Turkish Journal of Botany

Volume 46 | Number 5 Article 2

1-1-2022

# Role of MORE AXILLARY GROWTH2 (MAX2) protein in regulation of karrikin and strigolactone signalling pathways

SARIKA SINGH

MOIN UDDIN

M. MASROOR A. KHAN

SOBIA AMAN CHISHTI

SANGRAM SINGH

*See next page for additional authors*

# Role of MORE AXILLARY GROWTH2 (MAX2) protein in regulation of karrikin and strigolactone signalling pathways

Authors
SARIKA SINGH, MOIN UDDIN, M. MASROOR A. KHAN, SOBIA AMAN CHISHTI, SANGRAM SINGH, and UROOJ HASSAN BHATT

TÜBİTAK

Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Review Article

Turk J Bot
(2022) 46: 417-434

doi:10.55730/1300-008X.2720

# Role of MORE AXILLARY GROWTH 2 (MAX2) protein in regulation of karrikin and strigolactone signalling pathways

**Sarika SINGH[1,*], Moin UDDIN[2], M. Masroor A. KHAN[1], Sobia Aman CHISHTI[1], Sangram SINGH[1], Urooj Hassan BHATT[1]**

[1]Section of Plant Physiology, Department of Botany, Faculty of Life Sciences, Aligarh Muslim University, India

[2]Section of Botany, Women's College, Aligarh Muslim University, India

**Received:** 03.05.2022 • **Accepted/Published Online:** 11.08.2022 • **Final Version:** 19.09.2022

**Abstract:** MORE AXILLARY GROWTH 2 (MAX2) is an F-box protein, containing leucine-rich repeats. It is a common regulator in signalling pathways of both karrikin and strigolactone, and has several homologs such as MAX1, MAX3, and MAX4, which play a key role in the biosynthesis of strigolactone. It also interacts with various receptors and repressors of karrikin and strigolactone. Karrikins are a group of plant growth regulators found in the smoke of burning plant material and had the ability to stimulate seed germination, whereas strigolactone is a newly discovered plant hormone that regulates shoot and root branching and plays a vital role in hypocotyl growth and photomorphogenesis; strigolactone also helps in establishing the symbiosis between root and arbuscular mycorrhizal fungi regarding symbiosis. MAX2 protein also acts against drought, salt, and osmotic stresses. It interacts with various phytohormones in order to regulate seed germination as well as shoot and root branching. This review discusses about the relationship of MAX2 protein with other proteins and repressors during signalling pathways of karrikin and strigolactone and their antagonistic effects on seed and plant's life.

**Key words:** MAX2, F-box protein, strigolactone, karrikin, KAI2, SMXL

## 1. Introduction

The five major plant growth hormones are auxin, gibberellin, cytokinin, abscisic acid and ethylene, which help in growth and development of plant. In addition, there are several chemical substances like brassinosteroids, strigolactone, polyamines, karrikins, nitric oxide, etc., which exert regulatory effects on the growth and development of plants. Besides, karrikin and strigolactone are the two paralogs of butenolide class molecules that show distinct effects on plant growth (Brewer et al., 2013; Nelson et al., 2012). Karrikin is derived from smoke saturated water (SSW), whereas strigolactone is a plant hormone. Both of these growth regulators display similarity in signalling mechanism (Morffy et al., 2016).

### 1.1. Karrikin, a smoke derived compound

Karrikin ($KAR_1$) is a member of butenolide family, found in the smoke, generated by burning the plant material (Morffy et al., 2016). Karrikin is a seed germination enhancer that regulates seedling photosensitivity, seed germination, seed outgrowth, and plant development. Karrikin was purified by chemists using spectroscopic analysis in 2004 from plant derived smoke, and was named 3-methyl-2H-furo [2, 3-c] pyran-2-one. It is effective in concentration as low as 1 nanomolar. $KAR_1$ and various other analogs ($KAR_2$-$KAR_6$) of butenolide form a family called Karrikins (Figure 1) (Flemmati et al., 2004; Flematti et al., 2007), are also detected in smoke, such as $KAR_2$-$KAR_6$ that shows regulatory effect on seed germination and seedling growth. For example, in a study on *Avena fatua* L, KAR1 was reported to regulate the antioxidant (ROS) status in the embryo and aleurone layer in addition to breaking the seed dormancy and boosting the seed germination (Kepczynski, 2018). According to a recent proteomic study, conducted by Baldrianova et al. (2015) on *Arabidopsis* seedlings, out of more than 1900 proteins, there were identified 113 proteins (involved in carbohydrate metabolism, photosynthesis, protein synthesis, protein transport and processing, redox homeostasis, protein degradation, etc.), which responded positively to karrikin treatment. In a recent report, both $KAR_1$ and $KAR_2$, found in smoke solutions, played a significant role in stimulation of seed germination and plant growth (Gupta et al., 2020).

### 1.2. Strigolactone

Strigolactone (SL) is a class of plant hormones that stimulates branching in plants and the growth of symbiotic arbuscular mycorrhizal fungi (AMF) in the soil (Umehara,

* Correspondence: sarasingh6494@gmail.com

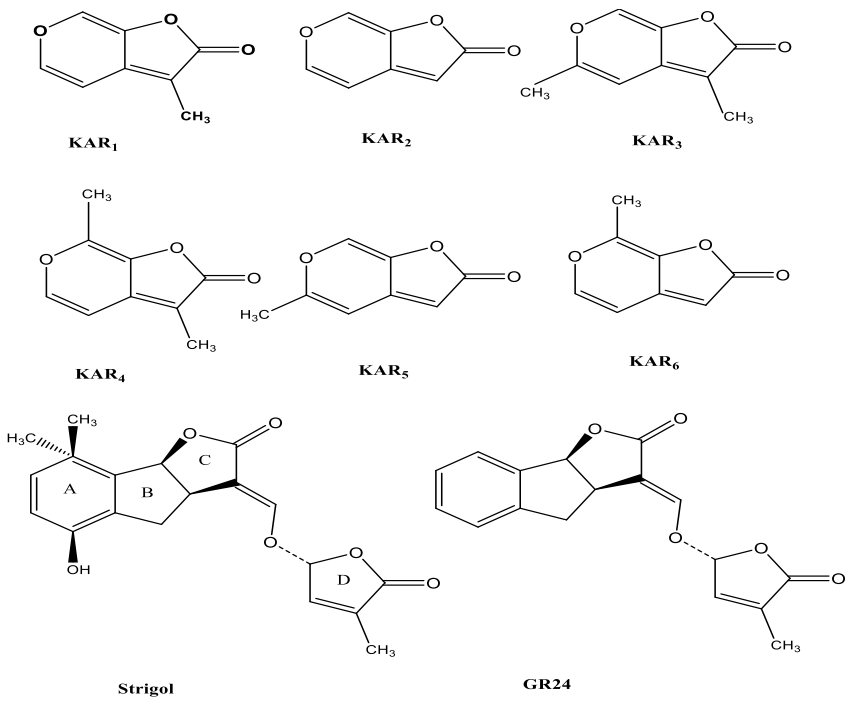


**Figure 1.** Structures of various karrikins ($KAR_1$– $KAR_6$), strigol and GR24 (synthetic strigol), showing common butenolide moieties, which attribute to their functional activities.

2011). Natural SL [(+)-strigol] was initially obtained from cotton root exudates, which were capable of stimulating the seed germination of *Striga lutea*, a root parasitic plant (Cook et al., 1972). From their roots, plants generally release multiple SL species (SLs) capable of inducing the seed germination of root parasitic-plant species (Xie et al., 2010). In fact, seeds of several obligate parasites germinate by the action of the SLs released by plant roots into the soil (Yoneyama et al., 2010). SLs, released by the plant roots, attract the AMF for building a symbiosis that provides the host plant with minerals and water, supplying the fungal partner (AMF) with carbohydrates in return (Gutjahr and Parniske, 2013).

In addition to stimulating the growth of symbiotic AMF in the soil, SLs have also been recognized as a class of plant hormones that regulate various plant development processes like root development, hypocotyls growth, secondary growth, etc. According to Kapulnik et al. (2011), SLs affected the root development in Arabidopsis, reducing the number of lateral roots and increasing the number of root hairs in the presence of a synthetic SL analog GR24. According to different studies (Koltai et al., 2011; Brewer et al., 2013), several species of SL inhibited the shoot branching, shaped the root architecture, promoted the leaf senescence, and regulated the secondary growth of plants. Several studies (de Saint et al., 2013; Qiao et al (2020)) suggested that SLs might also contribute to biotic and abiotic stress responses of plants. Under severe stress conditions, like those of drought, salinity, heat, and heavy metals, SL accumulates inside the plant cell and regulates various hormonal pathways, resulting in mitigation of stressful conditions (Bhoi et al., 2021).

Strigolactones are a group of terpenoid lactones that are synthesized from carotenoids (Mastusova et al., 2005). They are derived from a precursor, named carlactone, which is later converted into carlactonic acid (a carboxylated metabolite) with the help of MAX1 protein. Strigolactone is synthesized from all-trans-β-carotene by the sequential action of five significant components, i.e. *D27, CCD7 (MAX3, D17/HDT1, RMS5, DAD3), CCD8 (MAX4, D10, RMS1, DAD1), MAX1* and *LBO (LATERAL BRANCHING OXIDOREDUCTASE)* (Figure 2). All-trans-β-carotene is changed into 9-cis-β-carotene with the help of D27, which is later cleaved to 9-cis-β-apo-10'-carotenal by CCD7 (Burger and Chory, 2020). This is later converted into carlactone (biosynthetic precursor) via CCD8. This biosynthetic precursor then leads to the formation of carlactonic acid with the action of MAX1 via 19-hydroxy-carlactone. Carlactonic acid is later converted into methyl carlactonoate (MeCLA) with the help of methyltransferase. MeCLA suppresses the shoot branching, but the MeCLA can further be converted into strigol like compound, which plays as a final role in signalling mechanism (Dieckmann et al., 2018). Component D14 is the receptor of SL. In

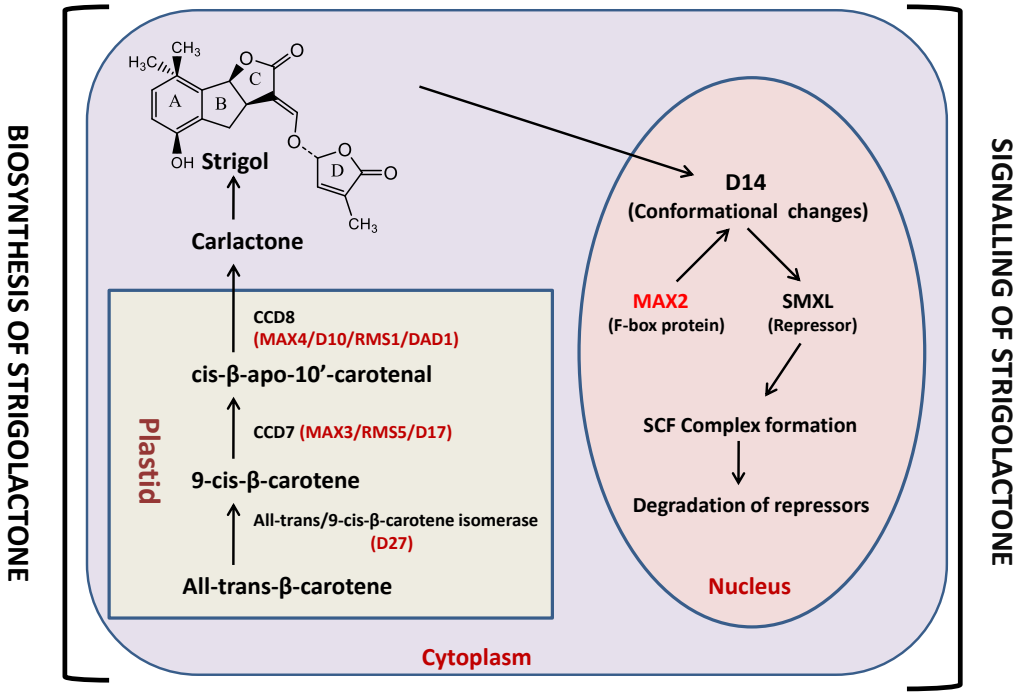


**Figure 2.** Strigolactone formation and signalling in the cell organelles. Strigolactone is synthesized in plastids from all-trans-β-carotene by the sequential action of the proteins *D27*, *MAX3*, *MAX4* and *MAX1*. Strigol hormone is later perceived by D14 receptor in the nucleus and forms a SCF complex (F-box containing complex) with *MAX2* and *SMXL7* (a repressor) for the degradation of repressors.
Abbreviations: *D10, DWARF10; D14, DWARF14; D27, DWARF27; DAD1, DECREASED APICAL DOMINANCE1; RMS1, RAMOSUS1; RMS5, RAMOSUS5; MAX1, MORE AXILLARY GROWTH1; MAX3, MORE AXILLARY GROWTH3; MAX4, MORE AXILLARY GROWTH4; SCF,* Skp, Cullin, F-Box*; SMXL7, SUPPRESSOR of MAX2 1 LIKE7.*

tomato, orthologs of Arabidopsis (MAX1 and SIMAX1) catalyse the formation of carlactonic acid from carlactone via formation of SID27, SICCD7, SICCD8 intermediates (Zhang et al., 2018). In the SL signalling pathway, AtDWARF14 (AtD14) is a paralogue of KAI2, which is a targeted SMXLs/DWARF53 for ubiquitin-mediated proteolysis (Soundappan et al., 2015).

### 1.3. MAX2: a common protein in strigolactone and karrikin signalling

Karrikin and SL share the partial structural similarities and both show common features in signalling mechanism and germination processes. A synthetic analog of SL, GR24, promotes seed germination like karrikin and inhibits hypocotyl elongation (Tsuchiya et al., 2010). Just like karrikin, SL also regulates COP1 ubiquitin ligase that later regulates the level of HY5 (light regulators). MAX2 is a part of SKP1-CULLIN-F-BOX (SCF) ubiquitin-ligase protein, which plays a crucial role in karrikin and SL signalling pathways (Strinberg et al., 2007; Zhao et al., 2014). MAX2 belongs to a protein subfamily of 33 members among the 692 F-box proteins found in Arabidopsis; they possess the receptors like those of auxin (*TIR1*, *AFB1*, *AFB2*, *AFB3*, *AFB5*) (Kepinski and Leyser, 2005; Walsh et al., 2006) and jasmonate (*COI1*) (Yan et al., 2009), and are the negative regulators (like *EBF1* and *EBF2*) of ethylene signalling pathway (Binder et al., 2007).

In this review, we highlight the relationship of MAX2 protein and its homologs with other receptors and with the repressors involving in karrikin and SL signalling pathways. As yet, we have also discussed the effect of MAX2 protein on seed germination, photomorphogenesis, various abiotic stresses and its crosstalk with other phytohormones.

## 2. Structural relationship between karrikin and strigolactone in signalling mechanism

There are structural and molecular similarities between karrikin and strigolactone, which may help in understanding the formation of complexes with various genes and proteins in signalling mechanism. In this section, structural similarities between chemical entities and their role in signalling mechanism are discussed. In addition, several genes and their orthologs are also compared in different plants.

### 2.1. Structural similarities in karrikin and strigolactone

Karrikin and SL share common structural moiety of a common butenolide ring, which is required for their activity. Various analogs of $KAR_1$ [2H-furo (2, 3-c) pyran-2-one] are observed with regard to methyl

group substitution at various carbon positions (C-3, C-4, C-5, and C-7) on pyran ring (Flematti et al., 2007). Accordingly, substitution of methyl group at C-3 position of $KAR_1$ accelerates seed germination activity, whereas $CH_3$-substitution at C-7 position of $KAR_6$ reduces such an activity (Flematti et al., 2007). Karrikin has a different structural identity than other plant growth hormones, but it has some structural similarity with SLs; for example, the A-ring of $KAR_1$ is analogous to the D-ring of SLs (Flematti et al., 2004). New strigolactone analogs, i.e. strigolactone 23 (3'-methyl-GR24), strigolactone 31 (Thia-3'-methyl-debranone-like molecule), and strigolactone AR36 carry the same dimethyl butenolide motifs, but they are different in structure in ABC part of the molecule. Strigolactone 23 has the same ABC part like that of GR24, whereas both strigolactone 31 and AR36 possess an aromatic ring and an acyclic carbon-ring; both are active in connection with repression of branching and elongation of main shoot in plants (Boyer et al., 2014).

Until now, there have been proposed many mechanisms that reveal how $KAR_1$ and SL are perceived by their receptors or how they elicit their responses. According to Mangnus and Zwanenburg (1992), CD part is responsible for the germination-promoting activity in GR24, in which the enol ether carbon double bond is replaced by a single bond to form a reduced analog of GR24. This double bond is essential for the activity of GR24. However, another report reveals an alternate method that supports hydrolysis of butenolide ring of karrikin and strigolactone. According to Scaffidi et al. (2012), hydrolysis of karrikin results into formation of a ketone that favors karrikin reformation by dehydrating with an acid, whereas in the case of strigolactone, cleavage of D ring from the ABC molecule takes place through Michael fashion, in which nucleophile attacks on the pyran ring and a product is obtained that further undergoes hydrolysis (Figure 3). This reaction supports that KAI2 and D14 may hydrolyze the $KAR_1$ and SL molecules, creating an intercellular signalling that changes the tertiary structure of protein.

**2.2. Molecular level analysis of karrikin and strigolactone signalling mechanism**

Two genes are essential for understanding the action of karrikin; one of them is *MAX2* (*MORE AXILARY GROWTH2*) (Smith and Li, 2014), and the other one is *KAI2* (*KARRIKIN INSENSITIVE2*) (Waters et al., 2014) (Figure 4). SL as well as of karrikin requires MAX2 for degradation of SMAX1/SMXL proteins, which in turn repress karrikin and SL (Soundappan et al., 2015). Products of these genes are analogous to DWARF14 (a SL receptor). Proposed mechanism of action of karrikin and SL starts with an addition of nucleophilic species via Michael fashion. According to Zwanenburg and Mwakaboko (2011), ABC

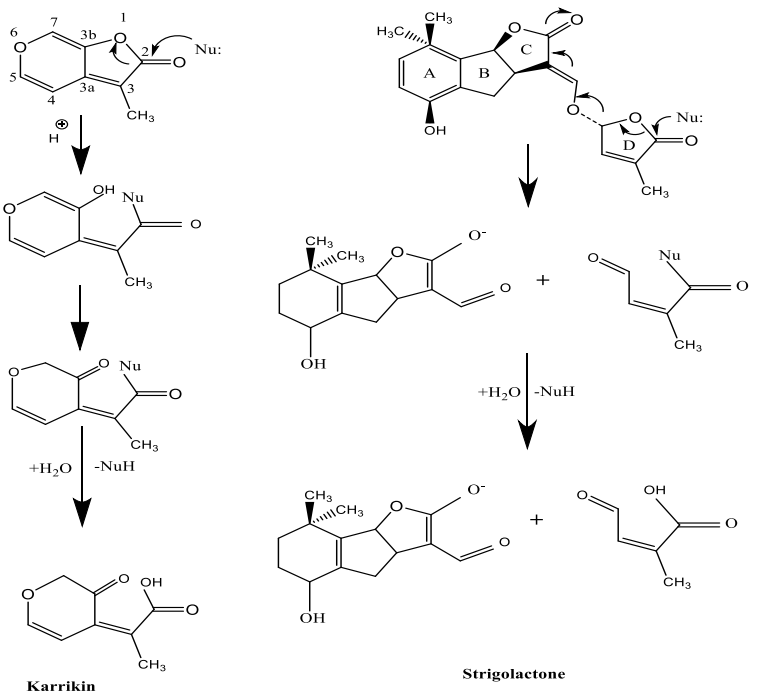


**Figure 3.** Perception of karrikin and strigolactone by KAI2 and D14 via Michael fashion and hydrolysis mechanism. Nucleophile attack at C7 position of karrikin and breakage of enol ether carbon double bond existing between C and D rings of strigolactone.

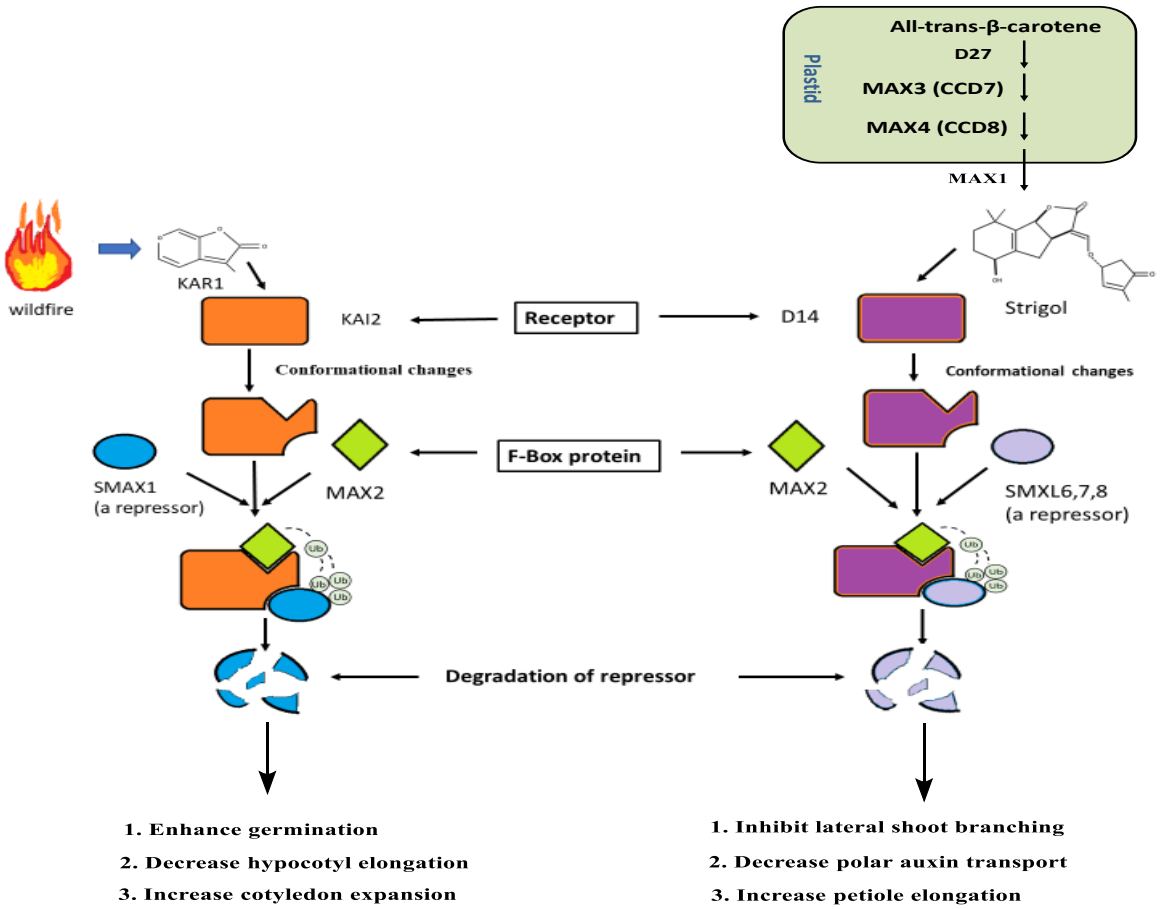


**Figure 4.** A Model of karrikin and strigolactone signaling pathways, showing the action of common F-box protein MAX2. In karrikin signalling pathway, karrikin is originated from wildfires, binds with the receptor KAI2 and makes a complex with MAX2 and the repressor SMAX1. The repressor is later degraded by the action of the SCF complex. Strigolactone biosynthesis takes place in plastids, in which carotenoids are cleaved and transformed into strigol precursor or intermediate carlactone by the sequential action of *D27*, *CCD7*, and *CCD8*. Carlactone is later transformed into strigol via MAX1. In the strigolactone signalling pathway, strigol fits in the active site of receptor D14 and makes a complex with common MAX2 protein and repressors SMXL6, 7 and 8. Later, it degrades them by proteasomal-mediated degradation.
Abbreviations: *KAI2, KARRIKIN INSENSITIVE2; D14, DWARF14; MAX2, MORE AXILLARY GROWTH2; SMXL6,7,8*, Suppressor of *MAX2 1 LIKE6,7,8; SMAX1*, Suppressor of *MAX2 1; D27, DWARF27; MAX3, MORE AXILLARY GROWTH3; MAX4, MORE AXILLLARY GROWTH4; CCD7, CAROTENOID CLEAVAGE DIOXYGENASE 7; CCD8, CAROTENOID CLEAVAGE DIOXYGENASE 8; MAX1, MORE AXILLARY GROWTH1.*

part of the SL and the enol ether bond do not contribute any important function to the activity of SL. However, Cohen et al. (2013) suggested that different substitutions at A-ring of SL affected its activity in receptor perception regarding three different organisms, i.e. Arabidopsis (root-hair elongation), *Orobanchea aegyptiaca* (seed germination) and the AMF *Glomus intraradices* (hyphal branching). According to Scaffidi et al. (2012), two potential sites (C5 and C7) of karrikin undergo nucleophilic addition on the 4-H pyran-ring (Figure 3). Each of KAI2 and D14 serves as the receptor as well as an enzyme; besides, both KAI2 and D14 are the members of the α/β hydrolase family, and each of which encodes a receptor for enzymatic activity with regard to signal transduction in plants. D14 acts with MAX2, forms a SCF complex, and degrades the proteins (repressor) of SMXL/D53 family, whereas KAI2 acts similar to D14 (Figure 4). SCF complex acts via ligating with ubiquitin moieties to target proteins, which results in their degradation via 26 proteasomal complexes (Stirnberg et al., 2007).

### 2.3. Interaction of various genes with karrikin and strigolactone in signalling/biosynthesis pathways

Different genes have been detected to regulate the karrikin and SL signalling/biosynthesis pathways in different plants as given in Table 1.

**Table 1.** Genes related to karrikin and strigolactone signalling/biosynthesis pathways.

| Pathway(s) | *Arabidopsis* | Rice | Pea | Gene function | References |
|---|---|---|---|---|---|
| Strigolactone signalling pathway | *AtD14* | *OsD14* | *RMS3* | Receptor of strigolactone and α/β fold hydrolase | Cooper et al., 2018; Waters et al., 2012; Arite et al., 2009 |
| Strigolactone biosynthesis pathway | *MAX4* | *D10* | *RMS1* | β – carotenoid cleavage (CCD8) in plastids | Challis et al., 2013; Arite et al., 2007 |
| Strigolactone biosynthesis pathway | *MAX1* | - | - | Catalytic function; it exists upstream of MAX2 | Challis et al., 2013; Strinberg et al., 2002 |
| Karrikin signalling pathway | *KAI2* | - | - | Receptor of karrikin and α/β fold hydrolase | Guo et al., 2013 |
| Karrikin and strigolactone signalling pathway | *MAX2* | *D3* | *RMS4* | F-Box leucine-rich protein, essential for arbuscular mycorrhizal fungi | Nelson et al., 2012; Yoshida et al., 2012; Johnson et al., 2006; Strinberg et al., 2002. |
| Strigolactone biosynthesis pathway | - | *D27* | - | β-carotene isomerase | Lin et al., 2009 |
| Strigolactone biosynthesis pathway | *MAX3* | *D17* | *RMS5* | β –carotenoid cleavage (CCD7) in plastids | Booker et al., 2004 |

**Abbreviations:** *AtD14,* Arabidopsis *DWARF14; CCD7, CAROTENOID CLEAVAGE DIOXYGENASE 7; CCD8, CAROTENOID CLEAVAGE DIOXYGENASE 8; D3, DWARF 3; D10, DWARF 10; D17, DWARF 17; D27, DWARF 27; KAI2, KARRIKIN INSENSITIVE 2; MAX1, MORE AXILLARY GROWTH1; MAX2, MORE AXILLARY GROWTH2; MAX3, MORE AXILLARY GROWTH3; MAX4, MORE AXILLARY GROWTH4; OsD14, Oryza sativa DWARF14; RMS1, RAMOSUS1; RMS3, RAMOSUS3; RMS4, RAMOSUS4; RMS5, RAMOSUS5.*

In Arabidopsis, gene KAI2 acts as a receptor of karrikin and forms a complex with MAX2 protein (Stirnberg et al., 2002) in order to degrade the repressors (Guo et al., 2013). Whereas in rice, different genes regulate the SL signalling pathway, such as OsD14, a paralog of AtD14 (Arabidopsis) acts as a SL receptor (Waters et al., 2012; Arite et al., 2009). On the other hand, *RMS3* acts as a SL receptor in pea (Cooper et al., 2018). As for SL biosynthesis process in Arabidopsis, MAX1, MAX3, and MAX4 act as catalytic genes, which transform all-trans-β-carotene into strigol (Booker et al., 2004). Genes *D17* and *D10* (in rice) and genes *RMS5* and *RMS1* (in pea) act as homologs of MAX3 and MAX4 (Sorefan et al., 2003; Arite et al., 2007). In rice, the homolog of MAX2 is *D3* (Yoshida et al., 2012), while in pea, it is *RMS4* (Johnson et al., 2006).

### 3. Homologs of MAX2 and their function

With regard to SL signalling pathways, there are four members of MAX protein,i.e. MAX1, MAX2, MAX3, and MAX4 in Arabidopsis. MAX1, MAX3, and MAX4 are similar to nonplant-specific genes, whereas MAX2 is related to plant genes (Challis et al., 2013). MAX2 protein is mainly conserved in land plants like Angiosperms, Gymnosperms, Pteridophytes (ferns, such as monilophytes and lycophytes), Bryophytes (mosses), etc., whereas ortholog of MAX2 protein is absent in charophyte algae (Delaux et al., 2012). A recent study conducted on *Physcomitrella patens* (a moss) supports an ancient role of SLs in land plants (Lopez-Obando et al., 2018). A MAX2 homolog, named as *PpMAX2*, is found in the cell-nucleus and helps in photomorphogenesis in the early development of *Physcomitrella patens* (Lopez-Obando et al., 2018). MAX2 protein of Arabidopsis expresses its role in leaf senescence, seedling photosensitivity, seed germination, and seedling outgrowth (Waters et al., 2012). With regard to stem and axillary bud of *Chrysanthemum*, Dong et al. (2013) reported that *DgMAX2b*, and *DgMAX2c* participated as MAX2 ortholog; in particular, these proteins helped in reducing the shoot branching. In *Glycine max*, two homologs of MAX2, i.e. *GmMAX2a* and *GmMAX2b*, exhibited maximum expression in the leaves as compared to that in the stem and root under salt stress (Qiao et al (2020)).

*MAX1* exists upstream of MAX2 in the SL signalling pathway; it shows functional diversification in Angiosperms (Challis et al., 2013). *MAX1 (CYP711A1)*, acting as cytochrome P450 monooxygenase, binds with carlactone and converts it into carlactonic acid in SL biosynthetic-pathway (Booker et al., 2005). MAX1 belongs to a member of CYP711 family that contains an anchor

in the endoplasmic reticulum towards the cytosolic side in Arabidopsis (Booker et al., 2005). *AtD27*, existing upstream of MAX1 in Arabidopsis, is another ortholog of DWARF27 (OsD27); its gene product is identified as a plastid-localized protein that inhibits secondary bud outgrowth (Waters et al., 2012). In Arabidopsis, lateral inflorescence is suppressed by exogenous application of carlactonic acid (CLA) or of its methyl ester [methyl carlactone (MeCLA)], which directly interacts with AtD14 to suppress the shoot branching (Abe et al., 2014).

For regulating shoot branching, MAX3 helps to cleave multiple carotenoids via plastidic dioxygenase (Booker et al., 2004). Besides, there is an ortholog of Arabidopsis MAX3 in rice, called *HIGH-TILLERING DWARF 1 (HTD1)*, which exercises the same function as MAX3, i.e. formation of carotenoid-derived signal molecule. *HTD1* is expressed in both root and shoot of plant, mainly in the tissues constituting the vascular bundles (Zou et al., 2006).

MAX4 is a protein utilized in the process of SL biosynthesis. In Arabidopsis, product of MAX4 protein is required for signal transduction of SL that inhibits shoot branching. Gene *RMS1 (RAMOSUS 1)* in rice and *DAD1 (DECREASED APICAL DOMINANCE 1)* in *Petunia* are orthologs to MAX4, showing similar functions (Sorefan et al., 2003; Snowden et al., 2005; Arite et al., 2007). However, location wise, *RMS1* gene, whose expression is stimulated by auxin (Foo et al., 2005), gets upregulated in nodal tissues of shoot, while MAX4 is upregulated in the root and hypocotyl region of the plant (Bainbridge et al., 2005). *Irregular xylem syndrome (irx)*, caused by defects in biosynthesis or deposition of plant secondary cell wall polymers, appears in response to stress factors such as drought and osmotic stress (Keppler and Showalter, 2010). In an Arabidopsis mutant *tbl29*, irx syndrome is dependent on MAX3 and MAX4; here, interaction of MAX4 is restricted to vascular tissues (Ramirez and Pulay, 2019).

### 3.2. Other protein homologs of karrikin and strigolactone related to signalling pathways

In karrikin and SL signalling pathways, many genes regulate the formation of new compounds or help in repressing the inhibitory compounds. For example, a homolog of MAX2 is MdMAX2, which is an F-Box component, regulates the photomorphogenesis and stress responses in apple plant (An et al., 2016). Table 2 shows the homologs of different genes that regulate various physiological processes in plants with regard to karrikin and strigolactone signalling pathways.

In Arabidopsis, there are several genes of SL signalling pathway, e.g., *SMXL6, 7* and *8* homologs of *SMAX* (repressor) and *ShMAX2* ortholog of *AtMAX2*, which help in mediating SL responses in addition to promoting shoot branching (Liu et al., 2014; Soundappan et al., 2015). *SMXL6, 7* and *8* (rice orthologs) form a complex with *MAX2* and *TPR2* (*TOPLESS-RELATED PROTEIN2*) to regulate shoot branching in Arabidopsis (Wang et al., 2015). In cotton, the ortholog of *MAX2* is *GhMAX2a/2b* that inhibits the lateral shoot branching via SL signalling pathway**.** According to Czarnecki et al. (2014), *MAX* genes of *Populus* and *Arabidopsis* exhibit functional identity and similarities at the amino acid level. Accordingly, *PtrMAX3* shows 62% identity and 71% similarity; *PtrMAX4a* shows 64% identity and 78% similarities; and *PtrMAX4b* shows 65% identity and 78% similarity with *AtMAX4*. *Populus* root represented one of the locations for SL synthesis as the highest level of *PtrMAX3* and *PtrMAX4a* expression was noted in the root (Czarnecki et al., 2014). Yang et al. (2020) revealed that the homolog of *D14* (*MdD14*) inhibited the root branching and provided the tolerance of apple plant against various stresses such as salt, drought and low temperature. Conserving the same function as that of *AtMAX2* in Arabidopsis, MAX2-ortholog (*PvMAX2*) in switch-grass (*Panicum virgatum* L.) reduced the dwarf and bushy phenotypes and restored the hypocotyl length phenotypes as a result of enhanced expression of *PvMAX2* in the stem and shoot through SL pathway (Cheng et al., 2018).

## 4. Function of KAI2/D14

In Arabidopsis, KAI2 is the receptor of karrikin, whereas AtD14 is a paralogue of KAI2 and receptor of SL in the signalling pathway (Waters et al., 2012). Both KAI2 and D14 have a catalytic triad of amino acid residues (*Ser*, *His*, and *Asp*) found in hydrolytic enzymes (Waters et al., 2014). *Ser* (serine residue) of KAI2 and AtD14 initiates a nucleophilic attack on the butenolide ring of $KAR_1$ and SL (Scaffidi et al., 2012). Binding of SL with D14 takes place through the binding and hydrolysis process, in which the receptor irreversibly binds to the product after completion of hydrolysis process. D14 hydrolyzes the bond between ABC lactone and the D-ring in SL. The ABC ring (ABC-formyl tricyclic lactone: ABC-FTL) of SL is hydrolyzed and gets separated from the D-ring (hydroxymethyl butenolide: HMB). D-ring gets covalently linked with the D14 receptor, forming a complex known as CLIM (covalently linked intermediate molecule). It is supposed that this catalytic reaction makes a conformational change in the D14 receptor so that its interaction with other molecules, like MAX2 and repressors, occurs (Marzec and Brewer, 2019). Therefore, strigolactone binds to D14 via hydrolysis mechanism, whereas in case of karrikin, it binds with KAI2 protein without showing clear mechanism of hydrolysis.

In KAI2-dependent signalling, karrikins are the potent activators in fire-prone as well as nonfire-prone plants by regulating various physiological responses that

**Table 2.** Homologs of different genes related to karrikin and strigolactone signalling pathways.

| Gene | Homolog | Plant species | Function | Reference |
|---|---|---|---|---|
| *MdD14* | *D14* | Apple *(Malus domestica)* | Ectopic interaction inhibits shoot branching, hypocotyl growth and increases tolerance to various stresses. | Yang et al., 2020 |
| *PvMAX2* | *MAX2* | Switch-grass (*Panicum virgatum*) | Plays important role in switchgrass tillering via strigolactone pathway. | Cheng et al., 2018 |
| *PpMAX2* | *MAX2* | Moss (*Physcomitrella patens*) | Functions in strigolactone signalling pathway, and plays role in early development and photomorphogenesis of moss. | Lopez-Obando et al., 2018 |
| *KAI2$^{ply2}$* | *KAI2* | Arabidopsis | α/β hydrolase acts as a receptor for karrikin in signalling mechanism | Lee et al., 2018 |
| *MdMAX2* | *MAX2* | Apple *(Malus domestica)* | F-box component of SCF complex regulates the plant photomorphogenesis and stress responses via karrikin and strigolactone biosignalling. | An et al., 2016 |
| *SMXL6, 7 and 8* | *SMXL* | Arabidopsis | Acts as a repressor and promotes the shoot branching, auxin transport and PIN1 accumulation. | Soundappan et al., 2015 |
| *SMXL6, 7 AND 8* | *D53* (Ortholog) | Arabidopsis | Promotes the lateral bud outgrowth | Wang et al., 2015 |
| *ShMAX2* | *AtMAX2* (Ortholog) | Arabidopsis | Mediates the strigolactone signalling and restores the branching | Liu et al., 2014 |
| *PtrMAX3* | *AtMAX3* | *Populus* (*Populus trichocarpa*) | Functions in the strigolactone signalling pathway | Czarnecki et al., 2014 |
| *SMAX1* | *HEAT SHOCK PROTEIN 101* | Arabidopsis | Reverses the Max2-dependent seed dormancy phenotype | Stanga et al., 2013 |
| *AtD27* | *OsD27* | Arabidopsis | Controls the plant development by acting upstream of MAX1 | Waters et al., 2012 |
| *AtD14* | *OsD14* (Ortholog) | Rice (*Oryza sativa*) | Inhibits the lateral shoot outgrowth | Waters et al., 2012; Arite et al., 2009 |

**Abbreviations:** *AtD14,* Arabidopsis *DWARF14; AtD27,* Arabidopsis *DWARF27; AtMAX2,* Arabidopsis *MORE AXILLARY GROWTH2; AtMAX3,* Arabidopsis *MORE AXILLARY GROWTH3; D14, DWARF14; D53, DWARF53; KAI2$^{ply2}$, KARRIKIN INSENITIVE2$^{Pleotropic\ long\ hypocotyl2}$; KAI2, KARRIKIN INSENSITIVE2; MdMAX2,Malus domestica MORE AXILLARY GROWTH2; MdD14,Malus domestica DWARF14; OsD27,Oryza sativa DWARF27; PpMAX2, Physcomitrella patens MORE AXILLARY GROWTH2; PtrMAX2, Populus trichocarpa MORE AXILLARY GROWTH2; PvMAX2, Panicum virgatum MORE AXILLARY GROWTH2; SMXL6, SUPPRESSOR of MAX2 1 LIKE6; SMXL7,SUPPRESSOR of MAX2 1 LIKE7; SMXL8, SUPPRESSOR of MAX2 1 LIKE8; SMXL,SUPPRESSOR of MAX2 1 LIKE; SMAX1, SUPPRESSOR of MAX2 1; ShMAX2, Striga hermonthica MAX2.*

are dependent on MAX2 (Dixon et al., 2009). Genetic screen of kai2-mutant shows a role of MAX2 protein in karrikin and SL dependent signalling with regard to seed and seedling development (Waters et al., 2012; Nelson et al., 2011). KAI2 forms a complex with MAX2 and SMAX1 in order to degrade the SMAX1 repressor through polyubiquitylation by 26 proteasomal complexes. On the other hand, D14 forms a complex with MAX2 and SMXL6, 7, and 8 repressors; later, this complex undergoes polyubiquitylation by 26 proteasomal complexes to enable the SL response. KAI2 (karrikin insensitive 2) is a member of α/β hydrolase family, which is initially from a photo morphogenetic mutant *HTL* (*Hyposensitive to Light*) (Sun and Ni, 2011). In pea, *RMS3* (*RAMOSUS3*) orthologue of *D14* (Rice) forms a RMS3-D ring complex, in which D-ring of strigolactone gets attached to *his* 247 of the

catalytic triad to show its enzyme specificity (de Saint et al., 2016). This result shows that, SL signalling takes place after the degradation of SL molecule. In a recent study, dual function of D14 protein has been shown, in which perception as well as hydrolytic deactivation of SL molecule takes place after transmission of signal (Seto et al., 2019). In another recent study on rice, D14-D3 was found to mediate the degradation of D53 repressor. D3 (ortholog of Arabidopsis MAX2) contains a C-terminal α helix, which can switch into two forms, i.e. 'engaged' and 'dislodged'. The 'dislodged form' inhibits the enzymatic activity of D14 through binding in an 'open state', whereas the 'engaged form' helps in binding of D3 and D14 with an intermediate of hydrolyzed SL (Shabek et al., 2018).

In weedy ephemerals, KAI2 is the receptor of karrikin, and specific amino acids at its active sites make conformational changes according to ligand specificity. In this case, KAI2 is sensitive to different karrikins and other compounds because of duplication and diversification of receptor protein (Sun et al., 2018). In rice, D14 acts as a new component to inhibit the tillers and suppress the shoot branching in rice via the SL pathway as the d14-mutant exhibits short plant height and more branches (Arite et al., 2009). D14, along with MAX2, acts on the aerial part of plants to inhibit the shoot branching locally. BRC1 and D14 show a relationship, according to which D14 regulates the transcription of BRC1 gene to suppress the shoot branching (Chevalier et al., 2014).

As per the evolutionary route, KAI2 is a protein that is conserved from the algae to the land plants to the angiosperms, and its primary function leads to the perception of compounds derived from smoke. In angiosperms, KAI2 occurs in one or two copies; but in parasitic algae, KAI2 occurs in more than 5–6 or as many as 13 copies (e.g., in Orobanchaceae) as a result of gene duplication (Conn et al., 2015). On the other hand, D14 is found as a single gene copy. According to Zhao et al. (2014) KAI2 also carries sequence similarity with RbsQ (a signalling protein in bacteria). In *Brassica tournefortii,* there were found three homologs of KAI2, i.e. BtKAI2a, BtKAI2b, and BtKAI2c, in which BtKAI2a represented the ancestor of KAI2 protein, whereas BtKAI2b and BtKAI2c were evolved by the genome triplication forms of KAI2 protein (Sun et al., 2018). A missense allele of KAI2 or KAI2$^{ply2}$ is also a putative receptor of karrikin in Arabidopsis, which helps in ligand binding and downstream signalling of karrikin (Lee et al., 2018). *Physcomitrella patens,* a moss that appeared 460 million years ago, shows some relation with ligand specificity against karrikin and nonnatural SL (Lopez-Obando et al., 2018). Therefore, KAI2/D14 is considered as a potent receptor of hormones and signalling compounds, degrading the repressors via MAX2-dependent manner.

**5. Function of SMAX1/SMXL protein and their degradation via MAX2**

SMAX1 and SMXL proteins act downstream of MAX2 (Soundappan et al., 2015) that controls various physiological and developmental processes in plants. SMAX1 belongs to a member of 8-gene family that shows weak phenotype similarities with ClpB protein of AtHSP101 that is revealed in BLAST technique (Stanga et al., 2013). In Arabidopsis, restoration of MAX2 phenotypes, related to seed germination and seedling photomorphogenesis, takes place by the *smax1* mutant (Stanga et al., 2013). In addition to this, in *smax1 max2* seedlings, three transcriptional markers (*D14-LIKE2, KAR-UP F-BOX1,* and *INDOLE-3-ACETIC ACID INDUCIBLE1)* have also been redeemed related to KAR/SL signalling. Max2 seed dormancy phenotype is also reversed by smax1 mutant (Stanga et al., 2013). In rice, SMAX1 also negatively regulates the biosynthesis of strigolactone and symbiosis of AMF with host plant roots (Choi et al., 2020). SMXL-LIKE genes, i.e. SMXL6, SMXL7, and SMXL8, are orthologs of D53 (rice), which promote shoot branching in Arabidopsis (Soundappan et al., 2015). SMXL7 is degraded with the help of MAX2 (from Arabidopsis) and D53 (from rice), but it can be prevented via deletion of putative P-loop (Soundappan et al., 2015). Degradation of SMXL6, 7, and 8 increases the lateral root density, auxin transport, and accumulation of auxin transport-related protein PIN1 (Soundappan et al., 2015). In Arabidopsis, MAX2-dependent degradation and ubiquitination of D53-like SMXL repressor proteins regulate the SL signalling, resulting in shoot development (Soundappan et al., 2015). Triple mutants (*smxl6, smxl7* and *smxl8*) suppress the highly branched phenotype of MAX2. Proteins SMXL6, 7, and 8 are degraded via making a complex with MAX2, D14 and TOPLESS-RELATED PROTEIN2 (TPR2) with the help of GR24 (SL analogue). TPR2, along with SMXL, represses the transcriptional activity and expression of *BRANCHED1* (a gene that controls the shoot branching in Arabidopsis), allowing the lateral bud outgrowth (Wang et al., 2015). During drought resistance, SMXL 6, 7 and 8 play various negative roles such as enhancing the rate of water transpiration (stomatal and nonstomatal), decreasing the ABA sensitivity as well as cell membrane integrity, reducing the antioxidant defense mechanism and upregulating the transcription of *LEA* genes that may protect plant from dehydration (Li et al., 2020; Yang et al., 2020).

In Arabidopsis, other SMXL genes (e.g., SMXL3, SMXL4, and SMXL5), which are independent of karrikin and SL signalling pathways, help in phloem formation and are expressed in tissues associated with phloem formation (Wallner et al., 2017). The function of *SMXL* genes is to regulate the formation of a cambium-based secondary

phloem in Arabidopsis. Loss of function of *SMXL5* gene results in the absence of secondary phloem, whereas loss of *SMXL4* gene results in cell proliferation in the cambium region rather than the formation of secondary phloem (Wallner et al., 2020). Promoters of *SMXL4* and *SMXL5* (MtSEO2: GFP-ER) activate the formation and differentiation of secondary phloem. According to a recent study on shoot development in Arabidopsis, D14 interacts with MAX2 and SMXL7 repressor in the nucleus and destroys the specific domains of SMXL7 repressor (Liang et al., 2016). Motif of *EAR* (*ETHYLENE-RESPONSE FACTOR* Amphiphilic repression) also contributes to SMXL7 functionality. Degradation of *SMAX1/SMXL* genes is the main target of MAX2 protein.

## 6. Physiological responses mediated by MAX2-dependent pathway

MAX2 is a member of F-box proteins that plays an antagonistic effect on various physiological and developmental processes through $KAR_1$ and SL signalling pathways. Previous findings support that MAX2 regulates seed germination, hypocotyl growth and root hair development through karrikin signalling module, whereas shoot branching, leaf senescence and root development are regulated through SL signalling pathways (Nelson et al., 2011). Some of the physiological responses regulated by MAX2 (Figure 5) are classified by the traits discussed below.

### 6.1. Seed germination and seedling growth

Seed germination itself is a complex process in which different physiological, biochemical and metabolic changes, like recovery from maturation drying, mobilization of reserve food material, regulation of phytohormones and breaking of seed coat, are mostly noted (Ali and Elozeiri, 2017). Seed germination and seedling development can be enhanced by MAX2-dependent karrikin signalling pathways. Both MAX2 and KAI2 are critical for light-dependent seedling development and plant growth (Zhou et al., 2013). In Arabidopsis, max2 seeds exhibit the hyposensitivity towards $GA_3$ and shows hypersensitivity towards ABA by increasing the dormancy of seeds. In Arabidopsis, degradation of SMAX1 repressors by AtHTL/KAI2 dependent pathways can induce seed germination in the presence of DELLA repressors. These results might overcome the GA-dependent seed germination in Arabidopsis and striga plants (Bunsick et al., 2020).

### 6.2. Shoot development

MAX2 is a member of F-box protein with Leucine-rich repeats and is identical to the product of ORE9 gene, a regulator of leaf senescence in plants (Strinberg et al., 2002; Woo et al., 2001). MAX1 and MAX2 control the branching of lateral shoots in Arabidopsis via repressing the formation of shoot primordia by axillary meristem (Strinberg et al., 2002). The action of MAX2 is generally found in local regions such as in the tissues of axillary bud, stem or petiole. Expression of the MAX2-GUS fusion-

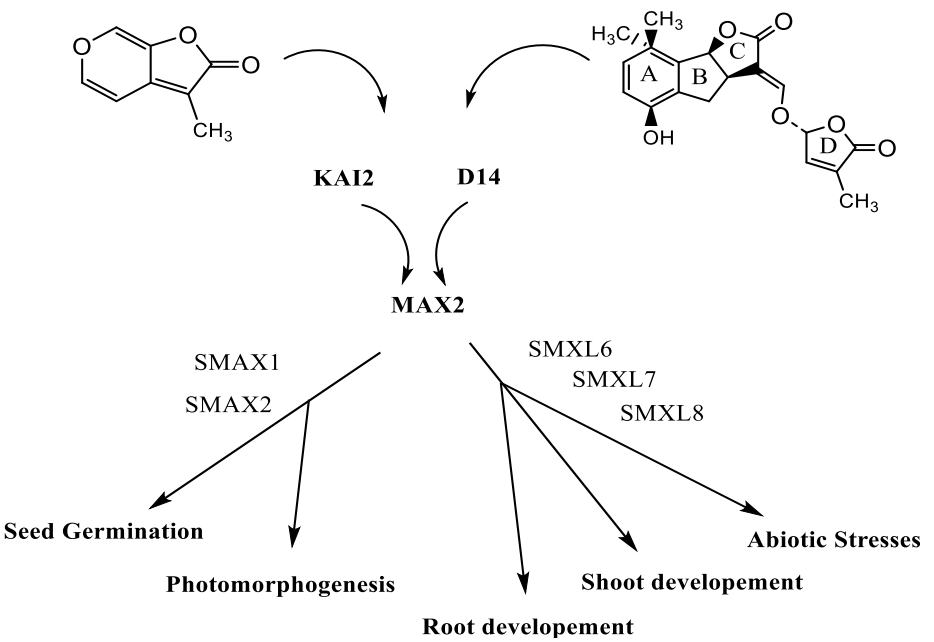


**Figure 5.** Regulation of various plant physiological mechanism by MAX2 protein via degradation of SMAX1 protein is through polyubiquitylation mechanism that leads to increases in seed germination, photomorphogenesis, seedling growth, lateral root development during flooding stress, and tolerance to plants facing severe stress conditions.

gene, detected in the whole plant body, including at the early reproductive stage (with cauline and rosette axillary buds), was highly expressed in the developing region of vasculature (Strinberg et al., 2007). In axillary buds, SL locally upregulates the expression of *BRANCHED1* (*BRC1*) gene, which contains a transcription factor domain called as *TEOSINTE BRANCHED1/PCNA/CYCLOIDEA* (Braun et al., 2012). According to a study, *BES1* is a substrate for MAX2 and acts as a negative regulator of SL signalling pathway; thus, MAX2 protein degrades the BES1 substrate and suppresses the shoot branching (Wang et al., 2013). In Arabidopsis, *ShMAX2* is a Striga ortholog of *AtMAX2* that helps in repressing the lateral branching of shoot through the SL signalling pathway. Through SL signalling, ShMAX2 shows various phenotypes of max2-1, such as root-shoot phenotype and high irradiance phenotype, but shows no response to fluence response phenotype (Liu et al., 2014).

### 6.3. Root development

Other than germination, $KAR_1$ also helps the development of lateral root formation and root skewing (deviation of root growth from direction of gravity) (Villaecija-Aguilar et al., 2019; Swarberck et al., 2019). Mutation in *KAI2* and *MAX2*, which together perceive $KAR_1$, resulted into alteration in root skewing in *Arabidopsis thaliana* (Davies et al., 2019). In Arabidopsis, new findings reveal that common components of karrikin and strigolactone signalling pathways, i.e. KAI2-MAX2-SMXL6, 7 and 8, might regulate the root skewing and junction root development under heterogeneous soil composition (Swarberck et al., 2020). Besides, MAX2, along with cytokinin, exhibited a negative role in regulating the root length and hypocotyl growth in Arabidopsis (Li et al., 2019).

### 6.4. Photomorphogenesis

In Arabidopsis, MAX2 plays essential roles in plant growth and development, photomorphogenesis, signalling pathway (karrikin), senescence, and drought tolerance regulation (Woo et al., 2001). Photomorphogenesis is a phenomenon, in which hypocotyl shortening as well as greening and expansion of cotyledon takes place in the presence of light. *VMdMAX2* acts as a positive regulator of plant photomorphogenesis, resulting in shorter cells of hypocotyl (An et al., 2016). MAX2 also regulates several phytohormones to promote photomorphogenesis (Shen et al., 2012). In Arabidopsis, max2 seeds exhibit the hyposensitivity towards $GA_3$ and show hypersensitivity towards ABA due to increase in the dormancy of seeds (Shen et al., 2012). In max2 seedlings, longer hypocotyl phenotype of seedlings is also observed due to the increase in auxin transport (Shen et al., 2012).

### 6.5. Abiotic stresses

Salinity and drought are stress factors that have a significant negative impact on growth and development of plants (Jones and Corlett, 1992). Drought is a significant environmental factor that affects arid and semiarid regions, comprising almost 60% of world's agricultural land. Drought and salinity stresses physiologically affect the plant because they exert osmotic stress inside the plant cells. Therefore, understanding the stress tolerance mechanism against drought and salinity is a crucial environmental research topic (Bartels and Sunkar, 2005). According to a study conducted by Bu et al. (2014), MAX2 protein plays an important role in regulating defense mechanisms in plants against abiotic stress conditions. Stomatal closure, cuticle thickness and sensitivity towards abscisic acid are found low in *max2* mutant as compared to the wild plant. In *max2* mutant of Arabidopsis, stress responsive genes, ABA biosynthesis, catabolism and signalling genes are impaired. Overexpression of *SsMAX2* results in higher resistance against drought, osmotic, and salt stresses in Arabidopsis. In addition to decreasing the water loss under drought stress, SsMAX2 also helps in decreasing chlorophyll degradation, while accumulating the soluble sugars and proline in the cells (Figure 5). In addition to increasing the anthocyanin biosynthesis, overexpression of SsMAX2 enhances the activities of several antioxidant enzymes like that of ascorbate peroxidase (APX), peroxidase (POD), and superoxide dismutase (SOD), which results in decreased hydrogen peroxide levels (Wang et al., 2019). MAX2 is also a component of plant defense towards bacteria like *Peclobacterium carotovorum* (a necrotroph) and *Pseudomonas syringae* (a hemibiotroph). However, *max2* mutants do not show resistance towards fungi like *Botrytis cinerea* (a necrotroph). In Arabidopsis, MAX2 contributes to ozone tolerance and provides tolerance to ROS (reactive oxygen species, such as $O_2^-$) (Piisila et al., 2015).

## 7. Crosstalk of MAX2

MAX2 protein itself plays a role as central regulator in karrikin and strigolactone signalling pathways (Li and Tran, 2015). It interacts with various phytohormones and regulates various physiological processes such as seed germination, seedling growth, shoot branching, drought tolerance, etc. (Bu et al., 2014). Here, we discuss a crosstalk of MAX2 with various plant growth regulators, like various phytohormones, karrikin and strigolactone in addition to phosphate deficiency in soil.

### 7.1. Phytohormones

Along with SL, auxin plays a vital role in regulating shoot branching by inhibiting bud outgrowth (Strinberg et al., 2010). SL affects the auxin-inducible flux by regulating the plasma membrane localized PIN proteins (auxin transporters) (Koltai, 2014). Expression of auxin-inducible genes and the genes related to light-induced signalling are regulated by MAX2 in the SL signalling pathway (Shen

et al., 2012). MAX2 related to TIR1 (auxin) and CoI1 (jasmonate) are members of LRR F-box protein, which later forms the SCF complex (Khosla and Nelson, 2016). In lateral root formation, NDL protein along with AGB1 (β subunit of heterotrimeric G-protein complex) affects the auxin transport and auxin gradients in root via AGB1-dependent regulation. MAX2 protein is regulated by *NDL* (*N-MYC DOWN-REGULATED-LIKE*) and AGB1 genes, which positively regulate the basipetal transport of auxin in flowers, meristem and inflorescence (Mudgil et al., 2013). In a recent study by Villaecija-Aguilar et al. (2019), kai2 and max2 mutants showed the reduced expression of auxin response factors, such as ARF7 and ARF17. In Arabidopsis, PIN proteins are significant in the root meristem and differentiation zone (Blilou et al., 2005). As revealed by Zou et al. (2006), auxin upregulates the HTD1 transcriptional gene (ortholog of MAX3) with regard to tillering in rice.

Gibberellin and karrikin function together in germination of dormant caryopses of *Avena fatua* through enhancing the activity of α- and β-amylase enzymes and also by increasing the synthesis of dehydrogenase proteins (Kepczynski et al., 2013). In Arabidopsis seedlings, action of both SL and gibberellic acid (GA) indicates the similar signal transduction pathways. Both of these hormones required the same receptors (α/β hydrolase) for degradation of repressors like SMXL7 (strigolactone) and DELLA (GA) by the method of E3 ubiquitin-mediated ligase proteasomal-degradation (Lantzouni et al., 2017). In a recent study on Arabidopsis (Meng et al., 2016), seed germination was delayed due to action of karrikin via enhancing the biosynthesis of abscisic acid and decreasing that of GA, under shade conditions. In another study (de Saint et al., 2013), SL repressed the axillary buds and increased the cell division in the stem of *Pisum sativum*, increasing the internode length independent of GA.

**7.2. Strigolactone and karrikin**

Strigolactone triggers the degradation of its receptor with the help of MAX2 protein (Chevalier et al., 2014). The receptor degradation is slower; it takes almost 1–2 h as compared to the degradation of D53 or BES1, which takes 8–30 min. When the SL - D14 - $SCF^{MAX2}$ complex degrades the repressors, the destabilization of D14 protein may take place. SL signalling mediates negative feedback regulation by regulating the stability of D14, in which functional MAX2 is required (Chevalier et al., 2014). Also, MAX2 acts as a negative regulator of seed size in Arabidopsis (Li et al., 2019). Cleavage of SL also takes place by D14 via interaction with SLR1 (repressor in GA signalling). Crystal structure of D14 shows that 5-hydroxy-3-methylbutenolide (D-OH), a reaction product of SLs, is trapped in the catalytic cavity of D14 (Nakamura et al., 2013).

Roots, being highly complex structure, provide nutrition to developing plant. Several plant hormones like auxins (Okada and Shimura, 1990), cytokinins (Kushwah et al., 2011), and brassinosteroids (Lanza et al., 2012) play a crucial role in root skewing. In a recent study on Arabidopsis, karrikin receptors regarding kai2 and max2 mutants showed root skewing rightward, which is independent of SL influence. Repressors, like SMAX1/SMXLs, are polyubiquitinated by MAX2-KAI2 complex. Mutant kai2 also shows a slow gravitropic response (Swabreck et al., 2019).

**7.3. Low phosphate induction**

For plant growth and development, phosphorus is an essential macronutrient as it plays a major role in various metabolic processes like biosynthesis of nucleic acid, phospholipids, ATP, etc. (Schachtman et al., 1998). To cope up with low inorganic phosphate (Pi) condition, Arabidopsis plant develops various metabolic strategies like elongation of root hairs, mycorrhizal symbiotic association, secretion of acid phosphatase enzyme, accumulation of anthocyanin pigment, etc. (Ito et al., 2015). In plants, SL hormone regulates the lateral root formation and root hair development in low Pi condition (Koltai, 2011). According to Mayzlish-Gati et al. (2012), SLs are regulators of plant perception and response to low inorganic phosphate (Pi) conditions. They showed that MAX2 mediated this response in Arabidopsis as a result of transcriptional induction of the auxin receptor TIR1. Mutant of SL signaling (*max2-1*) or of SL biosynthesis (*max4-1*) showed reduced response to low Pi conditions relative to wild type plant. *In max4-1* (but not in *max2-1*), the reduction in response to low Pi was compensated by the exogenous application of GR24, a synthetic analog of SL hormone.

In a decade back study on *Arabidopsis* under low Pi condition (Kohlen et al., 2011), there was noted alteration of genes, partial changes in the density of F-actin (a crucial protein used in cell functions and migration), and cellular trafficking (process of distribution of proteins and other macromolecules in the cell) in the root epidermis. Under low Pi condition, SL was transported via xylem to regulate shoot branching in Arabidopsis (nonarbuscular mycorrhizae). In Arabidopsis, expression of MAX2 protein was shown in the root endodermis under *SCR* (*SCARECROW*) promoter, which showed sensitivity towards GR24. MAX2 expression under SCARECROW promoter regulated low Pi responses as observed in *max2* mutant of Arabidopsis (Madmon et al., 2016).

Like MAX2 protein, ORE9 (an F-box protein) contains 693 amino acids and 18 leucine-rich repeats, which makes a complex with *ASK1* (Arabidopsis Skp1-like1) for constructing the SCF complex that was first identified in Arabidopsis as a regulator of leaf senescence (Woo et al., 2001). SL regulates the leaf senescence in rice under

Pi deficiency, causing redistribution of phosphate from old leaves to young leaves (Poirier and Bucher, 2002). Yamada et al. (2014) showed that chlorophyll degradation, ion leakage and leaf senescence could be delayed by treating the foliage of rice mutant with synthetic strigol and GR24. Stromules are the protrusions of plastids filled with stroma, which play an important role in exchanging of galactolipids from plastids to other membranes under low Pi conditions (Vismans et al., 2016). Low Pi conditions stimulate the synthesis of SL hormone in plastids. In Arabidopsis, SL influences the formation of stromule, independent of MAX2 protein (Vismans et al., 2016).

## 8. Conclusion and future prospects

MAX2 protein plays an important role in the signalling of both strigolactone and karrikin. It participates in modulating several physiological processes like germination, seed dormancy, plant growth and development. Furthermore, MAX2 protein plays an essential role in strigolactone perception and photomorphogenesis. MAX2 causes degradation of SMAX1/SMXL genes, which further modulates the germination traits. In different plants and in different plant organs, MAX2 carries several homologs. These homologs contribute to plant growth and developmental processes, including reduction of hypocotyls growth. MAX2 protein also plays a vital role in mitigating environmental stresses. In a very recent research, MAX2 protein was found to play a differential role in guard cell signalling related with $CO_2$-linked mechanism, plant defense mechanism against pathogens and environmental pollutants like ozone (Kalliola et al., 2020). Additionally, MAX2 enhances the plants physiological processes and makes the plant tolerant against stresses, like drought and salinity. MAX2 protein also interacts with natural phytohormones, strigolactone, and karrikin as well as with phosphorous for modulating several plant physiological processes. MAX2 also regulates low phosphate induction in plants, interacting with strigolactone and several other plant hormones, including karrikin.

These findings support the pleiotropic role of MAX2 protein. In context of signalling mechanism, MAX2 protein acts as a common regulator, whereas other homologs of MAX2 (MAX1, MAX3 and MAX4) are restricted to strigolactone biosynthesis mechanism only. These chemical entities (karrikin and strigolactone) are perceived by KAI2 and D14 receptors, which are paralogue to each other and share common mechanism of perception via hydrolysis. MAX2 protein, by modulating its action, drives the whole signalling mechanism via ubiquitylation of repressors.

Apart from above discussion, there are still many questions, which need to be answered regarding the mechanism of proper signalling of karrikin, characterization of various genes and transporters involved in karrikin and strigolactone signalling. Investigations must also be made regarding the role of MAX2 in mitigating various types of environmental stress. Further, role of MAX2 protein at different stages of karrikin and strigolactone signalling must be explored. Additionally, interdisciplinary research needs to be conducted to reveal different transcription factors or promoters that are involved in MAX2 functioning towards identification of their role in perception of receptors and ubiquitylation of repressors through omics approaches.

## Contribution of authors

SS drafted the original manuscript. SC, SS and UHB prepared a draft of the figures. MMAK and MU edited the final version of the manuscript and figures. All authors have read and approved the final manuscript.

## Conflict of interest

The authors declare that they have no conflict of interest.

## Acknowledgments

Sarika Singh acknowledges the receipt of Senior Research Fellowship granted by the Council of Scientific and Industrial Research (CSIR), Government of India, New Delhi.

## References

Abe S, Sado A, Tanaka K, Kisugi T, Asami K et al. (2014) Carlactone is converted to carlactonoic acid by MAX1 in Arabidopsis and its methyl ester can directly interact with AtD14 in vitro. Proceedings of the National Academy of Sciences 111: 18084-18089. doi:10.1073/pnas.1410801111

Ali AS, Elozeiri AA (2017). Metabolic processes during seed germination. Advances in Seed Biology 141-166.

An JP, Li R, Qu FJ, You CX, Wang XF et al. (2016) Apple F-box protein MdMAX2 regulates plant photomorphogenesis and stress response. Frontiers in Plant Science 7: 1685. doi:10.3389/fpls.2016.01685

Arite T, Iwata H, Ohshima K, Maekawa M, Nakajima M et al. (2007) DWARF10, an RMS1/MAX4/DAD1 ortholog, controls lateral bud outgrowth in rice. The Plant Journal 51: 1019-1029. doi:10.1111/j.1365-313x.2007.03210.x

Arite T, Umehara M, Ishikawa S, Hanada A, Maekawa M et al. (2009) d14, a strigolactone-insensitive mutant of rice, shows an accelerated outgrowth of tillers. Plant and Cell Physiology 50: 1416-1424.doi:10.1093/pcp/pcp091

Bainbridge K, Sorefan K, Ward S, Leyser O (2005). Hormonally controlled expression of the Arabidopsis MAX4 shoot branching regulatory gene. The Plant Journal 44: 569-580. doi:10.1111/j.1365-313x.2005.02548.x

Baldrianová J, Černý M, Novák J, Jedelský PL, Divíšková E et al. (2015) Arabidopsis proteome responses to the smoke-derived growth regulator karrikin. Journal of Proteomics 120: 7-20. doi:10.1016/j.jprot.2015.02.011

Bartels D, Sunkar R (2005). Drought and salt tolerance in plants. Critical reviews in plant sciences 24: 23-58. doi:10.1080/07352680590910410

Bhoi A, Yadu B, Chandra J, Keshavkant S (2021). Contribution of strigolactone in plant physiology, hormonal interaction and abiotic stresses. *Planta*, *254*: 1-21. doi: 10.1007/s00425-021-03678-1

Binder BM, Walker JM, Gagne JM, Emborg TJ, Hemmann G et al. (2007) The Arabidopsis EIN3 binding F-Box proteins EBF1 and EBF2 have distinct but overlapping roles in ethylene signaling. The Plant Cell 19: 509-523. doi:10.1105/tpc.106.048140

Blilou I, Xu J, Wildwater M, Willemsen V, Paponov I et al. (2005) The PIN auxin efflux facilitator network controls growth and patterning in Arabidopsis roots. Nature 433: 39-44. doi:10.1038/nature03184

Booker J, Auldridge M, Wills S, McCarty D, Klee H et al. (2004) MAX3/CCD7 is a carotenoid cleavage dioxygenase required for the synthesis of a novel plant signaling molecule. Current Biology 14: 1232-1238. doi: 10.1016/j.cub.2004.06.061

Booker J, Sieberer T, Wright W, Williamson L, Willett B et al. (2005) MAX1 encodes a cytochrome P450 family member that acts downstream of MAX3/4 to produce a carotenoid-derived branch-inhibiting hormone. Developmental Cell 8: 443-449. doi:10.1016/j.devcel.2005.01.009

Boyer FD, de Saint Germain A, Pouvreau JB, Clavé G, Pillot JP et al. (2014) New strigolactone analogs as plant hormones with low activities in the rhizosphere. Molecular plant 7: 675-690. doi:10.1093/mp/sst163

Braun N, de Saint Germain A, Pillot JP, Boutet-Mercey S, Dalmais M et al. (2012) The pea TCP transcription factor PsBRC1 acts downstream of strigolactones to control shoot branching. Plant physiology 158: 225-238. doi:10.1104/pp.111.182725

Brewer PB, Koltai H, Beveridge CA (2013). Diverse roles of strigolactones in plant development. Molecular plant 6: 18-28. doi:10.1093/mp/sss130

Bu Q, Lv T, Shen H, Luong P, Wang J et al. (2014) Regulation of drought tolerance by the F-box protein MAX2 in Arabidopsis. Plant Physiology 164: 424-439. doi:10.1104/pp.113.226837

Bunsick M, Toh S, Wong C, Xu Z, Ly G et al. (2020) SMAX1-dependent seed germination bypasses GA signalling in Arabidopsis and *Striga*. Nature Plants 1-7.doi: 10.1038/s41477-020-0653-z

Bürger M, Chory J (2020). The many models of strigolactone signaling. *Trends in Plant Science*, *25*: 395-405. doi: 10.1016/j.tplants.2019.12.009

Challis RJ, Hepworth J, Mouchel C, Waites R, Leyser O (2013). A role for more axillary growth1 (MAX1) in evolutionary diversity in strigolactone signaling upstream of MAX2. Plant Physiology 161: 1885-1902. doi:10.1104/pp.112.211383

Cheng T, Wang D, Wang Y, Zhang S, Zhang C et al. (2018) Identification and functional characterization of a MAX2 ortholog from switchgrass (*Panicum virgatum* L.). Plant Physiology and Biochemistry 128: 106-114. doi: 10.1016/j.plaphy.2018.05.016

Chevalier F, Nieminen K, Sánchez-Ferrero JC, Rodríguez ML, Chagoyen M et al. (2014) Strigolactone promotes degradation of DWARF14, an α/β hydrolase essential for strigolactone signaling in Arabidopsis. The Plant Cell 26: 1134-1150. doi:10.1105/tpc.114.122903

Choi J, Lee T, Cho J, Servante EK, Pucker B et al. (2020) The negative regulator SMAX1 controls mycorrhizal symbiosis and strigolactone biosynthesis in rice. Nature Communications *11*: 1-13. doi: 10.1038/s41467-020-16021-1

Cohen M, Prandi C, Occhiato EG, Tabasso S, Wininger S et al. (2013) Structure–function relations of strigolactone analogs: activity as plant hormones and plant interactions. Molecular Plant *6*: 141-152. doi: 10.1093/mp/sss134

Conn CE, Bythell-Douglas R, Neumann D, Yoshida S, Whittington B et al. (2015) Convergent evolution of strigolactone perception enabled host detection in parasitic plants. Science 349: 540-543. doi: 10.1126/science.aab1140

Cook CE, Whichard LP, Wall M, Egley GH, Coggon P et al. (1972) Germination stimulants. II. Structure of strigol, a potent seed germination stimulant for witchweed (*Striga lutea*). Journal of the American Chemical Society 94: 6198-6199.doi:10.1021/ja00772a048

Cooper JW, Hu Y, Beyyoudh L, YildizDasgan H, Kunert K et al. (2018) Strigolactones positively regulate chilling tolerance in pea and in Arabidopsis. Plant cell and environment 41: 1298-1310. doi:10.1111/pce.13147. 1298

Czarnecki O, Yang J, Wang X, Wang S, Muchero W et al. (2014) Characterization of MORE AXILLARY GROWTH genes in *Populus*. PLoS One 9: e102757.doi:10.1371/journal.pone.0102757

Davies J, Swarbreck S, Matthus E, Guerringue Y, Jamieson F (2019). Impairment in karrikin but not strigolactone sensing enhances root skewing in Arabidopsis thaliana. The Plant Journal 98: 607-621. doi: 10.1111/tpj.14233

de Saint Germain A, Clavé G, Badet-Denisot MA, Pillot JP, Cornu D et al. (2016) An histidine covalent receptor and butenolide complex mediates strigolactone perception. Nature Chemical Biology 12: 787.doi:10.1038/nchembio.2147

de Saint Germain A, Ligerot Y, Dun EA, Pillot JP, Ross JJ et al. (2013) Strigolactones stimulate internode elongation independently of gibberellins. Plant physiology 163: 1012-1025. doi:10.1104/pp.113.220541

Delaux PM, Xie X, Timme RE, Puech-Pages V, Dunand C et al. (2012) Origin of strigolactones in the green lineage. New Phytologist 195: 857-871. doi:10.1111/j.1469-8137.2012.04209.x

Dieckmann MC, Dakas PY, De Mesmaeker A (2018). Synthetic access to noncanonical strigolactones: syntheses of carlactonic acid and methyl carlactonoate. *The Journal of Organic Chemistry*, *83*: 125-135. doi: 10.1021/acs.joc.7b02465

Dixon KW, Merritt DJ, Flematti GR, Ghisalberti EL (2009). Karrikinolide–a phytoreactive compound derived from smoke with applications in horticulture, ecological restoration and agriculture. Acta Horticulturae 813: 155-170. doi:10.17660/ActaHortic.2009.813.20

Dong L, Ishak A, Yu J, Zhao R, Zhao L (2013). Identification and functional analysis of three MAX2 orthologs in chrysanthemum. Journal of Integrative Plant Biology 55: 434-442. doi:10.1111/jipb.12028

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD (2004). A compound from smoke that promotes seed germination. Science 305: 977-977. doi:10.1126/science.1099944

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD (2007). Germination Stimulant in Smoke: Isolation and Identification. In Bioactive Natural Products (pp. 545-568).CRC Press

Foo E, Bullier E, Goussot M, Foucher F, Rameau C et al. (2005) The branching gene RAMOSUS1 mediates interactions among two novel signals and auxin in pea. The Plant Cell 17: 464-474. doi:10.1105/tpc.104.026716

Guo Y, Zheng Z, La Clair JJ, Chory J, Noel JP (2013). Smoke-derived karrikin perception by the α/β-hydrolase KAI2 from Arabidopsis. Proceedings of the National Academy of Sciences 110: 8284-8289.doi:10.1073/pnas.1306265110

Gupta S, Hrdlička J, Ngoroyemoto N, Nemahunguni NK, Gucký T et al. (2020) Preparation and standardisation of smoke-water for seed germination and plant growth stimulation. *Journal of Plant Growth Regulation*, *39*: 338-345. doi: 10.1007/s00344-019-09985-y

Gutjahr C, Parniske M (2013). Cell and developmental biology of arbuscular mycorrhiza symbiosis. Annual review of cell and developmental biology 29: 593-617.doi:10.1146/annurev-cellbio-101512-122413

Ito S, Nozoye T, Sasaki E, Imai M, Shiwa Y et al. (2015) Strigolactone regulates anthocyanin accumulation, acid phosphatases production and plant growth under low phosphate condition in Arabidopsis. PLoS One 10 (3).doi:10.1371/journal.pone.0119724

Johnson X, Brcich T, Dun EA, Goussot M, Haurogné K et al. (2006) Branching genes are conserved across species. Genes controlling a novel signal in pea are coregulated by other long-distance signals. Plant physiology 142: 1014-1026. doi:10.1104/pp.106.087676

Jones HG, Corlett JE (1992). Current topics in drought physiology. The Journal of Agricultural Science 119: 291-296.doi:10.1017/S0021859600012144

Kalliola M, Jakobson L, Davidsson P, Pennanen V, Waszczak C et al. (2020) Differential role of MAX2 and strigolactones in pathogen, ozone, and stomatal responses. Plant direct 4: e00206.doi:10.1002/pld3.206

Kapulnik Y, Delaux PM, Resnick N, Mayzlish-Gati E, Wininger S et al. (2011) Strigolactones affect lateral root formation and root-hair elongation in Arabidopsis. Planta 233: 209-216. doi:10.1007/s00425-010-1310-y

Kępczyński J (2018). Induction of agricultural weed seed germination by smoke and smoke-derived karrikin (KAR 1), with a particular reference to *Avena fatua* L. Acta Physiologiae Plantarum 40: 87.doi:10.1007/s11738-018-2663-2

Kępczyński J, Cembrowska-Lech D, Van Staden J (2013). Necessity of gibberellin for stimulatory effect of KAR 1 on germination of dormant *Avena fatua* L. caryopses. Acta physiologiae Plantarum 35: 379-387.doi:10.1007/s11738-012-1080-*1*

Kepinski S, Leyser O (2005). The Arabidopsis F-box protein TIR1 is an auxin receptor. Nature 435: 446-451.doi:10.1038/nature03543

Keppler BD, Showalter AM (2010). IRX14 and IRX14-LIKE, two glycosyltransferases involved in glucuronoxylan biosynthesis and drought tolerance in Arabidopsis. Molecular Plant 3834-841. doi:10.1093/mp/ssq028

Kohlen W, Charnikhova T, Liu Q, Bours R, Domagalska MA et al. (2011) Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host Arabidopsis. Plant Physiology 155: 974-987. doi:10.1104/pp.110.164640

Koltai H (2011). Strigolactones are regulators of root development. *New Phytologist*, *190*: 545-549. doi: 10.1111/j.1469-8137.2011.03678.x

Koltai H (2014). Receptors, repressors, PINs: a playground for strigolactone signaling. Trends in plant Science 19: 727-733. doi:10.1016/j.tplants.2014.06.008

Koltai H, Cohen M, Chesin O, Mayzlish-Gati E, Bécard G et al. (2011) Light is a positive regulator of strigolactone levels in tomato roots. Journal of plant physiology 168: 1993-1996. doi:10.1016/j.jplph.2011.05.022

Kushwah S, Jones AM, Laxmi A (2011). Cytokinin interplay with ethylene, auxin, and glucose signaling controls Arabidopsis seedling root directional growth. Plant physiology 156: 1851-1866. doi:10.1104/pp.111.175794

Lantzouni O, Klermund C, Schwechheimer C (2017). Largely additive effects of gibberellin and strigolactone on gene expression in Arabidopsis thaliana seedlings. The Plant Journal 92: 924-938. doi:10.1111/tpj.13729

Lanza M, Garcia-Ponce B, Castrillo G, Catarecha P, Sauer M et al. (2012) Role of actin cytoskeleton in brassinosteroid signaling and in its integration with the auxin response in plants. Developmental cell 22: 1275-1285. doi:10.1016/j.devcel.2012.04.008

Lee I, Kim K, Lee S, Hwang E (2018) A missense allele of KARRIKIN-INSENSITIVE2 impairs ligand-binding and downstream signaling in Arabidopsis thaliana. Journal of Experimental Botany 69: 3609-3623. doi:10.1093/jxb/ery164

Li W, Nguyen KH, Tran CD, Watanabe Y, Tian C et al. (2020) Negative Roles of Strigolactone-Related SMXL6, 7 and 8 Proteins in Drought Resistance in Arabidopsis. Biomolecules 10: 607. doi: 10.3390/biom10040607

Li W, Nguyen KH, Van Ha C, Watanabe Y, Tran LSP (2019). Crosstalk between the cytokinin and MAX2 signaling pathways in growth and callus formation of Arabidopsis thaliana. Biochemical and biophysical research and communications 511: 300-306. doi:10.1016/j.bbrc.2019.02.038

Li W, Tran LSP (2015). Are karrikins involved in plant abiotic stress responses? Trends in plant science 20: 535-538. doi:10.1016/j.tplants.2015.07.006

Liang Y, Ward S, Li P, Bennett T, Leyser O (2016). SMAX1-LIKE7 signals from the nucleus to regulate shoot development in Arabidopsis via partially EAR motif-independent mechanisms. The Plant Cell 28: 1581-1601. doi:10.1105/tpc.16.00286

Liu Q, Zhang Y, Matusova R, Charnikhova T, Amini M et al. (2014) *Striga hermonthica* MAX2 restores branching but not the Very Low Fluence Response in the Arabidopsis thaliana max2 mutant. *New Phytologist*, *202*: 531-541.doi: 10.1111/nph.12692

Lopez-Obando M, de Villiers R, Hoffmann B, Ma L, de Saint Germain A et al. (2018) *Physcomitrella patens* MAX2 characterization suggests an ancient role for this F-box protein in photomorphogenesis rather than strigolactone signalling. New Phytologist 219: 743-756. doi:10.1111/nph.15214

Madmon O, Mazuz M, Kumari P, Dam A, Ion A et al. (2016) Expression of MAX2 under SCARECROW promoter enhances the strigolactone/MAX2 dependent response of Arabidopsis roots to low-phosphate conditions. Planta 243: 1419-1427. doi:10.1007/s00425-016-2477-7

Mangnus EM, Zwanenburg B (1992). Tentative molecular mechanism for germination stimulation of *Striga* and *Orobanche* seeds by strigol and its synthetic analogs. Journal of Agricultural and Food Chemistry 40: 1066-1070.doi:10.1021/jf00018a032

Marzec M, Brewer P (2019). Binding or Hydrolysis? How Does the Strigolactone Receptor Work?. Trends in Plant Science 24: 571-574. doi:10.1016/j.tplants.2019.05.001

Matusova R, Rani K, Verstappen FW, Franssen MC, Beale MH et al. (2005) The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanche* spp. are derived from the carotenoid pathway. Plant physiology 139: 920-934. doi:10.1104/pp.105.061382.

Mayzlish-Gati E, De-Cuyper C, Goormachtig S, Beeckman T, Vuylsteke M et al. (2012) Strigolactones are involved in root response to low phosphate conditions in Arabidopsis. Plant physiology 160: 1329-1341. doi:10.1104/pp.112.202358

Meng Y, Chen F, Shuai H, Luo X, Ding J et al. (2016) Karrikins delay soybean seed germination by mediating abscisic acid and gibberellin biogenesis under shaded conditions. Scientific reports 6: 1-12.doi:10.1038/srep22073

Morffy N, Faure L, Nelson DC (2016). Smoke and hormone mirrors: action and evolution of karrikin and strigolactone signaling. Trends in Genetics 32: 176-188.doi:10.1016/j.tig.2016.01.002

Mudgil Y, Ghawana S, Jones AM (2013). N-MYC down-regulated-like proteins regulate meristem initiation by modulating auxin transport and MAX2 expression. PloS one 8: e77863. doi:10.1371/journal.pone.0077863

Nakamura H, Xue YL, Miyakawa T, Hou F, Qin HM et al. (2013) Molecular mechanism of strigolactone perception by DWARF14. Nature Communications 4: 1-10.doi:10.1038/ncomms3613

Nelson DC, Flematti GR, Ghisalberti EL, Dixon KW, Smith SM (2012). Regulation of seed germination and seedling growth by chemical signals from burning vegetation. Annual Review of Plant Biology 63: 2012.doi:10.1146/annurev-arplant-042811-105545

Nelson DC, Scaffidi A, Dun EA, Waters MT, Flematti GR et al. (2011) F-box protein MAX2 has dual roles in karrikin and strigolactone signaling in Arabidopsis thaliana. Proceedings of the National Academy of Sciences 108: 8897-8902. doi:10.1073/pnas.1100987108

Okada K, Shimura Y (1990). Reversible root tip rotation in Arabidopsis seedlings induced by obstacle-touching stimulus. Science 250: 274-276. doi:10.1126/science.250.4978.274

Piisilä M, Keceli MA, Brader G, Jakobson L, Jõesaar I et al. (2015) The F-box protein MAX2 contributes to resistance to bacterial phytopathogens in Arabidopsis thaliana. BMC plant biology 15: 53.doi:10.1186/s12870-015-0434-4

Poirier Y, Bucher M (2002). Phosphate transport and homeostasis in Arabidopsis. The Arabidopsis book/American Society of Plant Biologists 1. doi:10.1199/tab.0024

Qiao Y, Lu W, Wang R, Nisa Z, Yu Y et al. (2020). Identification and expression analysis of strigolactone biosynthetic and signaling genes in response to salt and alkaline stresses in soybean (Glycine max). DNA and Cell Biology 39 (10): 1850-1861.

Ramírez V, Pauly M (2019). Genetic dissection of cell wall defects and the strigolactone pathway in Arabidopsis. Plant Direct 3: e00149. doi:10.1002/pld3.149

Scaffidi A, Waters MT, Bond CS, Dixon KW, Smith SM et al. (2012) Exploring the molecular mechanism of karrikins and strigolactones. Bioorganic and medicinal chemistry letters 22: 3743-3746.doi: 10.1016/j.bmcl.2012.04.016

Schachtman DP, Reid RJ, Ayling SM (1998). Phosphorus uptake by plants: from soil to cell. Plant physiology 116: 447-453. doi:10.1104/pp.116.2.447

Seto Y, Yasui R, Kameoka H, Tamiru M, Cao M et al. (2019) Strigolactone perception and deactivation by a hydrolase receptor DWARF14. Nature Communications 10: 191.doi:10.1038/s41467-018-08124-7

Shabek N, Ticchiarelli F, Mao H, Hinds TR, Leyser O et al. (2018) Structural plasticity of D3–D14 ubiquitin ligase in strigolactone signalling. Nature 563: 652.doi:10.1038/s41586-018-0743-5

Shen H, Zhu L, Bu QY, Huq E (2012). MAX2 affects multiple hormones to promote photomorphogenesis. Molecular plant 5:750-762. doi:10.1093/mp/sss029

Smith SM, Li J (2014). Signalling and responses to strigolactones and karrikins. Current opinion in Plant Biology 21: 23-29.doi:10.1016/j.pbi.2014.06.003

Snowden KC, Simkin AJ, Janssen BJ, Templeton KR, Loucas HM et al. (2005) The Dad1/PhCCD8 gene affects branch production and has a role in leaf senescence, root growth and flower development. The Plant Cell 17: 746-759.doi:10.1105/tpc.104.027714

Sorefan K, Booker J, Haurogné K, Goussot M, Bainbridge K et al. (2003) MAX4 and RMS1 are orthologous dioxygenase-like genes that regulate shoot branching in Arabidopsis and pea. Genes and development 17: 1469-1474.doi: 10.1101/gad.256603

Soundappan I, Bennett T, Morffy N, Liang Y, Stanga JP et al. (2015) SMAX1-LIKE/D53 family members enable distinct MAX2-dependent responses to strigolactones and karrikins in Arabidopsis. The Plant Cell 27: 3143-3159. doi:10.1105/tpc.15.00562

Stanga JP, Smith SM, Briggs WR, Nelson DC (2013). SUPPRESSOR OF MORE AXILLARY GROWTH2 1 controls seed germination and seedling development in Arabidopsis. Plant Physiology 163: 318-330. doi:10.1104/pp.113.221259

Stirnberg P, Furner IJ, Ottoline Leyser HM (2007). MAX2 participates in an SCF complex which acts locally at the node to suppress shoot branching. The Plant Journal 50: 80-94. doi:10.1111/j.1365-313X.2007.03032.x

Stirnberg P, van De Sande K, Leyser HO (2002). MAX1 and MAX2 control shoot lateral branching in Arabidopsis. Development 129: 1131-1141.doi: 10.1242/dev.129.5.1131

Stirnberg P, Ward S, Leyser O (2010) Auxin and strigolactones in shoot branching: intimately connected? Biochemical Society Transactions, 38: 717-722. doi: 10.1042/BST0380717

Sun XD, Ni M (2011) Hyposensitive to light, an alpha/beta fold protein, acts downstream of elongated Hypocotyl 5 to regulate seedling de-etiolation. Molecular Plant 4:116-126.doi:10.1093/mp/ssq055

Sun YK, Scaffidi A, Yao J, Melville K, Smith SM et al. (2018) Divergent receptor proteins confer responses to different karrikins in two ephemeral weeds. Nature communications 11:1-13. doi:10.1038/s41467-020-14991-w

Swarbreck SM, Guerringue Y, Matthus E, Jamieson FJ, Davies JM (2019). Impairment in karrikin but not strigolactone sensing enhances root skewing in Arabidopsis thaliana. The Plant Journal 98:607-621. doi:10.1111/tpj.14233

Swarbreck SM, Mohammad-Sidik A, Davies JM (2020). Common components of the strigolactone and karrikin signaling pathways suppress root branching in Arabidopsis thaliana. Plant Physiol*ogy* 184:18-22.doi: 10.1104/pp.19.00687

Tsuchiya Y, Vidaurre D, Toh S, Hanada A, Nambara E et al. (2010) A small-molecule screen identifies new functions for the plant hormone strigolactone. Nature Chemical Biology 6:741-749. doi:10.1038/nchembio.435.

Umehara M (2011). Strigolactone, a key regulator of nutrient allocation in plants. *Plant Biotechnology*, *28*:429-437. doi: 10.5511/plantbiotechnology.11.1109a

Villaecija-Aguilar JA, Hamon-Josse M, Carbonnel S, Kretschmar A, Ljung K et al. (2019) KAI2 regulates root and root hair development by modulating auxin distribution. bioRxiv 539734.doi:10.1101/539734

Vismans G, van der Meer T, Langevoort O, Schreuder M, Bouwmeester H et al. (2016) Low-phosphate induction of plastidalstromules is dependent on strigolactones but not on the canonical strigolactone signaling component MAX2. Plant Physiology 172:2235-2244. doi:10.1104/pp.16.01146

Wallner ES, López-Salmerón V, Belevich I, Poschet G, Jung I et al. (2017) Strigolactone-and karrikin-independent SMXL proteins are central regulators of phloem formation. Current Biology 27:1241-1247.doi: 10.1016/j.cub.2017.03.014

Wallner ES, Tonn N, Shi D, Jouannet V, Greb T (2020). SUPPRESSOR OF MAX2 1-LIKE 5 promotes secondary phloem formation during radial stem growth. The Plant Journal 102: 903-915.doi: 10.1111/tpj.14670

Walsh TA, Neal R, Merlo AO, Honma M, Hicks GR et al. (2006) Mutations in an auxin receptor homolog AFB5 and in SGT1b confer resistance to synthetic picolinate auxins and not to 2, 4-dichlorophenoxyacetic acid or indole-3-acetic acid in Arabidopsis. Plant Physiology 142:542-552. doi:10.1104/pp.106.085969

Wang L, Wang B, Jiang L, Liu X, Li X et al. (2015) Strigolactone signaling in Arabidopsis regulates shoot development by targeting D53-like SMXL repressor proteins for ubiquitination and degradation. The Plant Cell 27:3128-3142. doi:10.1105/tpc.15.00605

Wang Q, Ni J, Shah F, Liu W, Wang D et al. (2019) Overexpression of the Stress-Inducible SsMAX2 Promotes Drought and Salt Resistance via the Regulation of Redox Homeostasis in Arabidopsis. International Journal of Molecular Sciences 20:837. doi:10.3390/ijms20040837

Wang Y, Sun S, Zhu W, Jia K, Yang H et al. (2013) Strigolactone/MAX2-induced degradation of brassinosteroid transcriptional effector BES1 regulates shoot branching. Developmental cell 27:681-688. doi:10.1016/j.devcel.2013.11.010

Waters MT, Nelson DC, Scaffidi A, Flematti GR, Sun YK et al. (2012) Specialisation within the DWARF14 protein family confers distinct responses to karrikins and strigolactones in Arabidopsis. Devlopment 139:1285-1295. doi:10.1242/dev.074567

Waters MT, Scaffidi A, Sun YK, Flematti GR, Smith SM (2014). The karrikin response system of Arabidopsis. The Plant Journal 79:623-631. doi:10.1111/tpj.12430

Woo HR, Chung KM, Park JH, Oh SA, Ahn T et al. (2001) ORE9, an F-box protein that regulates leaf senescence in Arabidopsis. The Plant Cell 13:1779-1790.doi: 10.1105/TPC.010061

Xie X, Yoneyama K, Yoneyama K (2010). The strigolactone story. Annual Review of phytopathology 48.doi:10.1146/annurev-phyto-073009-114453

Yamada Y, Furusawa S, Nagasaka S, Shimomura K, Yamaguchi S et al. (2014) Strigolactone signaling regulates rice leaf senescence in response to a phosphate deficiency. Planta 240:399-408. doi:10.1007/s00425-014-2096-0

Yan J, Zhang C, Gu M, Bai Z, Zhang W et al. (2009) The Arabidopsis CORONATINE INSENSITIVE1 protein is a jasmonate receptor. The Plant Cell 21:2220-2236. doi:10.1105/tpc.109.065730

Yang T, Lian Y, Kang J, Bian Z, Xuan L et al. (2020) The suppressor of MAX2 1 (SMAX1)-LIKE SMXL6, SMXL7, and SMXL8 Act as Negative Regulators in Response to Drought Stress in Arabidopsis. Plant Cell Physiology *61*:1477-1492. doi: 10.1093/pcp/pcaa066

Yoneyama K, Awad AA, Xie X, Yoneyama K, Takeuchi Y (2010) Strigolactones as germination stimulants for root parasitic plants. Plant and Cell Physiology 51:1095-1103. doi:10.1093/pcp/pcq055

Yoshida S, Kameoka H, Tempo M, Akiyama K, Umehara M et al. (2012) The D3 F-box protein is a key component in host strigolactone responses essential for arbuscular mycorrhizal symbiosis. New Phytologist 196:1208-1216. doi:10.1111/j.1469-8137.2012.04339.x

Zhang Y, Cheng X, Wang Y, Díez-Simón C, Flokova K et al. (2018) The tomato MAX1 homolog, SlMAX1, is involved in the biosynthesis of tomato strigolactones from carlactone. New Phytologist 219:297-309. doi:10.1111/nph.15131

Zhao J, Wang T, Wang M, Liu Y, Yuan S et al. (2014) DWARF3 participates in an SCF complex and associates with DWARF14 to suppress rice shoot branching. Plant and Cell Physiology 55:1096-1109.doi: 10.1093/pcp/pcu045

Zou J, Zhang S, Zhang W, Li G, Chen Z et al. (2006) The rice HIGH-TILLERING DWARF1 encoding an ortholog of Arabidopsis MAX3 is required for negative regulation of the outgrowth of axillary buds. The Plant Journal 48:687-698. doi:10.1111/j.1365-313X.2006.02916.x

Zwanenburg B, Mwakaboko AS (2011). Strigolactone analogues and mimics derived from phthalimide, saccharine, p-tolylmalondialdehyde, benzoic and salicylic acid as scaffolds. Bioorganic and Medicinal Chemistry 19:7394-7400. doi: 10.1016/j.bmc.2011.10.057