Journal of Experimental Botany, Vol. 74, No. 4 pp. 1198–1206, 2023
https://doi.org/10.1093/jxb/erab508 Advance Access Publication 20 November 2021

REVIEW PAPER

Roles of the wound hormone jasmonate in plant regeneration

Guifang Zhang[1,2,3,†], Wu Liu[4,†], Zewei Gu[4,5,†], Shasha Wu[4,6], Yilan E[1], Wenkun Zhou[7,*], Jinxing Lin[1,2,3,*] and Lin Xu[4,*]

[1] National Engineering Laboratory for Tree Breeding, College of Biological Sciences and Biotechnology, Beijing Forestry University, Beijing 100083, China
[2] Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, Beijing Forestry University, Beijing 100083, China
[3] Institute of Tree Development and Genome Editing, Beijing Forestry University, Beijing 100083, China
[4] National Key Laboratory of Plant Molecular Genetics, CAS Center for Excellence in Molecular Plant Sciences, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, 300 Fenglin Road, Shanghai 200032, China
[5] University of Chinese Academy of Sciences, 19A Yuquan Road, Beijing 100049, China
[6] College of Life Sciences, Shanghai Normal University, Shanghai 200234, China
[7] State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China

[†] These authors contributed equally to this work.
* Correspondence: zhouwenkun@cau.edu.cn, linjx@ibcas.ac.cn, or xulin@cemps.ac.cn

Received 17 September 2021; Editorial decision 16 November 2021; Accepted 18 November 2021

Editor: Ziqiang Zhu, Nanjing Normal University, China

Abstract

Plants have remarkable abilities to regenerate in response to wounding. How wounding triggers rapid signal transduction to induce a cellular response is a key topic for understanding the molecular mechanism of plant regeneration. An increasing body of evidence indicates that jasmonate, a hormone that is produced rapidly in response to wounding, plays multiple roles in different plant regeneration processes. In this review, we summarize recent advances on the roles of jasmonate in tissue repair, the formation of wound-induced callus, *de novo* organ regeneration, and somatic embryogenesis. Physiological and molecular analyses indicate that jasmonate can regulate stem cell activities, cell proliferation, cell fate transition, and auxin production, thereby contributing to plant regeneration. In addition, jasmonate is strictly controlled in plant cells via restriction of the jasmonate concentration and its signalling pathway in a spatial and temporal manner during regeneration. Overall, jasmonate acts as the hormone linking wounding to distinct types of regeneration in plants.

Keywords: Callus, *de novo* root regeneration, *de novo* shoot regeneration, jasmonate, plant regeneration, somatic embryogenesis, tissue repair, wounding.

Abbreviations: ANAC071, NAC DOMAIN CONTAINING PROTEIN71; ASA1, ANTHRANILATE SYNTHASE α1; CIM, callus-inducing medium; COI1, CORONATINE INSENSITIVE1; ERF, ETHYLENE RESPONSE FACTOR; ESR1, ENHANCER OF SHOOT REGENERATION1; H3K36me3, histone H3 lysine 36 trimethylation; JA, jasmonate; JAZ, JASMONATE-ZIM-DOMAIN; miR156, microRNA156; NO, nitric oxide; RAP2.6L, RELATED TO AP2.6L; PGB2, PHYTOGLOBIN2; PLT, PLETHORA; QC, quiescent centre; RBR, RETINOBLASTOMA-RELATED; SA, salicylic acid; SCR, SCARECROW; SHR, SHORTROOT; SIM, shoot-inducing medium; SPL, SQUAMOSA PROMOTER BINDING PROTEIN-LIKE; WIND1, WOUND-INDUCED DEDIFFERENTIATION1; WOX5, WUSCHEL-RELATED HOMEOBOX5.

Introduction

Plants can undergo multiple regenerative processes after wounding to repair wounded tissues, form new organs, and produce somatic embryos (Xu and Huang, 2014). The regenerative abilities of plants have been widely exploited in agricultural technologies such as cutting, grafting, and vegetative propagation in tissue culture (Sussex, 2008; Ikeuchi *et al.*, 2019). Wounding is the first event in plant regeneration, and the underlying theme of plant regeneration is the cell fate transition in response to wounding (Chen *et al.*, 2016; Lup *et al.*, 2016).

In plants, most wound-induced responses occur in a relatively narrow time window. Wound signals occur in two waves, the first soon after wounding and the second later (León *et al.*, 2001; Maffei *et al.*, 2007; Hilleary and Gilroy, 2018; Wasternack, 2019). Very soon after wounding, plants quickly produce the first wave of wound signals, such as electrical pulses, calcium ion (Ca^{2+}) signals, and reactive oxygen species. The second wave of wound signals mainly involves plant hormones, such as jasmonate (JA), salicylic acid (SA), and ethylene. Among these signals, JA has been well characterized as the wound hormone (Han, 2017; Wasternack and Song, 2017; Ruan *et al.*, 2019). Usually, JA is kept at a low concentration in plant tissues, but it quickly accumulates in response to wounding (Chung *et al.*, 2008; Glauser *et al.*, 2008; Koo *et al.*, 2009). In its signalling pathway, jasmonoyl-isoleucine binds to the F-box protein receptor CORONATINE INSENSITIVE1 (COI1) (Feys *et al.*, 1994; Xie *et al.*, 1998; Yan *et al.*, 2009) and then COI1 is able to bind JASMONATE-ZIM-DOMAIN (JAZ) proteins, leading to the ubiquitination and degradation of JAZs, thereby activating the JA-signalling pathway (Yan *et al.*, 2007; Chini *et al.*, 2007; Thines *et al.*, 2007).

In this review, we summarize recent advances in research on how the wound hormone JA links wounding to plant regeneration, and discuss the possibility of the involvement of JA in crosstalk with other wounding signals and hormones.

Roles of JA in stem tissue repair and grafting

Research using injured Arabidopsis stems suggests that auxin, ethylene, and JA are involved in the reunion of the wounded tissues (Asahina *et al.*, 2011) (Fig. 1A). When the stem is injured, the tissues near the wounded site can trigger cell division to repair and heal the wound. The gap created by the wound blocks the flux of auxin from the shoot to the root, resulting in the accumulation of auxin in the upper region of the cut gap and the deprivation of auxin in the lower region of the cut gap. The unbalanced auxin distribution in the two regions of the cut gap is critical for tissue repair, because either removal of the source of auxin production (e.g., cauline leaves, shoot apices, or lateral buds) or inhibition of polar auxin transport may result in defective stem wound reunion. At the molecular level, the high auxin concentration together with ethylene promotes the expression of *NAC DOMAIN CONTAINING PROTEIN71* (*ANAC071*) in the upper region of the cut gap, and the low auxin concentration together with JA promotes the expression of *RELATED TO AP2.6L* (*RAP2.6L*) in the lower region of the cut gap. The gene *LIPOXYGENASE2* (*LOX2*), which encodes the JA-biosynthesis enzyme, is also up-regulated, and its expression profile is similar to that of *RAP2.6L*. The expression of *RAP2.6L* can also be up-regulated by exogenous JA treatment. Genetic evidence indicates that both *ANAC071* and *RAP2.6L* are required for stem wound reunion. Overall, the unbalanced distribution of auxin at the cut gap, together with wound-induced ethylene and JA, controls the asymmetrical expression patterns of the transcription factor genes *ANAC071* and *RAP2.6L*, thereby regulating the repair of the wounded stem tissues (Asahina *et al.*, 2011).

Grafting is a biotechnology in which two wounded plants are physically joined to generate a chimeric plant (Melnyk *et al.*, 2015, 2018; Melnyk, 2017; Notaguchi *et al.*, 2020). During grafting, some tissues of the scion and stock, such as the cortex, endodermis, cambium, and/or pericycle, undergo cell division and differentiation to heal the graft junction (Jeffree and Yeoman, 1983; Melnyk *et al.*, 2015). The rapid accumulation of JA and the up-regulation of JA-responsive genes, including *RAP2.6L*, occur during grafting (Yin *et al.*, 2012; Gasperini *et al.*, 2015; Nanda and Melnyk, 2018; Matsuoka *et al.*, 2018; Wang *et al.*, 2020*a*). However, JA-deficient Arabidopsis mutants can also be grafted successfully (Gasperini *et al.*, 2015; Nanda and Melnyk, 2018). In addition, the induction of JA and *RAP2.6L* expression upon wounding during Arabidopsis hypocotyl grafting is not necessary for cell proliferation for healing (Matsuoka *et al.*, 2018). Therefore, further research is needed to clarify the roles of JA in regeneration after grafting.

Roles of JA in root tip repair

Laser ablation, root tip excision, and the use of DNA-damaging reagents are the main methods used to investigate root tip repair and regeneration (Feldman, 1976; van den Berg *et al.*, 1995; Xu *et al.*, 2006; Sena *et al.*, 2009). Many studies have established the framework of root tip repair, involving the wounding response, the redistribution of auxin and cytokinin, and quiescent centre (QC) and stem cell niche re-establishment (Matosevich and Efroni, 2021). These processes require the expression of the wound response genes *ETHYLENE RESPONSE FACTOR115* (*ERF115*) and *PHYTOCHROME A SIGNAL TRANSDUCTION1* (*PAT1*), and the stem cell regulation genes *PLETHORA* (*PLT*), *SHORTROOT* (*SHR*), *SCARECROW* (*SCR*), and *WUSCHEL-RELATED HOMEOBOX5* (*WOX5*) (van den Berg *et al.*, 1995, 1997; Xu *et al.*, 2006; Sena *et al.*, 2009; Heyman *et al.*, 2013, 2016; Efroni

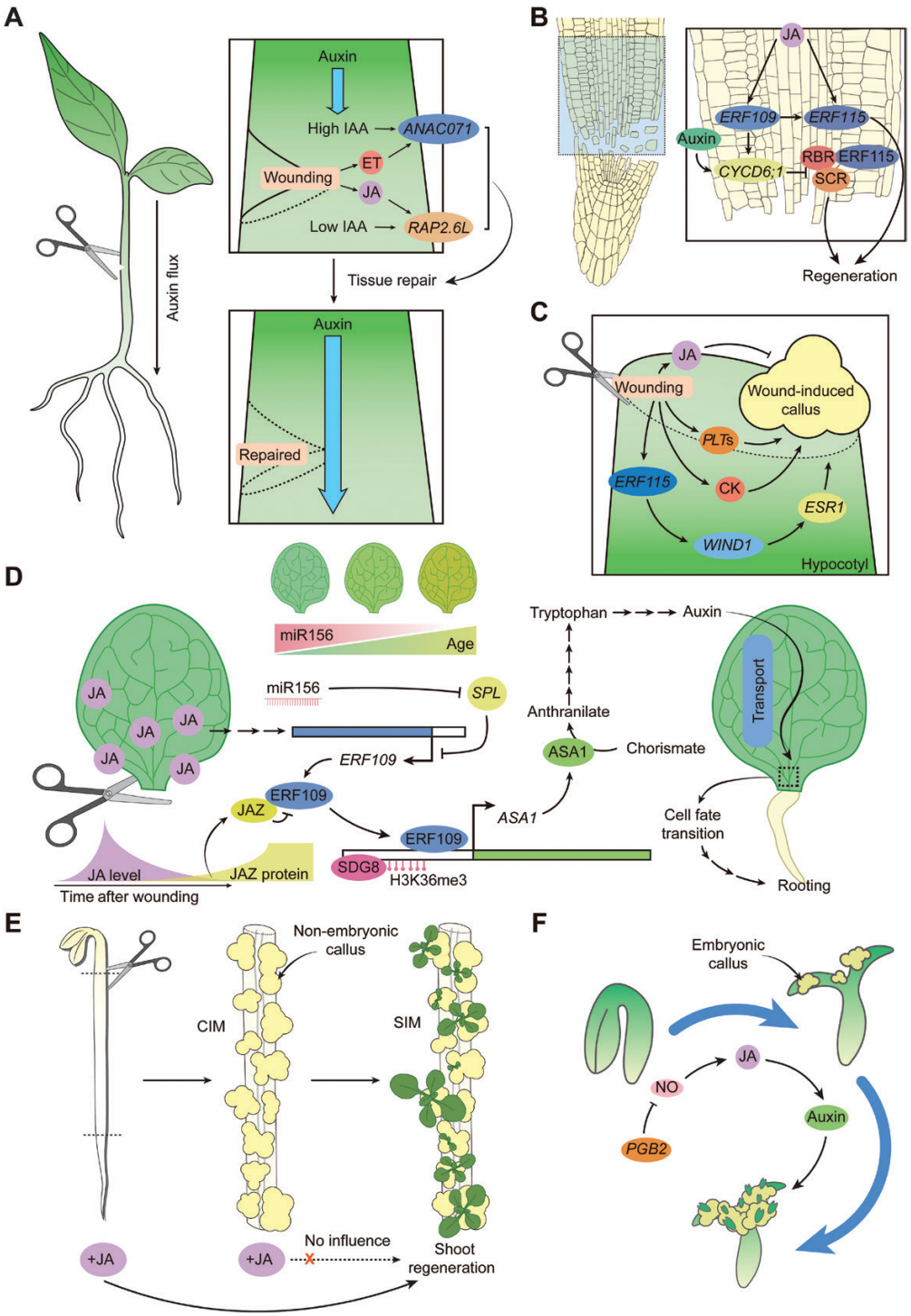

Fig. 1. Summary of the roles of jasmonate (JA) in Arabidopsis regeneration. (A) Stem tissue repair (Asahina *et al.*, 2011). Wounding induces ethylene (ET) and JA accumulation. ET, together with a high auxin concentration, activates *ANAC071* expression; JA, together with a low auxin concentration, activates *RAP2.6L* expression. Both pathways are required for tissue repair. (B) Root tip repair (Heyman *et al.*, 2013; Zhou *et al.*, 2019). JA acts as the wound hormone to promote cell division and cell fate transition via the activation of *ERF*s expression in the wounded root tip. (C) Wound-induced callus formation (Ikeuchi *et al.*, 2017). Wounding promotes many pathways, including JA, cytokinin (CK), *PLT*s, and *ERF115-WIND1-ESR1*, which regulate the formation of wound-induced callus from wounded hypocotyls. (D) *De novo* root regeneration from detached leaves (Zhang *et al.*, 2019; Ye *et al.*, 2020). JA serves as the wound hormone to accelerate auxin production in detached leaves, thereby promoting adventitious root regeneration. This process is also regulated by the miR156-*SPL* age pathway. (E) *De novo* shoot regeneration from non-embryonic callus (Park *et al.*, 2019). Pre-treatment of hypocotyl explants with JA can promote shoot regeneration in tissue culture. (F) Somatic embryogenesis (Elhiti *et al.*, 2013; Mira *et al.*, 2016). JA is involved in somatic embryogenesis via crosstalk with nitric oxide (NO) and auxin.

et al., 2016; Marhava *et al.*, 2019; Hellmann and Helariutta, 2019).

After both laser ablation and root tip excision, JA is the key hormone involved in root tip repair via activation of the QC and stem cell niche (Zhou *et al.*, 2019) (Fig. 1B). On the one hand, JA can activate cell division of the QC through the network of *WOX5*, *SHR*, *SCR*, and *RETINOBLASTOMA-RELATED* (*RBR*). On the other hand, JA promotes the expression of *ERF109* and *ERF115* during regeneration. The ERF109 transcription factor and locally accumulated auxin promote the expression of *CyclinD6;1* (*CYCD6;1*), which participates in the activation of cell division. ERF115 interacts with RBR and acts upstream of the *RBR-SCR-SHR* pathway in the regeneration of the QC and stem cell niche. Additionally, soil penetration and nematode herbivory induce JA-mediated wound responses and regeneration. Overall, the study of Zhou *et al.* (2019) revealed a genetic network from wounding to root tip repair.

Roles of JA in wound-induced callus formation

Wounded hypocotyls of Arabidopsis can produce a group of wound-induced callus cells, whose cell identity differs from that of non-embryonic callus cells produced in tissue culture (Iwase *et al.*, 2011). The tissue organization of non-embryonic callus produced in tissue culture is similar to that of the root primordium or root apical meristem (Sugimoto *et al.*, 2010, 2011; Fan *et al.*, 2012; He *et al.*, 2012). In contrast, wound-induced callus at the wounded site of the hypocotyl after decapitation does not exhibit root primordium or root apical meristem identity (Iwase *et al.*, 2011; Ikeuchi *et al.*, 2013). The AP2/ERF transcription factor gene *WOUND-INDUCED DEDIFFERENTIATION1* (*WIND1*) is involved in wound-induced callus formation by forming a regulatory network with *ERF115* and *ENHANCER OF SHOOT REGENERATION1* (*ESR1*), and *PLT*s also contribute to wound-induced callus formation (Iwase *et al.*, 2011, 2017; Ikeuchi *et al.*, 2017).

Time-course RNA-sequencing analyses identified that many hormone pathways are involved in wound-induced callus formation (Ikeuchi *et al.*, 2017) (Fig. 1C). The JA-biosynthesis genes and JA-response genes are quickly up-regulated upon wounding at the hypocotyl. However, mutations in JA-biosynthesis or JA-signalling pathway genes do not block the formation of wound-induced callus, but lead to increased efficiency of wound-induced callus formation (Ikeuchi *et al.*, 2017). Therefore, JA may play a negative role in the regulation of wound-induced callus formation. Genes involved in cytokinin synthesis are also up-regulated at the wounded site of hypocotyls. The cytokinin that accumulates at the wounded site can activate, via its signalling pathway, the expression of the cell-cycle-related genes *CYCD3;1*, *CYCD3;2*, and *CYCD3;3* to promote wound-induced callus formation. Therefore, JA and cytokinin might play opposing roles in the regulation of wound-induced callus formation (Ikeuchi *et al.*, 2017). Further research will shed light on the molecular mechanism by which JA negatively regulates wound-induced callus formation.

Roles of JA in *de novo* root regeneration in cuttings

De novo root regeneration is the process by which adventitious roots form from wounded or detached plant organs. The regeneration of adventitious roots from cuttings is a commonly used biotechnology for vegetative propagation of plants in the forestry and horticultural industries. Auxin is the key hormone that controls root organogenesis (Thimann and Went, 1934; Zimmerman and Wilcoxon, 1935; Hitchcock and Zimmerman, 1936) and it activates many key genes involved in cell fate transition during root primordium establishment (Xu, 2018).

Many studies have shown that JA plays a positive role in the promotion of *de novo* root regeneration from stem cuttings. In stem cuttings of *Petunia hybrida* and pea (*Pisum sativum*), JA rapidly accumulates in the stem base and promotes root formation (Ahkami *et al.*, 2009; Rasmussen *et al.*, 2015; Lischweski *et al.*, 2015). In the thin cell layers of tobacco or Arabidopsis that produce adventitious roots, treatment with JA at a low concentration can increase root formation (Fattorini *et al.*, 2009, 2018).

Detached leaves of Arabidopsis can regenerate adventitious roots on hormone-free medium, thereby providing a platform to study the molecular mechanism controlling *de novo* root regeneration from leaf cuttings (Chen *et al.*, 2014; Liu *et al.*, 2014; Xu, 2018). From 10 min to 2 h after leaf detachment, a wave of JA is rapidly produced in detached leaves in response to wounding, but this wave disappears by 4 h after wounding (Zhang *et al.*, 2019). Mutation of the JA-signalling pathway gene *COI1* leads to a reduced ability to form roots from detached leaves (Zhang *et al.*, 2019). Through its signalling pathway, JA activates the expression of the transcription factor gene *ERF109*, and ERF109 in turn up-regulates the expression of *ANTHRANILATE SYNTHASE α1* (*ASA1*) (Sun *et al.*, 2009; Cai *et al.*, 2014). ASA1 is involved in the biosynthesis of tryptophan (Niyogi and Fink, 1992), which is the precursor for auxin production (Zhao, 2010). The rapid up-regulation of *ASA1* expression by ERF109 within 2 h of wounding is dependent on an epigenetic modification, that is, the pre-deposition of a trimethyl group at histone H3 lysine 36 (H3K36me3) on the *ASA1* locus by SET DOMAIN GROUP8 (SDG8) before wounding (Zhang *et al.*, 2019). This H3K36me3 epigenetic marker might be required for the rapid up-regulation of many genes induced by JA (Zhang *et al.*, 2019). After 2 h, the JA concentration decreases, resulting in the accumulation of the JAZ protein, which can directly interact with

and inhibit ERF109 to turn off the wounding signal (Zhang *et al.*, 2019). Turning off the wound signal is important, because constant JA treatment or disruption of endogenous JA homeostasis is harmful for root organogenesis (Gutierrez *et al.*, 2012; Zhang *et al.*, 2019; Lakehal *et al.*, 2019, 2020; Alallaq *et al.*, 2020). Recent studies have indicated that JA inhibits adventitious rooting from Arabidopsis hypocotyls via repression of the cytokinin degradation pathway gene *CYTOKININ OXIDASE/DEHYDROGENASE1* (*CKX1*) and activation of the expression of *RAP2.6L* and *ERF115* (Lakehal *et al.*, 2020; Dob *et al.*, 2021; Pan *et al.*, 2021), and that red light can promote adventitious rooting by preventing the accumulation of JA and cytokinin (Alallaq *et al.*, 2020). Overall, the JA peak after wounding boosts auxin production to promote *de novo* root regeneration from leaf cuttings, and a strict turning-off of the JA signal is also required for root organogenesis (Fig. 1D).

The root regenerative capacity declines as plants age (Greenwood *et al.*, 2001; Díaz-Sala, 2014; Rasmussen *et al.*, 2015; Xu *et al.*, 2016; Pan *et al.*, 2019; Ye *et al.*, 2020). A recent study revealed that the age pathway can crosstalk with JA and auxin in the regulation of *de novo* root regeneration (Ye *et al.*, 2020) (Fig. 1D). In Arabidopsis, as the plant ages, the microRNA156 (miR156) level decreases, resulting in the accumulation of transcripts of its targets, *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE* (*SPL*) genes (Poethig, 2009; Wang, 2014). *SPL2*, *SPL10,* and *SPL11* are specifically involved in the regulation of rooting from leaf cuttings (Ye *et al.*, 2020). In aged leaves, SPL2, SPL10, and SPL11 can inhibit JA-mediated auxin biosynthesis by repressing the expression of the AP2/ERF transcription factor genes *ERF109* and *ABSCISIC ACID REPRESSOR1* (*ABR1*), both of which are involved in wound- and JA-induced auxin production (Zhang *et al.*, 2019; Ye *et al.*, 2020). Therefore, as the plant ages, it becomes less sensitive to the wound hormone JA during regeneration.

Roles of JA in *de novo* shoot regeneration in tissue culture

Adventitious shoots can regenerate from non-embryonic callus in tissue culture. In tissue culture, detached explants are cultured on callus-inducing medium (CIM), which has a high ratio of auxin to cytokinin, to produce non-embryonic callus. The callus can then be moved to shoot-inducing medium (SIM), which has a high ratio of cytokinin to auxin, to regenerate adventitious shoots (Skoog and Miller, 1957).

The role of JA in *de novo* shoot regeneration is less well understood. An indication came from experiments using Arabidopsis hypocotyl explants treated with JA (Park *et al.*, 2019) (Fig. 1E). In that study, hypocotyl explants pre-treated with JA before culture on CIM showed enhanced shoot regeneration on SIM, while JA treatment of explants already on CIM did not enhance shoot regeneration on SIM. This might indicate that pre-treatment with JA activates some regeneration-promoting genes in the hypocotyl explants (Park *et al.*, 2019). The authors also showed that mutations in the JA-signalling pathway gene *COI1* impair shoot regeneration in tissue culture (Park *et al.*, 2019), suggesting that the endogenous JA-signalling pathway is involved in *de novo* shoot regeneration. However, the molecular mechanism underlying the role of JA in *de novo* shoot regeneration in tissue culture is still largely unclear. A recent study indicated that endogenous auxin accumulation in callus is important for organ regeneration (Zhai and Xu, 2021). In future studies, it will be interesting to test whether pre-treatment with JA affects the accumulation of endogenous auxin in hypocotyl explants.

Roles of JA in somatic embryogenesis

Plant somatic cells can undergo dedifferentiation to form somatic embryos (Horstman *et al.*, 2017; Méndez-Hernández *et al.*, 2019; Wójcik *et al.*, 2020; Salaün *et al.*, 2021). Usually, somatic embryos form either directly from somatic cells or indirectly from embryonic callus in tissue culture. Auxin is the key hormone that triggers cell dedifferentiation and somatic embryo formation (Su *et al.*, 2009; Wang *et al.*, 2020*b*). Several studies have indicated that JA might also have a role in the regulation of somatic embryogenesis in diverse species.

During somatic embryogenesis in *Medicago sativa*, endogenous JA accumulates in the developing somatic embryos (Ruduś *et al.*, 2005, 2009). However, JA treatment can inhibit somatic embryogenesis in *M. sativa* (Kepczynski and Florek, 1997; Ruduś *et al.*, 2001, 2006) and carrot (*Daucus carota*) (Tokuji *et al.*, 1995). In *Brassica napus,* the application of exogenous JA as well as abscisic acid and SA at an appropriate concentration can promote microspore embryogenesis (Ahmadi *et al.*, 2014). The application of JA can also promote somatic embryogenesis in saffron (*Crocus sativus*) (Blázquez *et al.*, 2004).

Studies on Arabidopsis have shed light on the role of JA in somatic embryogenesis (Elhiti *et al.*, 2013; Mira *et al.*, 2016) (Fig. 1F). Supplying JA at an appropriate concentration in the medium can promote somatic embryogenesis, whereas JA at a very high concentration inhibits somatic embryogenesis in Arabidopsis. Thus, the concentration of JA is critical for its function. Mutations in the genes involved in JA biosynthesis result in the reduced formation of somatic embryos. JA promotes somatic embryogenesis through promoting the expression of genes involved in auxin production (e.g. *ASA1* and *YUCCA*). In addition, nitric oxide (NO), which is negatively regulated by *PHYTOGLOBIN2* (*PGB2*), promotes JA biosynthesis and regulates the JA-signalling pathway. Therefore, the *PGB2*-NO-JA-auxin crosstalk might form a regulatory network that controls the efficiency of cell dedifferentiation and somatic embryo formation (Mira *et al.*, 2016).

Because JA has been found to both inhibit and promote somatic embryogenesis in diverse plant species, it is possible that plants are very sensitive to the concentration of JA as well as its spatial and temporal patterns. This could be the same in *de novo* root regeneration and probably other plant regeneration processes as well. One possibility is that JA may crosstalk with auxin and/or cytokinin under different physiological conditions (Zhang *et al.*, 2019; Alallaq *et al.*, 2020; Lakehal *et al.*, 2020; Dob *et al.*, 2021; Pan *et al.*, 2021).

Conclusion

JA is involved in many types of plant regeneration, including tissue repair, wound-induced callus formation, *de novo* organ regeneration, and somatic embryogenesis (summarized in Fig. 1). The common theme of JA in plant regeneration is the link between wounding and cell fate transition, and JA might be very strictly sensed and controlled by the cell during regeneration. Currently, our understanding of the network of wound signals involved in regeneration is very limited. To improve our understanding, first, the molecular mechanisms of JA in different types of plant regeneration need to be further explored. Auxin and cytokinin are key hormones in almost all types of plant regeneration. Although there is some evidence for crosstalk between JA and cytokinin or auxin, the molecular framework of how these three hormones act together in regeneration—for example, in wound-induced callus formation, tissue repair, and *de novo* shoot regeneration—remains unknown. Second, wounding may produce many signals, some of which may act even faster than JA. Recent studies on wounding indicate important roles for electrical signals, Ca^{2+} waves, and glutamate in systemic wound responses (León *et al.*, 2001; Maffei *et al.*, 2007; Choi *et al.*, 2016; Hilleary and Gilroy, 2018; Toyota *et al.*, 2018; Wasternack, 2019; Moe-Lange *et al.*, 2021). Ethylene and SA are also important hormones induced by wounding. Research into the crosstalk between JA and other wound signals and hormones will shed light on the complex network involved in regeneration after wounding. Third, JA can spread very quickly through the wound site and to other tissues (Gasperini *et al.*, 2015). It will be important to determine whether JA functions as a mobile signal in plant regeneration. Fourth, single-cell damage in the Arabidopsis root activates the production of, and responses to, ethylene, but not JA or SA (Marhavý *et al.*, 2019). This might indicate that, in some cases, different types of wounding trigger responses through different signals. Overall, a comprehensive understanding of wound signalling pathways is necessary to understand how different types of regeneration are triggered in plants under different conditions.

Author contributions

GZ, WL, WZ, JL, and LX conceived and wrote the review; GZ, ZG, WZ, and LX prepared the figure; all authors discussed and revised the review.

Conflict of interest

The authors declare no competing interests.

Funding

This work was supported by the National Natural Science Foundation of China (32001293/31630007/32000175/32070874/31761133009), the National Postdoctoral Program for Innovative Talents of China (BX20200060), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB27030103), and a China Postdoctoral Science Foundation Grant (2019M660506).

References

Ahkami AH, Lischewski S, Haensch K-T, *et al*. 2009. Molecular physiology of adventitious root formation in *Petunia hybrida* cuttings: involvement of wound response and primary metabolism. New Phytologist **181**, 613–625.

Ahmadi B, Shariatpanahi ME, Teixeira da Silva JA. 2014. Efficient induction of microspore embryogenesis using abscisic acid, jasmonic acid and salicylic acid in *Brassica napus* L. Plant Cell, Tissue and Organ Culture **116**, 343–351.

Alallaq S, Ranjan A, Brunoni F, Novák O, Lakehal A, Bellini C. 2020. Red light controls adventitious root regeneration by modulating hormone homeostasis in *Picea abies* seedlings. Frontiers in Plant Science **11**, 586140.

Asahina M, Azuma K, Pitaksaringkarn W, *et al*. 2011. Spatially selective hormonal control of RAP2.6L and ANAC071 transcription factors involved in tissue reunion in *Arabidopsis*. Proceedings of the National Academy of Sciences, USA **108**, 16128–16132.

Blázquez S, Piqueras A, Serna MD, Casas JL, Fernández J-A. 2004. Somatic embryogenesis in saffron: optimisation through temporary immersion and polyamine metabolism. Acta Horticulturae **650**, 269–276.

Cai X-T, Xu P, Zhao P-X, Liu R, Yu L-H, Xiang C-B. 2014. *Arabidopsis* ERF109 mediates cross-talk between jasmonic acid and auxin biosynthesis during lateral root formation. Nature Communications **5**, 5833.

Chen X, Qu Y, Sheng L, Liu J, Huang H, Xu L. 2014. A simple method suitable to study *de novo* root organogenesis. Frontiers in Plant Science **5**, 1–6.

Chen L, Sun B, Xu L, Liu W. 2016. Wound signaling: the missing link in plant regeneration. Plant Signaling & Behavior **11**, e1238548.

Chini A, Fonseca S, Fernández G, *et al*. 2007. The JAZ family of repressors is the missing link in jasmonate signalling. Nature **448**, 666–671.

Choi W-G, Hilleary R, Swanson SJ, Kim S-H, Gilroy S. 2016. Rapid, long-distance electrical and calcium signaling in plants. Annual Review of Plant Biology **67**, 287–307.

Chung HS, Koo AJK, Gao X, Jayanty S, Thines B, Jones AD, Howe GA. 2008. Regulation and function of Arabidopsis *JASMONATE ZIM*-domain genes in response to wounding and herbivory. Plant Physiology **146**, 952–964.

Díaz-Sala C. 2014. Direct reprogramming of adult somatic cells toward adventitious root formation in forest tree species: the effect of the juvenile-adult transition. Frontiers in Plant Science **5**, 310.

Dob A, Lakehal A, Novak O, Bellini C. 2021. Jasmonate inhibits adventitious root initiation through repression of *CKX1* and activation of RAP2.6L transcription factor in Arabidopsis. Journal of Experimental Botany **72**, 7107–7118.

Efroni I, Mello A, Nawy T, Ip P-L, Rahni R, DelRose N, Powers A, Satija R, Birnbaum KD. 2016. Root regeneration triggers an embryo-like sequence guided by hormonal interactions. Cell **165**, 1721–1733.

Elhiti M, Hebelstrup KH, Wang A, Li C, Cui Y, Hill RD, Stasolla C. 2013. Function of type-2 Arabidopsis hemoglobin in the auxin-mediated

formation of embryogenic cells during morphogenesis. The Plant Journal **74**, 946–958.

Fan M, Xu C, Xu K, Hu Y. 2012. LATERAL ORGAN BOUNDARIES DOMAIN transcription factors direct callus formation in *Arabidopsis* regeneration. Cell Research **22**, 1169–1180.

Fattorini L, Falasca G, Kevers C, Mainero Rocca L, Zadra C, Altamura MM. 2009. Adventitious rooting is enhanced by methyl jasmonate in tobacco thin cell layers. Planta **231**, 155–168.

Fattorini L, Hause B, Gutierrez L, Veloccia A, Della Rovere F, Piacentini D, Falasca G, Altamura MM. 2018. Jasmonate promotes auxin-induced adventitious rooting in dark-grown *Arabidopsis thaliana* seedlings and stem thin cell layers by a cross-talk with ethylene signalling and a modulation of xylogenesis. BMC Plant Biology **18**, 182.

Feldman LJ. 1976. The *de novo* origin of the quiescent center regenerating root apices of *Zea mays*. Planta **128**, 207–212.

Feys B, Benedetti CE, Penfold CN, Turner JG. 1994. Arabidopsis mutants selected for resistance to the phytotoxin coronatine are male sterile, insensitive to methyl jasmonate, and resistant to a bacterial pathogen. The Plant Cell **6**, 751–759.

Gasperini D, Chauvin A, Acosta IF, Kurenda A, Stolz S, Chetelat A, Wolfender J-L, Farmer EE. 2015. Axial and radial oxylipin transport. Plant Physiology **169**, 2244–2254.

Glauser G, Grata E, Dubugnon L, Rudaz S, Farmer EE, Wolfender J-L. 2008. Spatial and temporal dynamics of jasmonate synthesis and accumulation in *Arabidopsis* in response to wounding. Journal of Biological Chemistry **283**, 16400–16407.

Greenwood MS, Cui X, Xu F. 2001. Response to auxin changes during maturation-related loss of adventitious rooting competence in loblolly pine (*Pinus taeda*) stem cuttings. Physiologia Plantarum **111**, 373–380.

Gutierrez L, Mongelard G, Floková K, *et al*. 2012. Auxin controls *Arabidopsis* adventitious root initiation by regulating jasmonic acid homeostasis. The Plant Cell **24**, 2515–2527.

Han G-Z. 2017. Evolution of jasmonate biosynthesis and signaling mechanisms. Journal of Experimental Botany **68**, 1323–1331.

He C, Chen X, Huang H, Xu L. 2012. Reprogramming of H3K27me3 is critical for acquisition of pluripotency from cultured *Arabidopsis* tissues. PLoS Genetics **8**, e1002911.

Hellmann E, Helariutta Y. 2019. Plant genetics: advances in regeneration pathways. Current Biology **29**, R702–R704.

Heyman J, Cools T, Canher B, *et al*. 2016. The heterodimeric transcription factor complex ERF115–PAT1 grants regeneration competence. Nature Plants **2**, 16165.

Heyman J, Cools T, Vandenbussche F, *et al*. 2013. ERF115 controls root quiescent center cell division and stem cell replenishment. Science **342**, 860–863.

Hilleary R, Gilroy S. 2018. Systemic signaling in response to wounding and pathogens. Current Opinion in Plant Biology **43**, 57–62.

Hitchcock AE, Zimmerman PW. 1936. Effect of the use of growth substances on the rooting response of cuttings. Contributions from Boyce Thompson Institute **8**, 63–79.

Horstman A, Li M, Heidmann I, Weemen M, Chen B, Muino JM, Angenent GC, Boutilier K. 2017. The BABY BOOM transcription factor activates the LEC1-ABI3-FUS3-LEC2 network to induce somatic embryogenesis. Plant Physiology **175**, 848–857.

Ikeuchi M, Favero DS, Sakamoto Y, Iwase A, Coleman D, Rymen B, Sugimoto K. 2019. Molecular mechanisms of plant regeneration. Annual Review of Plant Biology **70**, 377–406.

Ikeuchi M, Iwase A, Rymen B, *et al*. 2017. Wounding triggers callus formation via dynamic hormonal and transcriptional changes. Plant Physiology **175**, 1158–1174.

Ikeuchi M, Sugimoto K, Iwase A. 2013. Plant callus: mechanisms of induction and repression. The Plant Cell **25**, 3159–3173.

Iwase A, Harashima H, Ikeuchi M, *et al*. 2017. WIND1 promotes shoot regeneration through transcriptional activation of *ENHANCER OF SHOOT REGENERATION1* in Arabidopsis. The Plant Cell **29**, 54–69.

Iwase A, Mitsuda N, Koyama T, *et al*. 2011. The AP2/ERF transcription factor WIND1 controls cell dedifferentiation in *Arabidopsis*. Current Biology **21**, 508–514.

Jeffree CE, Yeoman MM. 1983. Development of intercellular connections between opposing cells in a graft union. New Phytologist **93**, 491–509.

Kepczynski J, Florek I. 1997. The influence of JA-Me and ABA on induction of somatic embryogenesis in *Medicago sativa* L. tissue cultures. In: Ellis RH, Black M, Murdoch AJ, Hong TD, eds. Basic and applied aspects of seed biology. Current Plant Science and Biotechnology in Agriculture, vol. **30**. Dordrecht: Springer, 137–140.

Koo AJK, Gao X, Daniel Jones A, Howe GA. 2009. A rapid wound signal activates the systemic synthesis of bioactive jasmonates in Arabidopsis. The Plant Journal **59**, 974–986.

Lakehal A, Dob A, Novák O, Bellini C. 2019. A DAO1-mediated circuit controls auxin and jasmonate crosstalk robustness during adventitious root initiation in *Arabidopsis*. International Journal of Molecular Sciences **20**, 4428.

Lakehal A, Dob A, Rahneshan Z, Novák O, Escamez S, Alallaq S, Strnad M, Tuominen H, Bellini C. 2020. *ETHYLENE RESPONSE FACTOR 115* integrates jasmonate and cytokinin signaling machineries to repress adventitious rooting in *Arabidopsis*. New Phytologist **228**, 1611–1626.

León J, Rojo E, Sánchez-Serrano JJ. 2001. Wound signalling in plants. Journal of Experimental Botany **52**, 1–9.

Lischweski S, Muchow A, Guthörl D, Hause B. 2015. Jasmonates act positively in adventitious root formation in petunia cuttings. BMC Plant Biology **15**, 229.

Liu J, Sheng L, Xu Y, Li J, Yang Z, Huang H, Xu L. 2014. *WOX11* and *12* are involved in the first-step cell fate transition during de novo root organogenesis in *Arabidopsis*. The Plant Cell **26**, 1081–1093.

Lup SD, Tian X, Xu J, Pérez-Pérez JM. 2016. Wound signaling of regenerative cell reprogramming. Plant Science **250**, 178–187.

Maffei ME, Mithöfer A, Boland W. 2007. Before gene expression: early events in plant–insect interaction. Trends in Plant Science **12**, 310–316.

Marhava P, Hoermayer L, Yoshida S, Marhavý P, Benková E, Friml J. 2019. Re-activation of stem cell pathways for pattern restoration in plant wound healing. Cell **177**, 957–969.e13.

Marhavý P, Kurenda A, Siddique S, Dénervaud Tendon V, Zhou F, Holbein J, Hasan MS, Grundler FM, Farmer EE, Geldner N. 2019. Single-cell damage elicits regional, nematode-restricting ethylene responses in roots. The EMBO Journal **38**, e100972.

Matosevich R, Efroni I. 2021. The quiescent center and root regeneration. Journal of Experimental Botany **72**, 6739–6745.

Matsuoka K, Yanagi R, Yumoto E, Yokota T, Yamane H, Satoh S, Asahina M. 2018. RAP2.6L and jasmonic acid–responsive genes are expressed upon Arabidopsis hypocotyl grafting but are not needed for cell proliferation related to healing. Plant Molecular Biology **96**, 531–542.

Melnyk CW. 2017. Plant grafting: insights into tissue regeneration. Regeneration **4**, 3–14.

Melnyk CW, Gabel A, Hardcastle TJ, Robinson S, Miyashima S, Grosse I, Meyerowitz EM. 2018. Transcriptome dynamics at *Arabidopsis* graft junctions reveal an intertissue recognition mechanism that activates vascular regeneration. Proceedings of the National Academy of Sciences, USA **115**, E2447–E2456.

Melnyk CW, Schuster C, Leyser O, Meyerowitz EM. 2015. A developmental framework for graft formation and vascular reconnection in *Arabidopsis thaliana*. Current Biology **25**, 1306–1318.

Méndez-Hernández HA, Ledezma-Rodríguez M, Avilez-Montalvo RN, Juárez-Gómez YL, Skeete A, Avilez-Montalvo J, De-la-Peña C, Loyola-Vargas VM. 2019. Signaling overview of plant somatic embryogenesis. Frontiers in Plant Science **10**, 77.

Mira MM, Wally OSD, Elhiti M, El-Shanshory A, Reddy DS, Hill RD, Stasolla C. 2016. Jasmonic acid is a downstream component in the modulation of somatic embryogenesis by Arabidopsis Class 2 phytoglobin. Journal of Experimental Botany **67**, 2231–2246.

Moe-Lange J, Gappel NM, Machado M, *et al*. 2021. Interdependence of a mechanosensitive anion channel and glutamate receptors in distal wound signaling. Science Advances **7**, eabg4298.

Nanda AK, Melnyk CW. 2018. The role of plant hormones during grafting. Journal of Plant Research **131**, 49–58.

Niyogi KK, Fink GR. 1992. Two anthranilate synthase genes in Arabidopsis: defense-related regulation of the tryptophan pathway. The Plant Cell **4**, 721–733.

Notaguchi M, Kurotani K, Sato Y, *et al*. 2020. Cell-cell adhesion in plant grafting is facilitated by β-1,4-glucanases. Science **369**, 698–702.

Pan X, Yang Z, Xu L. 2021. Dual roles of jasmonate in adventitious rooting. Journal of Experimental Botany **72**, 6808–6810.

Pan J, Zhao F, Zhang G, *et al*. 2019. Control of *de novo* root regeneration efficiency by developmental status of *Arabidopsis* leaf explants. Journal of Genetics and Genomics **46**, 133–140.

Park O-S, Bae SH, Kim S-G, Seo PJ. 2019. JA-pretreated hypocotyl explants potentiate *de novo* shoot regeneration in Arabidopsis. Plant Signaling & Behavior **14**, 1618180.

Poethig RS. 2009. Small RNAs and developmental timing in plants. Current Opinion in Genetics & Development **19**, 374–378.

Rasmussen A, Hosseini SA, Hajirezaei M-R, Druege U, Geelen D. 2015. Adventitious rooting declines with the vegetative to reproductive switch and involves a changed auxin homeostasis. Journal of Experimental Botany **66**, 1437–1452.

Ruan J, Zhou Y, Zhou M, Yan J, Khurshid M, Weng W, Cheng J, Zhang K. 2019. Jasmonic acid signaling pathway in plants. International Journal of Molecular Sciences **20**, 2479.

Ruduś I, Kępczyński J, Kępczyńska E. 2001. The influence of the jasmonates and abscisic acid on callus growth and somatic embryogenesis in *Medicago sativa* L. tissue culture. Acta Physiologiae Plantarum **23**, 103–107.

Ruduś I, Kępczyńska E, Kępczyński J, Wasternack C, Miersch O. 2005. Changes in jasmonates and 12-oxophytodienoic acid contents of *Medicago sativa* L. during somatic embryogenesis. Acta Physiologiae Plantarum **27**, 497–504.

Ruduś I, Kępczyńska E, Kępczyński J. 2006. Comparative efficacy of abscisic acid and methyl jasmonate for indirect somatic embryogenesis in *Medicago sativa* L. Plant Growth Regulation **48**, 1–11.

Ruduś I, Weiler EW, Kępczyńska E. 2009. Do stress-related phytohormones, abscisic acid and jasmonic acid play a role in the regulation of *Medicago sativa* L. somatic embryogenesis? Plant Growth Regulation **59**, 159–169.

Salaün C, Lepiniec L, Dubreucq B. 2021. Genetic and molecular control of somatic embryogenesis. Plants **10**, 1467.

Sena G, Wang X, Liu HY, Hofhuis H, Birnbaum KD. 2009. Organ regeneration does not require a functional stem cell niche in plants. Nature **457**, 1150–1153.

Skoog F, Miller CO. 1957. Chemical regulation of growth and organ formation in plant tissues cultured in vitro. Symposia of the Society for Experimental Biology **11**, 118–130.

Su YH, Zhao XY, Liu YB, Zhang CL, O'Neill SD, Zhang XS. 2009. Auxin-induced *WUS* expression is essential for embryonic stem cell renewal during somatic embryogenesis in Arabidopsis. The Plant Journal **59**, 448–460.

Sugimoto K, Gordon SP, Meyerowitz EM. 2011. Regeneration in plants and animals: dedifferentiation, transdifferentiation, or just differentiation? Trends in Cell Biology **21**, 212–218.

Sugimoto K, Jiao Y, Meyerowitz EM. 2010. *Arabidopsis* regeneration from multiple tissues occurs via a root development pathway. Developmental Cell **18**, 463–471.

Sun J, Xu Y, Ye S, *et al*. 2009. *Arabidopsis ASA1* is important for jasmonate-mediated regulation of auxin biosynthesis and transport during lateral root formation. The Plant Cell **21**, 1495–1511.

Sussex IM. 2008. The scientific roots of modern plant biotechnology. The Plant Cell **20**, 1189–1198.

Thimann KV, Went FW. 1934. On the chemical nature of the root forming hormone. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and Medical Sciences **37**, 456–459.

Thines B, Katsir L, Melotto M, Niu Y, Mandaokar A, Liu G, Nomura K, He SY, Howe GA, Browse J. 2007. JAZ repressor proteins are targets of the SCF^{COI1} complex during jasmonate signalling. Nature **448**, 661–665.

Tokuji Y, Mizue Y, Masuda H. 1995. Effects of methyljasmonate and concanavalin A on embryogenesis and the induction of secondary somatic embryos of carrot. Bioscience, Biotechnology, and Biochemistry **59**, 1675–1678.

Toyota M, Spencer D, Sawai-Toyota S, Jiaqi W, Zhang T, Koo AJ, Howe GA, Gilroy S. 2018. Glutamate triggers long-distance, calcium-based plant defense signaling. Science **361**, 1112–1115.

van den Berg C, Willemsen V, Hage W, Weisbeek P, Scheres B. 1995. Cell fate in the *Arabidopsis* root meristem determined by directional signalling. Nature **378**, 62–65.

van den Berg C, Willemsen V, Hendriks G, Weisbeek P, Scheres B. 1997. Short-range control of cell differentiation in the *Arabidopsis* root meristem. Nature **390**, 287–289.

Wang J-W. 2014. Regulation of flowering time by the miR156-mediated age pathway. Journal of Experimental Botany **65**, 4723–4730.

Wang J, Li D, Chen N, Chen J, Mu C, Yin K, He Y, Liu H. 2020a. Plant grafting relieves asymmetry of jasmonic acid response induced by wounding between scion and rootstock in tomato hypocotyl. PLoS One **15**, e0241317.

Wang F-X, Shang G-D, Wu L-Y, Xu Z-G, Zhao X-Y, Wang J-W. 2020b. Chromatin accessibility dynamics and a hierarchical transcriptional regulatory network structure for plant somatic embryogenesis. Developmental Cell **54**, 742–757.e8.

Wasternack C. 2019. New light on local and systemic wound signaling. Trends in Plant Science **24**, 102–105.

Wasternack C, Song S. 2017. Jasmonates: biosynthesis, metabolism, and signaling by proteins activating and repressing transcription. Journal of Experimental Botany **68**, 1303–1321.

Wójcik AM, Wójcikowska B, Gaj MD. 2020. Current perspectives on the auxin-mediated genetic network that controls the induction of somatic embryogenesis in plants. International Journal of Molecular Sciences **21**, 1333.

Xie DX, Feys BF, James S, Nieto-Rostro M, Turner JG. 1998. *COI1*: an *Arabidopsis* gene required for jasmonate-regulated defense and fertility. Science **280**, 1091–1094.

Xu L. 2018. *De novo* root regeneration from leaf explants: wounding, auxin, and cell fate transition. Current Opinion in Plant Biology **41**, 39–45.

Xu J, Hofhuis H, Heidstra R, Sauer M, Friml J, Scheres B. 2006. A molecular framework for plant regeneration. Science **311**, 385–388.

Xu L, Huang H. 2014. Genetic and epigenetic controls of plant regeneration. Current Topics in Developmental Biology **108**, 1–33.

Xu M, Hu T, Zhao J, Park M-Y, Earley KW, Wu G, Yang L, Poethig RS. 2016. Developmental functions of miR156-regulated *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL)* genes in *Arabidopsis thaliana*. PLoS Genetics **12**, e1006263.

Yan Y, Stolz S, Chételat A, Reymond P, Pagni M, Dubugnon L, Farmer EE. 2007. A downstream mediator in the growth repression limb of the jasmonate pathway. The Plant Cell **19**, 2470–2483.

Yan J, Zhang C, Gu M, *et al*. 2009. The *Arabidopsis* CORONATINE INSENSITIVE1 protein is a jasmonate receptor. The Plant Cell **21**, 2220–2236.

Ye B-B, Shang G-D, Pan Y, Xu Z-G, Zhou C-M, Mao Y-B, Bao N, Sun L, Xu T, Wang J-W. 2020. AP2/ERF transcription factors integrate age and wound signals for root regeneration. The Plant Cell **32**, 226–241.

Yin H, Yan B, Sun J, Jia P, Zhang Z, Yan X, Chai J, Ren Z, Zheng G, Liu H. 2012. Graft-union development: a delicate process that involves cell–cell communication between scion and stock for local auxin accumulation. Journal of Experimental Botany **63**, 4219–4232.

Zhai N, Xu L. 2021. Pluripotency acquisition in the middle cell layer of callus is required for organ regeneration. Nature Plants **7**, 1453–1460.

Zhang G, Zhao F, Chen L, *et al*. 2019. Jasmonate-mediated wound signalling promotes plant regeneration. Nature Plants **5**, 491–497.

Zhao Y. 2010. Auxin biosynthesis and its role in plant development. Annual Review of Plant Biology **61**, 49–64.

Zhou W, Lozano-Torres JL, Blilou I, Zhang X, Zhai Q, Smant G, Li C, Scheres B. 2019. A jasmonate signaling network activates root stem cells and promotes regeneration. Cell **177**, 942–956.e14.

Zimmerman PW, Wilcoxon F. 1935. Several chemical growth substances which cause initiation of roots and other responses in plants. Contributions from Boyce Thompson Institute **7**, 209–229.