawa Y, Bae TW, Wells DM, Owen MR, Band LR, Dyson RJ, Jensen OE, King JR, Tracy SR, Sturrock CJ, Mooney SJ, Roberts JA, Bhalerao RP, Dinneny JR, Rodriguez PL, Nagatani A, Hosokawa Y, Baskin TI, Pridmore TP, De Veylder L, Takahashi H, Bennett MJ (2017) Root hydrotropism is controlled via a cortex-specific growth mechanism. Nat Plants 3: 1-8
Google Scholar: Author Only Title Only Author and Title

Dolgikh VA, Pukhovaya EM, Zemlyanskaya EV (2019) Shaping Ethylene Response: The Role of EIN3/EIL1 Transcription Factors. Front Plant Sci 10: 1030
Google Scholar: Author Only Title Only Author and Title

Dong L, Li L, Liu C, Liu C, Geng S, Li X, Huang C, Mao L, Chen S, Xie C (2018) Genome Editing and Double-Fluorescence Proteins Enable Robust Maternal Haploid Induction and Identification in Maize. Mol Plant 11: 1214-1217
Google Scholar: Author Only Title Only Author and Title

Feng XJ, Jia L, Cai YT, Guan HR, Zheng D, Zhang WX, Xiong H, Zhou HM, Wen Y, Hu Y, Zhang XM, Wang QJ, Wu FK, Xu J, Lu YL (2022) ABA-inducible improves adaptation of maize to water deficiency. Plant Biotechnol J 20: 2077-2088
Google Scholar: Author Only Title Only Author and Title

Frankowski K, Kesy J, Kopcewicz J (2007) Regulation of ethylene biosynthesis in plants. Postepy Biochem 53: 66-73
Google Scholar: Author Only Title Only Author and Title

Fusi R, Rosignoli S, Lou H, Sangiorgi G, Bovina R, Pattem JK, Borkar AN, Lombardi M, Forestan C, Milner SG, Davis JL, Lale A, Kirschner GK, Swarup R, Tassinari A, Pandey BK, York LM, Atkinson BS, Sturrock CJ, Mooney SJ, Hochholdinger F, Tucker MR, Himmelbach A, Stein N, Mascher M, Nagel KA, De Gara L, Simmonds J, Uauy C, Tuberosa R, Lynch JP, Yakubov GE, Bennett MJ, Bhosale R, Salvi S (2022) Root angle is controlled by EGT1 in cereal crops employing an antigravitropic mechanism. Proc Natl Acad Sci U S A 119: e2201350119
Google Scholar: Author Only Title Only Author and Title

Gallie DR, Young TE (2004) The ethylene biosynthetic and perception machinery is differentially expressed during endosperm and embryo development in maize. Mol Genet Genomics 271: 267-281
Google Scholar: Author Only Title Only Author and Title

Giri J, Bhosale R, Huang G, Pandey BK, Parker H, Zappala S, Yang J, Dievart A, Bureau C, Ljung K, Price A, Rose T, Larrieu A, Mairhofer S, Sturrock CJ, White P, Dupuy L, Hawkesford M, Perin C, Liang W, Peret B, Hodgman CT, Lynch J, Wissuwa M, Zhang D, Pridmore T, Mooney SJ, Guiderdoni E, Swarup R, Bennett MJ (2018) Rice auxin influx carrier OsAUX1 facilitates root hair elongation in response to low external phosphate. Nat Commun 9: 1408
Google Scholar: Author Only Title Only Author and Title

Guo T, Chen K, Dong NQ, Ye WW, Shan JX, Lin HX (2020) Tillering and small grain 1 dominates the tryptophan aminotransferase family required for local auxin biosynthesis in rice. J Integr Plant Biol 62: 581-600
Google Scholar: Author Only Title Only Author and Title

Hanzawa E, Sasaki K, Nagai S, Obara M, Fukuta Y, Uga Y, Miyao A, Hirochika H, Higashitani A, Maekawa M, Sato T (2013) Isolation of a novel mutant gene for soil-surface rooting in rice (Oryza sativa L.). Rice (N Y) 6: 30
Google Scholar: Author Only Title Only Author and Title

Huang G, Kilic A, Karady M, Zhang J, Mehra P, Song X, Sturrock CJ, Zhu W, Qin H, Hartman S, Schneider HM, Bhosale R, Dodd IC, Sharp RE, Huang R, Mooney SJ, Liang W, Bennett MJ, Zhang D, Pandey BK (2022) Ethylene inhibits rice root elongation in compacted soil via ABA- and auxin-mediated mechanisms. Proc Natl Acad Sci U S A 119: e2201072119
Google Scholar: Author Only Title Only Author and Title

Huang G, Liang W, Sturrock CJ, Pandey BK, Giri J, Mairhofer S, Wang D, Muller L, Tan H, York LM, Yang J, Song Y, Kim YJ, Qiao Y, Xu J, Kepinski S, Bennett MJ, Zhang D (2018) Rice actin binding protein RMD controls crown root angle in response to external phosphate. Nat Commun 9: 2346
Google Scholar: Author Only Title Only Author and Title

Huang YH, Han JQ, Ma B, Cao WQ, Li XK, Xiong Q, Zhao H, Zhao R, Zhang X, Zhou Y, Wei W, Tao JJ, Zhang WK, Qian WF, Chen SY, Yang C, Yin CC, Zhang JS (2023) A translational regulator MHZ9 modulates ethylene signaling in rice. Nat Commun 14: 4674
Google Scholar: Author Only Title Only Author and Title

Ju C, Chang C (2015) Mechanistic Insights in Ethylene Perception and Signal Transduction. Plant Physiol 169: 85-95
Google Scholar: Author Only Title Only Author and Title

Kirschner GK, Rosignoli S, Guo L, Vardanega I, Imani J, Altmuller J, Milner SG, Balzano R, Nagel KA, Pflugfelder D, Forestan C, Bovina R, Koller R, Stocker TG, Mascher M, Simmonds J, Uauy C, Schoof H, Tuberosa R, Salvi S, Hochholdinger F (2021) ENHANCED GRAVITROPISM 2 encodes a STERILE ALPHA MOTIF-containing protein that controls root growth angle in barley and wheat. Proc Natl Acad Sci U S A 118: e2101526118
Google Scholar: Author Only Title Only Author and Title

Kitomi Y, Hanzawa E, Kuya N, Inoue H, Hara N, Kawai S, Kanno N, Endo M, Sugimoto K, Yamazaki T, Sakamoto S, Sentoku N, Wu J, Kanno H, Mitsuda N, Toriyama K, Sato T, Uga Y (2020) Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields. Proc Natl Acad Sci U S A 117: 21242-21250
Google Scholar: Author Only Title Only Author and Title

Liao H, Rubio G, Yan X, Cao A, Brown KM, Lynch JP (2001) Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil 232: 69-79
Google Scholar: Author Only Title Only Author and Title

Liu HJ, Jian L, Xu J, Zhang Q, Zhang M, Jin M, Peng Y, Yan J, Han B, Liu J (2020) High-Throughput CRISPR/Cas9 Mutagenesis Streamlines Trait Gene Identification in Maize. Plant Cell 32: 1397-1413
Google Scholar: Author Only Title Only Author and Title

Ma B, He SJ, Duan KX, Yin CC, Chen H, Yang C, Xiong Q, Song QX, Lu X, Chen HW, Zhang WK, Lu TG, Chen SY, Zhang JS (2013) Identification of Rice Ethylene-Response Mutants and Characterization of in Distinct Ethylene Response and Yield Trait Regulation. Mol Plant 6: 1830-1848
Google Scholar: Author Only Title Only Author and Title

Ma B, Yin CC, He SJ, Lu X, Zhang WK, Lu TG, Chen SY, Zhang JS (2014) Ethylene-induced inhibition of root growth requires abscisic acid function in rice (Oryza sativa L.) seedlings. PLoS Genet 10: e1004701
Google Scholar: Author Only Title Only Author and Title

Ma B ZY, Chen H, He SJ, Huang YH, Zhao H, Lu X, Zhang WK, Pang JH, Chen SY, Zhang JS (2018) Membrane protein MHZ3 stabilizes OsEIN2 in rice by interacting with its Nramp-dlike domain. Proc Natl Acad Sci U S A 115: 2520-2525
Google Scholar: Author Only Title Only Author and Title

Mao JL, Miao ZQ, Wang Z, Yu LH, Cai XT, Xiang CB (2016) Arabidopsis ERF1 Mediates Cross-Talk between Ethylene and Auxin Biosynthesis during Primary Root Elongation by Regulating ASA1 Expression. Plos Genet 12: e1005760
Google Scholar: Author Only Title Only Author and Title

Mashiguchi K, Tanaka K, Sakai T, Sugawara S, Kawaide H, Natsume M, Hanada A, Yaeno T, Shirasu K, Yao H, McSteen P, Zhao Y, Hayashi K, Kamiya Y, Kasahara H (2011) The main auxin biosynthesis pathway in Arabidopsis. Proc Natl Acad Sci U S A 108: 18512-18517
Google Scholar: Author Only Title Only Author and Title

Miao R, Yuan W, Wang Y, Garcia-Maquilon I, Dang XL, Li Y, Zhang JH, Zhu YY, Rodriguez PL, Xu WF (2021) Low ABA concentration promotes root growth and hydrotropism through relief of ABA INSENSITIVE 1-mediated inhibition of plasma membrane H-ATPase 2. Sci Adv 7: eabd4113
Google Scholar: Author Only Title Only Author and Title

Muday GK, Rahman A, Binder BM (2012) Auxin and ethylene: collaborators or competitors? Trends Plant Sci 17: 181-195
Google Scholar: Author Only Title Only Author and Title

Okushima Y, Overvoorde PJ, Arima K, Alonso JM, Chan A, Chang C, Ecker JR, Hughes B, Lui A, Nguyen D, Onodera C, Quach H, Smith A, Yu G, Theologis A (2005) Functional genomic analysis of the AUXIN RESPONSE FACTOR gene family members in Arabidopsis thaliana: unique and overlapping functions of ARF7 and ARF19. Plant Cell 17: 444-463
Google Scholar: Author Only Title Only Author and Title

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol 58: 93-113
Google Scholar: Author Only Title Only Author and Title

Peret B, Desnos T, Jost R, Kanno S, Berkowitz O, Nussaume L (2014) Root architecture responses: in search of phosphate. Plant Physiol 166: 1713-1723
Google Scholar: Author Only Title Only Author and Title

Qin H, Zhang Z, Wang J, Chen X, Wei P, Huang R (2017) The activation of OsEIL1 on YUC8 transcription and auxin biosynthesis is required for ethylene-inhibited root elongation in rice early seedling development. PLoS Genet 13: e1006955
Google Scholar: Author Only Title Only Author and Title

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
Google Scholar: Author Only Title Only Author and Title

Ren W, Zhao L, Liang J, Wang L, Chen L, Li P, Liu Z, Li X, Zhang Z, Li J, He K, Zhao Z, Ali F, Mi G, Yan J, Zhang F, Chen F, Yuan L, Pan Q (2022) Genome-wide dissection of changes in maize root system architecture during modern breeding. Nat Plants 8: 1408-1422
Google Scholar: Author Only Title Only Author and Title

Rogers ED, Benfey PN (2015) Regulation of plant root system architecture: implications for crop advancement. Curr Opin Biotechnol 32: 93-98
Google Scholar: Author Only Title Only Author and Title

Roychoudhry S, Del Bianco M, Kieffer M, Kepinski S (2013) Auxin controls gravitropic setpoint angle in higher plant lateral branches. Curr Biol 23: 1497-1504
Google Scholar: Author Only Title Only Author and Title

Ruzicka K, Ljung K, Vanneste S, Podhorska R, Beeckman T, Friml J, Benkova E (2007) Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. Plant Cell 19: 2197-2212
Google Scholar: Author Only Title Only Author and Title

Savada RP, Ozga JA, Jayasinghege CPA, Waduthanthri KD, Reinecke DM (2017) Heat stress differentially modifies ethylene biosynthesis and signaling in pea floral and fruit tissues. Plant Mol Biol 95: 313-331
Google Scholar: Author Only Title Only Author and Title

Schneider HM, Lor VSN, Hanlon MT, Perkins A, Kaeppler SM, Borkar AN, Bhosale R, Zhang X, Rodriguez J, Bucksch A, Bennett MJ, Brown KM, Lynch JP (2022) Root angle in maize influences nitrogen capture and is regulated by calcineurin B-like protein (CBL)-interacting serine/threonine-protein kinase 15 (ZmCIPK15). Plant Cell Environ 45: 837-853
Google Scholar: Author Only Title Only Author and Title

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
Google Scholar: Author Only Title Only Author and Title

Stepanova AN, Robertson-Hoyt J, Yun J, Benavente LM, Xie DY, DoleZal K, Schlereth A, Jurgens G, Alonso JM (2008) TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. Cell 133: 177-191
Google Scholar: Author Only Title Only Author and Title

Stepanova AN, Yun J, Likhacheva AV, Alonso JM (2007) Multilevel interactions between ethylene and auxin in Arabidopsis roots. Plant Cell 19: 2169-2185
Google Scholar: Author Only Title Only Author and Title

Swarup R, Perry P, Hagenbeek D, Van Der Straeten D, Beemster GT, Sandberg G, Bhalerao R, Ljung K, Bennett MJ (2007) Ethylene upregulates auxin biosynthesis in Arabidopsis seedlings to enhance inhibition of root cell elongation. Plant Cell 19: 2186-2196
Google Scholar: Author Only Title Only Author and Title

Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K, Kanno N, Inoue H, Takehisa H, Motoyama R, Nagamura Y, Wu J, Matsumoto T, Takai T, Okuno K, Yano M (2013) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat Genet 45: 1097-1102

Google Scholar: Author Only Title Only Author and Title

Woo YM, Park HJ, Su'udi M, Yang JI, Park JJ, Back K, Park YM, An G (2007) Constitutively wilted 1, a member of the rice YUCCA gene family, is required for maintaining water homeostasis and an appropriate root to shoot ratio. Plant Mol Biol 65: 125-136
Google Scholar: Author Only Title Only Author and Title

Yang J, Yuan Z, Meng Q, Huang G, Perin C, Bureau C, Meunier AC, Ingouff M, Bennett MJ, Liang W, Zhang D (2017) Dynamic Regulation of Auxin Response during Rice Development Revealed by Newly Established Hormone Biosensor Markers. Front Plant Sci 8: 256
Google Scholar: Author Only Title Only Author and Title

Yin CC, Ma B, Collinge DP, Pogson BJ, He SJ, Xiong Q, Duan KX, Chen H, Yang C, Lu X, Wang YQ, Zhang WK, Chu CC, Sun XH, Fang S, Chu JF, Lu TG, Chen SY, Zhang JS (2015) Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-mediated abscisic acid pathway. Plant Cell 27: 1061-1081
Google Scholar: Author Only Title Only Author and Title

Yoshikawa T, Ito M, Sumikura T, Nakayama A, Nishimura T, Kitano H, Yamaguchi I, Koshiba T, Hibara KI, Nagato Y, Itoh JI (2014) The rice FISH BONE gene encodes a tryptophan aminotransferase, which affects pleiotropic auxin-related processes. Plant J 78: 927-936
Google Scholar: Author Only Title Only Author and Title

Zhang Z, Zhang Y, Tan H, Wang Y, Li G, Liang W, Yuan Z, Hu J, Ren H, Zhang D (2011) RICE MORPHOLOGY DETERMINANT encodes the type II formin FH5 and regulates rice morphogenesis. Plant Cell 23: 681-700
Google Scholar: Author Only Title Only Author and Title

Zhao H, Duan KX, Ma B, Yin CC, Zhang JS (2020) Histidine kinase MHZ1/OsHK1 interacts with ethylene receptors to regulate root growth in rice. Nature Communications 11
Google Scholar: Author Only Title Only Author and Title

Zhao H, Ma B, Duan KX, Li XK, Zhang JS (2020) The GDSL Lipase MHZ11 Modulates Ethylene Signaling in Rice Roots. The Plant Cell 32: tpc.00840.02019
Google Scholar: Author Only Title Only Author and Title

Zhao H, Yin CC, Ma B, Chen SY, Zhang JS (2021) Ethylene signaling in rice and Arabidopsis: New regulators and mechanisms. J Integr Plant Biol 63: 102-125
Google Scholar: Author Only Title Only Author and Title

Zhao Y (2018) Essential Roles of Local Auxin Biosynthesis in Plant Development and in Adaptation to Environmental Changes. Annu Rev Plant Biol 69: 417-435
Google Scholar: Author Only Title Only Author and Title

Zhou SQ, Zhang YK, Kremling KA, Ding YZ, Bennett JS, Bae JS, Kim DK, Ackerman HH, Kolomiets MV, Schmelz EA, Schroeder FC, Buckler ES, Jander G (2019) Ethylene signaling regulates natural variation in the abundance of antifungal acetylated diferuloylsucroses and Fusarium graminearum resistance in maize seedling roots. New Phytol 221: 2096-2111
Google Scholar: Author Only Title Only Author and Title

Zhou Y, Ma B, Tao JJ, Yin CC, Hu Y, Huang YH, Wei W, Xin PY, Chu JF, Zhang WK, Chen SY, Zhang JS (2022) Rice EIL1 interacts with OsIAAs to regulate auxin biosynthesis mediated by the tryptophan aminotransferase MHZ10/OsTAR2 during root ethylene responses. Plant Cell 34: 4366-4387
Google Scholar: Author Only Title Only Author and Title