



The role of methane in plant physiology: a review

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Received: 13 August 2019 / Revised: 18 September 2019 / Accepted: 3 October 2019 / Published online: 23 October 2019
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Abstract

Methane (CH₄), one of the most important greenhouse gases, has conventionally been considered as a physiologic inert gas. However, this perspective has been challenged by the observation that CH₄ has diverse biological functions in animals, such as anti-inflammatory, antioxidant, and anti-apoptosis. Meanwhile, it has now been identified as a possible candidate of gaseous signaling molecule in plants, although its biosynthetic and metabolic pathways as well as the mechanism(s) of CH₄ signaling have not fully understood yet. This paper aims to review the available evidence for the biological roles of CH₄ in regulating plant physiology. Although currently available reports do not fully support the notion of CH₄ as a gasotransmitter, they do show that CH₄ might be produced by an aerobic, non-microbial pathway from plants, and plays important roles in enhancing plant tolerance against abiotic stresses, such as salinity, drought, heavy metal exposure, and promoting root development, as well as delaying senescence and browning. Further results showed that CH₄ could interact with reactive oxygen species (ROS), other gaseous signaling molecules [e.g., nitric oxide (NO), carbon monoxide (CO), and hydrogen sulfide (H₂S)], and glutathione (GSH). These reports thus support the idea that plant-produced CH₄ might be a component of a survival strategy of plants. Finally, the possibility of CH₄ application in agriculture is preliminarily discussed.

Keywords Abiotic stress · Biological functions · Methane · Plant methanogenesis · Root organogenesis

Introduction

Methane (CH₄) is a ubiquitous, colorless, odorless, and volatile gaseous molecule. Normally, this gas is considered to be a significant greenhouse gas with potential to substantially impact the planet's climate. CH₄ is intrinsically non-toxic to animals, but at high concentrations, it will cause headaches and even asphyxia (Boros et al. 2015). Conventionally, CH₄ is considered to be biologically inactive. However, a previous review suggested that CH₄ could exhibit a wide range of protective effects in many human disease models, and thus was proposed to be a new functional gas with the possible

medical applications (Liu et al. 2012). For example, methane-rich saline can ameliorate ischemia/reperfusion injury of small intestine (Boros et al. 2012), liver (Ye et al. 2015; Wang et al. 2017), myocardium (Chen et al. 2016), kidney (Meng et al. 2018), and sepsis-induced injury (Jia et al. 2018; Li et al. 2019) via anti-oxidation, anti-inflammation, and anti-apoptosis pathways. It also has been reported that CH₄ has analgesic effects for monoarthritis in a rat model of chronic inflammatory pain (Zhou et al. 2018).

Previously, it was proposed the six criteria for identifying a gasotransmitter (Wang 2014) and it was shown that CH₄ is a gasotransmitter candidate similar to nitric oxide (NO), carbon oxide (CO), and hydrogen sulfide (H₂S). Its gaseous characteristics, high membrane permeability, endogenous production and catabolism in mammals, and biological effects elicited by exogenous donors further highlighted the potential as a gasotransmitter (Ghyczy et al. 2008; Liu et al. 2012; Boros et al. 2015). Increasingly, studies of CH₄ have been performed in plants, so the evidence was steadily accumulated to support this hypothesis. For example, aerobic non-microbial emission of CH₄ (Keppler et al. 2006; Wang et al. 2013a, b; Liu et al. 2015; Martel and Qaderi 2017) and its biological activities in plants have been increasingly

Communicated by Neal Stewart.

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demonstrated (Cui et al. 2015, 2017; Zhu et al. 2016; Samma et al. 2017; Hu et al. 2018; Mei et al. 2019).

The objective of this review is to summarize the important progress in botanical functions of CH₄, including enhancing plants tolerance against stresses (salinity, drought, osmotic stress, and metal exposure, etc.), and regulating plant growth and development (lateral rooting and adventitious root development, etc.). These positive effects of CH₄ in plants indicated that it might be used in agricultural production as a novel plant growth regulator and not only for medical treatment.

CH₄ synthesis and emission

Microbial CH₄ production

CH₄ can be produced through abiotic or biotic pathways. CH₄ emissions from the three main abiotic pathways (volcanic activities, geothermal systems, and water–rock interactions) are considered to be insignificant, accounting for about 1% of the total global amount (Emmanuel and Ague 2007; Fiebig et al. 2009). In contrast, approximately 99% of CH₄ in the atmosphere is derived from decomposition of organic compounds and microbial CH₄ production that accounts more than 70% of CH₄ global production (Wang et al. 2013b).

Methanogenic microorganisms are obligate anaerobic members of the archaea that are distinguished from bacteria and eukaryotes, and produce CH₄ as a byproduct of metabolism under anaerobic conditions. Methanogens are often present in wetlands, rice paddy fields, landfills, oceans, and digestive tracts of humans and animals (Liu and Whitman 2008). Normally, methanogens existing in the gut are widely considered to be a major cause of CH₄ production in ruminants and humans (Costello et al. 2013). Archaea have been also isolated from trees that act as a significant contributor of methanogenesis (Covey et al. 2012; Wang et al. 2016; Yip et al. 2019). Methanogens can be divided into three major groups: (1) the first group reduces CO₂ to form CH₄ along with H₂ as an electron donor; (2) the second group decomposes acetate to form CH₄; and (3) the third one produces CH₄ by reducing methyl-group containing compounds, including methanol, methylated amines, and methylated sulfides (Liu and Whitman 2008).

Non-microbial CH₄ production and consumption

Non-microbial CH₄ production accounts less than 30% of global CH₄ production and has received less attention because of its lower proportion (Wang et al. 2013b). Previously, non-microbial CH₄ production has been confirmed in animals (Tuboly et al. 2013), plants (Keppler et al. 2008),

fungi (Lenhart et al. 2012), soils (Jugold et al. 2012; Wang et al. 2013a), and the surface of ocean (Bange and Uher 2005). It has also been observed that CH₄ can be produced in rat mitochondria under hypoxic conditions. In this, mitochondrial dysfunction elicited significant CH₄ production (Ghyczy et al. 2008), which occurs in mammalian cells after inhibition of cytochrome *c* oxidase (the last enzyme of mitochondrial electron transport chain) by sodium azide (NaN₃) (Tuboly et al. 2013).

Conventionally, plants have been considered as pathways for CH₄ transfer and emission from soil to atmosphere. It was only in 2006, that direct evidence of non-microbial CH₄ emission in the presence of oxygen was first reported (Keppler et al. 2006). However, much suspicion and controversy ensued, until it was subsequently confirmed that aerobic non-microbial CH₄ can be produced in the intact and detached plants under various stress conditions, including high temperature (Keppler et al. 2008; Vigano et al. 2008; Bruhn et al. 2009; Abdulmajeed et al. 2017), UV irradiation (Keppler et al. 2008; McLeod et al. 2008; Vigano et al. 2008; Bruhn et al. 2009, 2014; Messenger et al. 2009; Abdulmajeed et al. 2017), physical injury (Wang et al. 2009, 2011; Lenhart et al. 2015), hypoxia (Wang et al. 2011), drought (Qaderi and Reid 2011), low light (Bruggemann et al. 2009; Martel and Qaderi 2017), salinity (Zhu et al. 2016), metal exposure (Cui et al. 2017; Samma et al. 2017; Gu et al. 2018), reactive oxygen species (ROS) (Messenger et al. 2009; Althoff et al. 2010, 2014), and bacterial and fungi infection (Messenger et al. 2009; Hietala et al. 2015).

Identifying the specific precursor(s) of CH₄ production in plants is, therefore, a research priority. Various organic compounds containing functional groups, such as methyl (–CH₃), methoxyl (–O–CH₃), hydroxymethyl (–CH₂–OH), thiomethyl (–S–CH₃), etc., may serve as the intermediates for CH₄ production. Pectin was suggested to be a precursor for plant CH₄ production under heating and UV irradiation because of its high degree of methylation (Keppler et al. 2008; McLeod et al. 2008; Vigano et al. 2008; Messenger et al. 2009). Other plant components such as lignin (Vigano et al. 2008, 2009), cellulose (Vigano et al. 2008, 2009), ascorbic acid (AsA) (Althoff et al. 2010), leaf surface waxes (Bruhn et al. 2014), and methionine (Met) (Althoff et al. 2014; Lenhart et al. 2015; Han et al. 2017) have also been confirmed as potential sources for plant CH₄ release and production.

Substantive evidence has suggested that ROS, which can be stimulated or intensified under various types of stresses, is a conceivable driver of non-microbial CH₄ emissions. It has been demonstrated that aerobic non-microbial CH₄ production associated with ROS production, can be limited by ROS removal, and stimulated by the enzymes that inhibit ROS removal (Messenger et al. 2009). ROS may also be involved in CH₄ formation from cleavage of pectin and/or

lignin (Keppler et al. 2008; Messenger et al. 2009). Interestingly, a strong increase of CH_4 generation was discovered in plant cell cultures exposed to NaN_3 (Wishkerman et al. 2011). This result is consistent with an increase in NaN_3 -induced CH_4 generation in rat liver cells (Ghyczy et al. 2008). These findings indicated that interference of electron transport chains in mitochondria may be partially involved in CH_4 production in both animals and plants. However, Bruhn et al. (2012) subsequently questioned the specificity of NaN_3 , which can also inhibit the activities of some ROS-removing enzymes, including catalase (CAT) and peroxidase (POD). Together, although ROS may be an important hub for the stimulation of plant CH_4 production (Fig. 1), the complete mechanism(s) of plant CH_4 production has still to be unequivocally determined.

A well-studied source of CH_4 transfer is aerenchyma, a specialized tissue that forms in root and stems (Drew et al. 2000; Evans 2004). Regarding the mechanism, it was suggested that CH_4 in situ moves by diffusion rather than pressurized transport (Pangala et al. 2014). Moreover, transpiration has also been demonstrated to be a mechanism for transporting and emitting CH_4 to atmosphere (Rusch and Rennenberg 1998). Transpiration-driven CH_4 emission varies with CO_2 concentration and stomatal conductance (Garnet et al. 2005). CH_4 emission might be organ-specific, and

the stem was identified as the largest source (Abdulmajeed et al. 2017; Barba et al. 2019; Covey and Megonigal 2019).

Methanotrophy is a ubiquitous process for CH_4 consumption (Covey and Megonigal 2019). According to reports, CH_4 was consumed by symbiosis in *Sphagnum* mosses, part of which was consumed by endophytic methanotrophs (Raghoebarsing et al. 2005). Subsequently, the CH_4 uptake by trees of four species, including *Betula pubescens*, *Picea abies*, *Pinus sylvestris*, and *Sorbus aucuparia*, was observed both in the laboratory and in situ measurements (Sundqvist et al. 2012).

Plant support of microbial methanogenesis and methanotrophy

Plant root exudates and litter residues are important organic carbon sources (Phillips et al. 2011). Vegetation type and species composition have significant effects on methanogenic archaea diversity and activity, as well as CH_4 production (Ström et al. 2005; Godina et al. 2012). Vascular plants produce root exudates and easily degradable litter that provide abundant substrate to methanogenic archaea, which may substantially increase CH_4 emissions (Ström et al. 2005; Whalen 2005). Meanwhile, plant-transported O_2 diffuses into the rhizosphere (Armstrong et al. 2006), where CH_4 is consumed by methanotrophic bacteria (Sorrell et al. 2002; Raghoebarsing et al. 2005). However, in the presence of O_2 , methanogenesis can be suppressed (Fritz et al. 2011). It was also observed that in cushion plant lawns, CH_4 emissions were absent because of high root densities coincided with high soil oxygen, but in *Sphagnum* lawns, CH_4 emissions were substantial. Subsequent study suggested that methanotrophs were members of the nitrogen-fixing communities in all wood decay stages (Mäkipää et al. 2018). Together, plants might play important roles in regulating the production, oxidation, and export of CH_4 . However, it still requires more evidence to underlie its regulation mechanism.

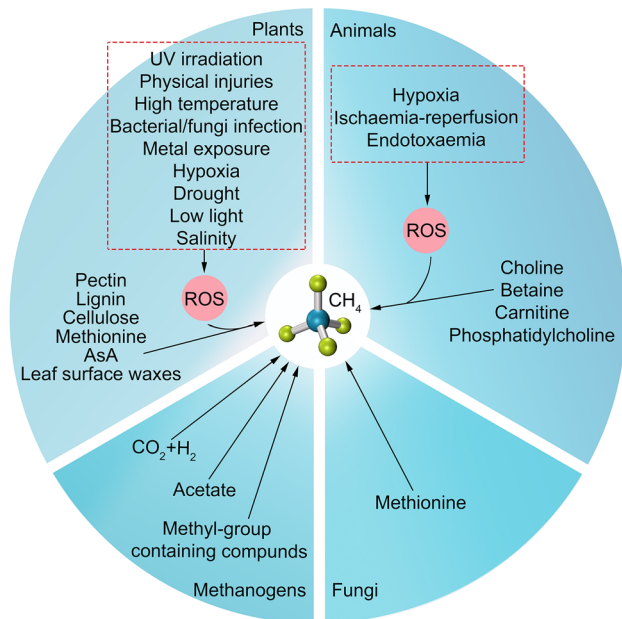


Fig. 1 The proposed mechanisms for CH_4 production in plant under abiotic stresses. The stimuli factors are shown as red dash-lined boxes. ROS are considered to play a vital role in CH_4 production. AsA ascorbic acid, CO_2 carbon dioxide, H_2 hydrogen, ROS reactive oxygen species. Integrated from Liu et al. (2015); Liu and Whitman (2008)

Roles for CH_4 in plants

Plant tolerance against abiotic stress

Ample evidence has clearly demonstrated the protective effects of CH_4 on various stresses in plants (Table 1). The protection achieved by CH_4 in animals has been proposed to be mediated by reducing oxidative stress (Boros et al. 2012; Wang 2014). Rapid overproduction of ROS is triggered by abiotic stresses, thus resulting in lipid peroxidation and oxidative damage (Møller et al. 2007). To counteract these toxic stress metabolites, plants possess defense systems that include antioxidant enzymes, superoxide dismutase (SOD), ascorbate peroxidase (APX), CAT, and POD. In addition,

Table 1 Examples of CH₄ involvement in plant abiotic stress tolerance

Plant species	Stress	Mechanism	References
<i>Medicago sativa</i>	NaCl toxicity	Up-regulation of HO1 expression and reestablishment of ion homeostasis	Zhu et al. (2016)
<i>Zea mays</i>	Osmotic stress	Improving sugar and AsA metabolism, thus suppressing ROS production	Han et al. (2017)
<i>Vigna radiata</i>	Osmotic stress	CH ₄ -induced NO-regulated redox homeostasis and starch metabolism	Zhang et al. (2018)
<i>Medicago sativa</i>	Cu stress	Reducing Cu accumulation, increasing amylase activities, and reestablishing redox homeostasis	Samma et al. (2017)
<i>Medicago sativa</i>	Al stress	Reducing Al accumulation via stimulating the organic acid metabolism and their transport for chelating Al, and reestablishing redox homeostasis	Cui et al. (2017)
<i>Medicago sativa</i>	Cd stress	Reducing Cd accumulation via the modulation of miR159 and miR167, and reestablishing redox and GSH homeostasis	Gu et al. (2018)

non-enzymatic components, such as AsA, glutathione (GSH), and glucose metabolism, could detoxify ROS to enhance plant tolerance against stress (Foyer and Noctor 2011; Noctor et al. 2012; Uzilday et al. 2014). It has been identified that there is a correlation between exposure to CH₄ and increase of antioxidant enzyme activity as well as their gene expression, thereby reestablishing redox homeostasis (Cui et al. 2015, 2017; Zhu et al. 2016).

Drought and salinity stress are considered as major limitations for crop productivity. CH₄ can alleviate polyethylene glycol (PEG) stress, a solute for mimicking water deficiency by inducing osmotic stress, through regulating ROS status by improving sugar, AsA, and GSH homeostasis (Han et al. 2017). Subsequent result discovered that NO might be involved in CH₄-ameliorated seed germination inhibition triggered by PEG, and CH₄-reestablished redox homeostasis is NO-dependent (Zhang et al. 2018). Salinity stress also imposes an ionic imbalance somewhat like osmotic stress and certain nutrition disorders (Zhu 2001, 2003; Kurniasih et al. 2013), resulting in the inhibition of seed germination and seedling growth, and a decline in productivity (Turner et al. 2013). CH₄-rich water (MRW) may also reestablish ionic homeostasis by increasing K⁺ and Ca²⁺ contents, and by decreasing Na⁺ content (Zhu et al. 2016). It was also observed that heme oxygenase1/carbon monoxide (HO1/CO) might be involved in CH₄-alleviated salinity stress in *Medicago sativa*.

Metal exposure is an acute problem of crop production in some production areas. More importantly, it poses a serious threat to animal and human health (Jarup and Akesson 2009). Metal exposure causes severe inhibition in seed germination and plant growth, even to the extent of plant death (Foy et al. 1978). Biochemical and genetic evidence shows that metal imposes oxidative stress by inducing excessive levels of ROS production (Cui et al. 2017; Samma et al. 2017; Gu et al. 2018). Methane generally provides protective effects toward plant metal toxicity through at least two mechanisms: reducing metal accumulation and reestablishing redox homeostasis in plant cells. This hypothesis has been supported by strong evidence. For instance, CH₄

noticeably alleviated an excess of copper (Cu)-induced inhibition of the seed germination and seedling growth of *Medicago sativa* (Samma et al. 2017). This was in accordance with a reduction in the accumulation of Cu and Cu-induced proline, concomitant with an increase of α/β -amylase activities and total sugar content. The reestablishment of redox homeostasis was also observed.

Application of a CH₄ solution can also block cadmium (Cd) accumulation by modulating the expression levels of *miR159* and *miR167*, as well as their target genes *ABC transporter* and *Nramp6* in root tissues (Gu et al. 2018). Besides, CH₄ reestablishes redox and GSH homeostasis, which contributes to ameliorate Cd toxicity in *M. sativa*. In addition, CH₄ could suppress aluminum (Al) accumulation by regulating the expression of organic acid metabolism and transport genes, including citrate synthase (CS), malate dehydrogenase1/2 (MDH1/2), aluminum-activated malate transporter1 (ALMT1), and aluminum-activated citrate transporter (AACT), to maintain nutrient homeostasis and improve Al-induced oxidative stress (Cui et al. 2017).

Participation in root organogenesis

Root development is of great importance for plants to thrive. Recent studies have shown that CH₄ acts as an inducer of root organogenesis (Table 2). Application of MRW can significantly induce the formation of adventitious roots (AR) in cucumber explants. Pharmacological and molecular evidence indicated the involvement of HO1/CO and Ca²⁺ pathways (Cui et al. 2015). Further studies indicated that NO (Qi et al. 2017), H₂S (Kou et al. 2018), and GSH (Jiang et al. 2019) operate as downstream components regulating CH₄-induced AR formation. The modulation of the cell division-related gene (*CsCDC6*), cell cycle regulatory genes (*CsDNAJ-1*, *CsCDPK1*, and *CsCDPK5*), auxin signaling-related genes (*CsAux22D-like* and *CsAux22B-like*), and auxin inducible genes (*AtCYCB1; 1*, *AtCDKA; 1*, and *AtGH3.3*, etc.) as well as genes encoding calcium-dependent protein kinases (CDPKs), were also involved. Interestingly, CH₄-induced NO-mediated S-nitrosylation and H₂S-dependent S-sulphydrylation, both

Table 2 Examples of CH₄ regulation of root organogenesis

Plant species	Organs	Mechanism	References
<i>Cucumis sativus</i>	Adventitious root formation	Regulating HO1/CO and Ca ²⁺ signal transduction	Cui et al. (2015)
<i>Cucumis sativus</i>	Adventitious root formation	Regulating downstream NO signal transduction	Qi et al. (2017)
<i>Cucumis sativus</i>	Adventitious root formation	Regulating downstream H ₂ S signal transduction	Kou et al. (2018)
<i>Cucumis sativus</i>	Adventitious root formation	Regulating γ -ECS-mediated GSH homeostasis	Jiang et al. (2019)
<i>Solanum lycopersicum</i>	Lateral root formation	Regulating downstream H ₂ S signal transduction	Mei et al. (2019)
<i>Solanum lycopersicum</i>	Lateral root formation	Regulating downstream H ₂ O ₂ signal transduction	Zhao et al. (2019)

of which belong to post-translational modification and play important roles in diverse biological processes (Yun et al. 2011; Aroca et al. 2015; Yang et al. 2015), were observed in cucumber explants (Qi et al. 2017; Kou et al. 2018). These results indicated that post-translational modification might be used to explain the mechanism underlying CH₄ functions in plants.

Although the origin of lateral roots (LRs) is different from ARs origin, it has been found that they share key elements with other gaseous signaling cascades. Recent study has demonstrated that CH₄ can trigger LR formation in alfalfa, rapeseed, *Arabidopsis*, and tomato (Mei et al. 2019). To date, hydrogen peroxide (H₂O₂) and H₂S have been found to be required for CH₄-induced LR formation (Mei et al. 2019; Zhao et al. 2019). Related studies provided the molecular mechanism for CH₄-induced tomato LR formation. This model postulates that CH₄ triggers a signaling cascade, and results in increased production of downstream molecules, nicotinamide adenine dinucleotide phosphate (NADPH)-dependent H₂O₂ and L-cysteine desulfhydrase (DES)-dependent H₂S, followed by the development of LR formation with the involvement of cell cycle regulatory genes, miRNAs, and their target genes (e.g., *ARFs*) (Mei et al. 2019; Zhao et al. 2019).

Participation in vegetable postharvest preservation

The postharvest storage of vegetables induces a redox imbalance. CH₄ could delay senescence and associated browning of daylily buds via regulating polyphenol oxidase activity to maintain redox homeostasis (Hu et al. 2018). Moreover, the decrease of the unsaturated/saturated fatty acid ratio and energy charge during storage was also attenuated. These results suggested that CH₄ can be used in postharvest practice.

The interaction between CH₄ and other signaling molecules

Cross talk between CH₄ and ROS

As mentioned above, ROS is one of the CH₄ inducers. CH₄ production was decreased by the removal of ROS and

increased by inhibiting ROS removal enzymes (Messenger et al. 2009). Meanwhile, CH₄ can significantly block the increased ROS overproduction through various mechanisms, including increasing antioxidant enzymes activities, reestablishing AsA and GSH homeostasis, and modulating glucose metabolism, thus enhancing plant tolerance against abiotic stresses (Han et al. 2017; Samma et al. 2017; Gu et al. 2018). Furthermore, CH₄ could increase NADPH oxidase-dependent H₂O₂ production, followed by the induction of LR formation in tomato seedlings (Zhao et al. 2019).

Cross talk between CH₄ and NO

NO is an essential gasotransmitter involved in multiple physiological functions. CH₄ interacts with NO in controlling adventitious rooting (Qi et al. 2017) and combating osmotic stress (Zhang et al. 2018). Using laser confocal scanning microscopy and inhibitor tests, we discovered that endogenous NO synthesis was induced by CH₄ via NO synthesis-like (NOS-like) protein and diamine oxidase (DAO), two NO synthetic enzymes. Afterwards, the modulation of target gene expression and post-translational modification were observed during the development of cucumber AR formation (Qi et al. 2017). Above CH₄ responses were reversed by 2-phenyl-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (PTIO) and 2,4-carboxyphenyl-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO) (two NO scavengers), N_G-nitro-L-arginylester hydrochloride (L-NAME) (a mammalian NOS-like enzyme inhibitor), and β -hydroxyethyl hydrazine (β -HEH) (a DAO inhibitor). This evidence showed that CH₄-induced AR formation was NO-dependent and partially mediated by NOS-like protein and DAO. Besides, CH₄ could enhance the plant tolerance against osmotic stress via maintaining redox homeostasis, and modulating starch metabolism (Zhang et al. 2018). Meanwhile, CH₄-triggered NO-dependent S-nitrosylation was observed either. Above results reflect the complexity of CH₄ signaling.

Cross talk between CH₄ and other gas molecules

Similar to NO, CO might be another second messenger in CH₄ signaling. For instance, HO1-dependent CO acts as

a downstream component during CH₄-induced cucumber AR formation via modulating *DNAJ-1* and *CDPK1/5* gene expression (Cui et al. 2015). Subsequent studies revealed that H₂S was also partially involved in CH₄-induced LR and AR formation by regulating the expression of cell cycle regulatory genes, *ARFs*, and miRNA, and the involvement of S-sulphydrylation was also suggested (Kou et al. 2018; Mei et al. 2019).

Cross talk between CH₄ and Ca²⁺

In rice LR formation, Ca²⁺ acts downstream of HO1-dependent CO signaling (Hsu et al. 2013). Similarly, exogenous Ca²⁺ strengthens CH₄-triggered cucumber AR formation (Cui et al. 2015), which was further impaired by the addition of its chelator ethylenediaminetetraacetic acid (EDTA) and a Ca²⁺ channel blocker lanthanum chloride (LaCl₃). These observations indicated that the Ca²⁺ might be involved in CH₄-elicited cucumber AR formation.

Cross talk between CH₄ and GSH

GSH is an important cellular antioxidant with multiple functions in plants, including redox signaling, antioxidant defense, and root organogenesis (Noctor et al. 2012). Some studies have shown that GSH homeostasis is reestablished by CH₄ in plants when subjected to Cd exposure (Gu et al. 2018) and osmotic stress (Han et al. 2017). Recent result showed that γ -glutamyl cysteine synthetase (γ -ECS)-dependent GSH might be required for CH₄-induced cucumber AR formation (Jiang et al. 2019).

Conclusion and perspectives

Some literature is now available that preliminarily illustrates the complex and integrated regulation of CH₄ synthesis, functions, and its signaling (Figs. 1, 2). Considerable advances have been made in the field of identifying the biological effects of CH₄. However, aerobic non-microbial CH₄ production still remains to be further and completely elucidated in plants. On the other hand, although direct targets of CH₄ in plant cells remain unknown, the molecular mechanism underlying the biological roles of CH₄ involves gene expression, miRNA, protein, plant hormone levels, and the regulation of protein post-translational modification.

It is clear that CH₄ plays valuable roles in plant development and adaptation against environmental stimuli. Since methanotroph activity may be increased under conditions with high concentration of CH₄ (Sorrell et al. 2002), and methanotrophs appear to be coupled with N₂ fixation (Mäkipää et al. 2018), we speculated that CH₄ might have

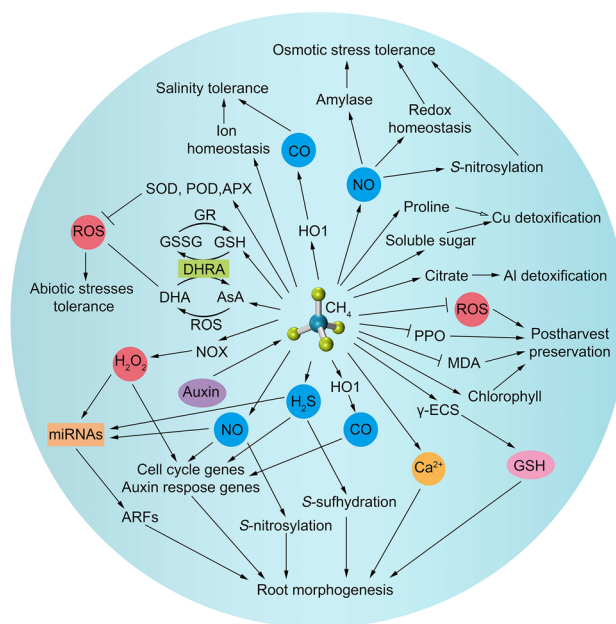


Fig. 2 Possible mechanism related to the botanical effects of CH₄. *APX* ascorbate peroxidase, *ARFs* auxin response factors, *CAT* catalase, *CO* carbon oxide, *DHA* oxidized ascorbic acid, *DHRA* dehydroascorbate reductase, γ -*ECS* gamma-glutamylcysteine synthetase, *GR* glutathione reductase, *GSH* glutathione, *GSSG* oxidized glutathione, *HO1* heme oxygenase 1, *H₂O₂* hydrogen peroxide, *H₂S* hydrogen sulfide, *MDA* malondialdehyde, *miRNA* microRNA, *NO* nitric oxide, *NOX* reduced nicotinamide adenine dinucleotide phosphate (NADPH) oxidase, *POD* peroxidase, *PPO* polyphenol oxidase, *ROS* reactive oxygen species, *SOD* superoxide dismutase

potential capacity to improve soil fertility by changing microbial community and increasing methanotrophic bacteria activity. Certainly, this hypothesis requires further validation.

Finally, it reminds us of some crucial challenges facing current application of CH₄. First, because of its innate flammability and difficulty in transport, CH₄ fumigation may be impractical for agriculture. Consequently, we proposed the application of MRW irrigation, which may provide a safe, portable, and easy approach. The reason is that the concentration of CH₄ in the saturated methane-rich water or methane-rich saline was about 1–1.5 mM (Ye et al. 2015; Zhou et al. 2018; Jiang et al. 2019), far below its lowest explosive concentration (5%; v/v) (Liu et al. 2012). Second, it should be noted that CH₄ is a potent climatic change gas, and its potential usage is a challenge.

Acknowledgements The authors would like to thank the financial support from the National Natural Science Foundation of China (Grant No. 31572116 and 31771696) and the Natural Science Foundation of Jiangsu Province (Grant No. BK20181317). We would like to thank Dr. Evan Evans (University of Tasmania; tassiebeerdr@gmail.com) for the English editing of this paper.

Author contribution statement LL, SW, and WS wrote and revised the manuscript. All authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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