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Jasmonic acid signalling and the plant holobiont

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The plant holobiont – which is the plant and its associated microbiome – is increasingly viewed as an evolving entity. Some interacting microbes that compose the microbiome assist plants in combating pathogens and herbivorous insects. However, knowledge of the factors that influence the microbiome in the context of defence signalling pathways is still in its infancy. Recent research reported that changes in jasmonic acid (JA) and salicylic acid signalling affects the root microbiome of *Arabidopsis thaliana*. This review aims to present the hypothesis that the JA pathway represents a novel mechanism for microbiome engineering for improved holobiont fitness in agricultural systems.

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Introduction

Advances in the field of microbial ecology indicate that macro-organisms are populated by diverse microbial communities that affect their fitness and evolution [1••]. For this reason, the host, together with its microbiome, is increasingly being viewed as a 'holobiont' in which mutualistic interactions are likely to prevail by collectively enhancing overall fitness [1••]. Plants have co-evolved with microorganisms for the entirety of their existence and as such have acquired mechanisms to mediate interactions with their symbionts that help to regulate holobiont fitness [3]. Current evidence suggests that plant defence signalling pathways are among these mechanisms and may play important roles in helping plants to recruit microbiomes that enhance stress tolerance [4]. In this review, we focus on how jasmonic acid (JA) signalling influences the plant microbiome and how this may affect holobiont fitness in response to attack by herbivorous insects and necrotrophic pathogens. We begin with an overview of the JA pathway and its evolution in terrestrial plants, then present evidence of how the plant microbiome influences biotic stress tolerance and how it is affected by JA signalling. Finally, we discuss potential mechanisms for JA mediated changes in the plant microbiome, how this may influence holobiont fitness and identify key knowledge gaps for future research.

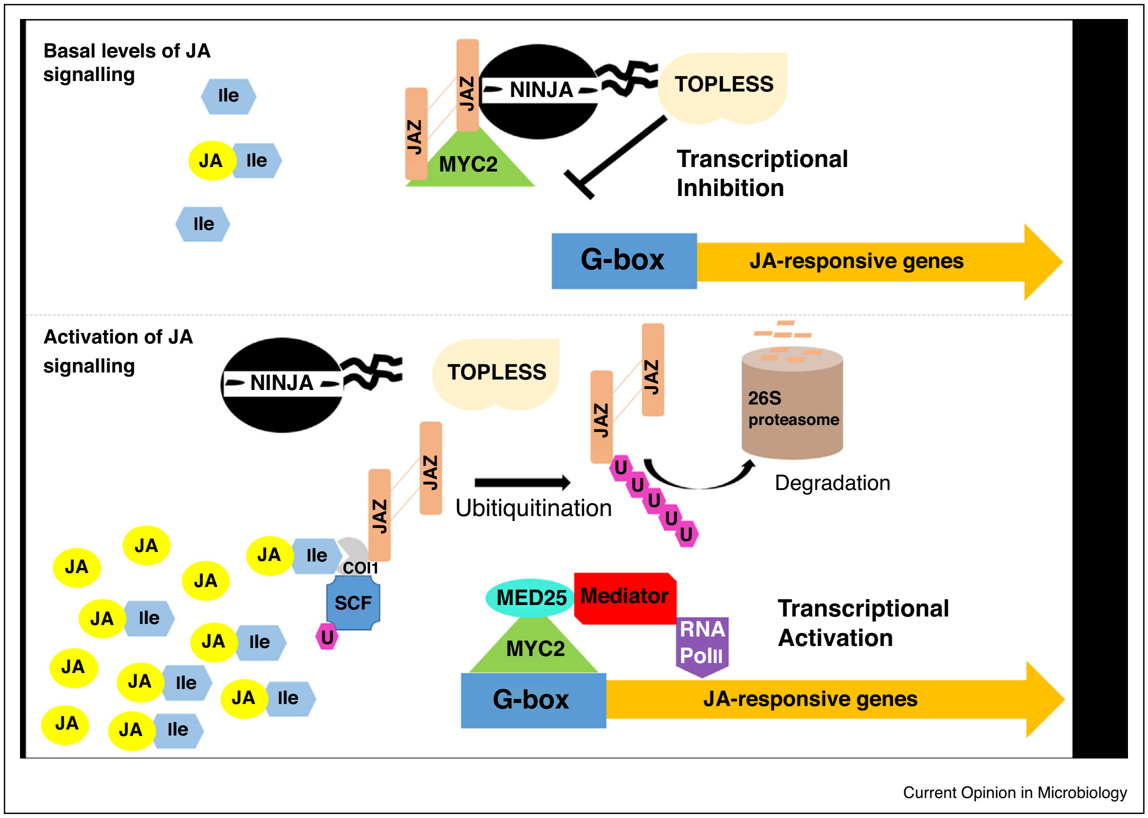
The JA signalling pathway

As sessile organisms plants have developed sophisticated ways to perceive and respond to environmental change and interact with other organisms. Of these, plant hormones are critically important as modulators of pathways that lead to phenotypic responses to a plethora of environmental stimuli. JA and its derivatives are particularly important as they not only mediate responses against certain pathogens and herbivores, but act as signalling molecules that facilitate interactions between plants and root-associated beneficial microorganisms [5]. In addition, they modulate stomatal opening, tendril coiling, root growth inhibition, anther development, fruit ripening, tuber formation, seed germination, senescence, and plant responses against wounding [6].

Coordination, prioritisation and cross-talk between pathways are essential to enable plants to efficiently respond to external cues. For example, JA defence signalling is often coordinated with ethylene (ET) signalling, but typically suppressed by abscisic acid (ABA) [7]. ABA is active during abiotic stress signalling via the basic helix loop helix transcription factor MYC2 that provides a powerful switch between both pathways [7,8•]. The reason for this is likely to be related to resource use efficiency. In this case i.e. plants must prioritise responses to abiotic stresses that are essential for survival, such as drought, rather than defence against biotic stresses. This antagonistic wiring of pathways may seem disadvantageous, as drought-stressed plants, for example, become more susceptible to pests and pathogens. Nonetheless, these detrimental organisms often encounter suboptimal conditions and are usually not as abundant during conditions of abiotic stress. A similar (at least partially) antagonistic relationship exists between JA and salicylic acid (SA) defence signalling, to enable the most appropriate action against pests and pathogens [9].

Enzymes of the lipoxygenase pathway catalyse the synthesis of jasmonates through the octadecanoid pathway from the precursor α-linolenic acid released from chloroplast membranes [10,11]. JA biosynthesis is regulated by a

Figure 1



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Schematic representation of the regulation of JA signalling pathway in *Arabidopsis*. The JA pathway is activated by the conjugation of JA to L-isoleucine (Ile), which leads to the production of the active hormone (3R, 7S)-jasmonoyl-L-isoleucine (JA-Ile) [42]. This hormone elicits the formation of a co-receptor complex formed by the interaction between the F-box protein CORONATINE INSENSITIVE1 (COI1) and a JASMONATE-ZIM DOMAIN PROTEIN (JAZ), which subsequently promotes the ubiquitin (U)-mediated degradation of JAZ proteins through the 26S proteasome pathway [42,43]. These proteins supress several basic-helix-loop-helix transcriptional factors such as MYC2, hence upon their breakdown, MYC2 is released. This makes it possible for JAZ proteins to up or down regulate distinct branches of the JA signalling pathway [8•]. Compelling evidence indicates that MYC2 (and related MYC3 and MYC4) form a regulatory hub, which integrates distinct signals that affect plant health and growth [8•]. Pathogen defence-related genes are negatively regulated by MYC2, which is also involved in other defence-related processes including Induced Systemic Resistance (ISR) or priming [44]. Responses to wounding and insect herbivory are positively regulated by MYC2 and are initiated by the induction of the VEGETATIVE STORAGE PROTEIN (VSP2) [45]. Generally, JAZ proteins repress transcription factors by: (1) competing with MEDIATOR25 (MED25), a subunit of the MEDIATOR protein complex that promotes transcriptional activation [46]; and (2) competing with the NOVEL INTERACTOR OF JAZZ (NINJA) adaptor protein, which recruits the co-repressor TOPLESS (TPL) [47]. U: Ubiquitin; SCF: Skp, Cullin, F-box containing E3 ubiquitin ligase complex; RNA PolII: RNA polymerase II.

positive feedback as genes that encode these enzymes are inducible by JA [12]. The JA signalling pathway of *Arabidopsis* has received greater attention than that of other plant species and as such is the most comprehensively understood (Figure 1).

Studies on *Arabidopsis thaliana* suggest that the ‘feeding’ behaviour of plant pathogens determines the hormone signalling transduction pathway that will be activated to trigger defence responses by plants. For example, an appropriate response to biotrophic pathogens (viz. those that feed on the contents of living cells) is induction of SA signalling and the production of reactive oxygen species (ROS) that lead to a hypersensitive response (HR) and localised programmed cell death [9]. However, ROS and SA signalling must be rapidly suppressed by JA signalling if the plant is under attack by necrotrophic pathogens (viz. those that feed on dead plant tissues). Nevertheless, a wide range of agriculturally significant plant pathogens alter their feeding behaviour throughout their lifecycle or trick the plant into inducing the wrong pathway [13]. Hence, predicting which defence signalling pathway will be induced in response to a particular pathogen is not straightforward. There is evidence to suggest that JA signalling has evolved during the colonisation of land by plants, which were then exposed to new biotic and abiotic stresses including novel pathogens (Box 1) [14]. Nonetheless, symbiotic relationships with microbes, in particular mycorrhizal fungi, may have facilitated the occupation of land by plants [15].

Box 1 The JA pathway emerged with land plants.

Recent evidence indicate that when plants colonised plants during the Silurian period JA signalling and other defence pathways evolved in plants. This hypothesis is based on analyses of complete genome sequences of nine representative species of all main plant lineages as well as transcriptome data of four charophytes and one liverwort [2•]. All genomes were found to contain orthologs representing core components of the JA signalling pathway. However, algal genomes encoded orthologs to only three of these components, namely TOPLESS, COI1 and MYC-RELATED TRANSCRIPTIONAL ACTIVATOR [2•]. In addition to JA signalling, SA and ABA signalling also seem to have emerged in the last common ancestor of land plants [2•], as both pathways are also involved in plant biotic and abiotic interactions [5]. ABA synthesis and the downstream signalling events in *Arabidopsis* and possibly in all Embryophyta may have been triggered mainly by limited water availability [2•].

The influence of microbiomes on host biotic stress tolerance

To colonise and remain in association with plants, microbes must overcome plant's innate immunity. Plants perceive molecules associated with microbes as 'danger signals' through high-affinity cell surface pattern-recognition receptors (PRR). These signals, which are known as evolutionarily conserved pathogen (or microbial)-associated molecular patterns (PAMPs or MAMPs, respectively), activate extracellular surface PRRs [16]. This activation then leads to signal transduction pathways that elicit mechanisms to restrict microbial colonisation [16]. Some plant beneficial microbes not only seem to circumvent this first line of defence but may also be actively recruited by the plant to provide the host with additional defences. These can then serve as biocontrol microbes by producing antimicrobial compounds, outcompeting pathogens and/or through 'defence priming', which is a process that leads to ISR in which the plant responds more rapidly and more intensely to pathogen or pest attacks [17]. JA and ET play essential roles in the regulation of rhizobacteria-conferred ISR, which is SA-independent [18••]. Upon attack by pathogens or insect herbivores, defence priming is typically followed by the formation of structural barriers such as increased cell wall appositions, callose depositions and enhanced stomatal closure [18••]. MYB72 is a transcriptional factor protein which belongs to the large R2R3-MYB gene family and is required in the roots during the onset of ISR [19]. MYC2 and transcripts from members of the AP2/ERF family are also involved in the regulation of priming [18••].

The influence of JA signalling on the plant microbiome

Microbes thrive in distinct plant-associated habitats including: (1) the rhizosphere, which is the region of soil affected by the presence and activities of roots; (2) the rhizoplane, which is the root surface; (3) the phyllosphere, which comprises the surfaces and inner tissues of aerial plant tissues (viz. stem and leaves, surface); and (4) the endosphere, which is the interior of the plant [20]. Each of these habitats comprise a different set of environmental conditions that strongly affect the diversity of the associated microbiome [20]. Current evidence indicates that JA influences the composition of the *Arabidopsis* root-associated microbiome [21••]. Induction of JA signalling pathway increased the relative abundances of bacterial populations closely related to taxa that are reported to suppress phytopathogens and insects [20]. This suggests that when under attack, plants may have evolved mechanisms to recruit symbionts that enhance their tolerance to biotic stress. Effects of altered JA signalling on epiphytic microbial communities on shoots were also observed. *Arabidopsis* plants that were impaired in the JA pathway harboured a higher diversity of cultured epiphytes colonising the phyllosphere, while the diversity of cultured endophytes was reduced upon induction of the SA pathway [22]. JA signalling has also been shown to restrict colonisation of rice (*Oryza sativa*) endophytic environments by incompatible strains of nitrogen-fixing *Azoarcus* bacteria and suppress nodulation in *Lotus japonicus* [23,24]. Nevertheless, distinct holobionts may respond differently to alterations in defence signalling pathways. JA signalling did not impact the structure of phyllosphere and root microbiomes of wild *Nicotiana attenuata* characterised over five developmental stages [25]. In addition, defence signalling pathways mediated by other hormones such as SA play a role in driving the selection of specific bacterial families for *Arabidopsis* root colonisation [26••]. Taken together, it appears that plants are quite selective in attracting and enabling colonisation by specific microbial taxa, presumably those that provide more benefits.

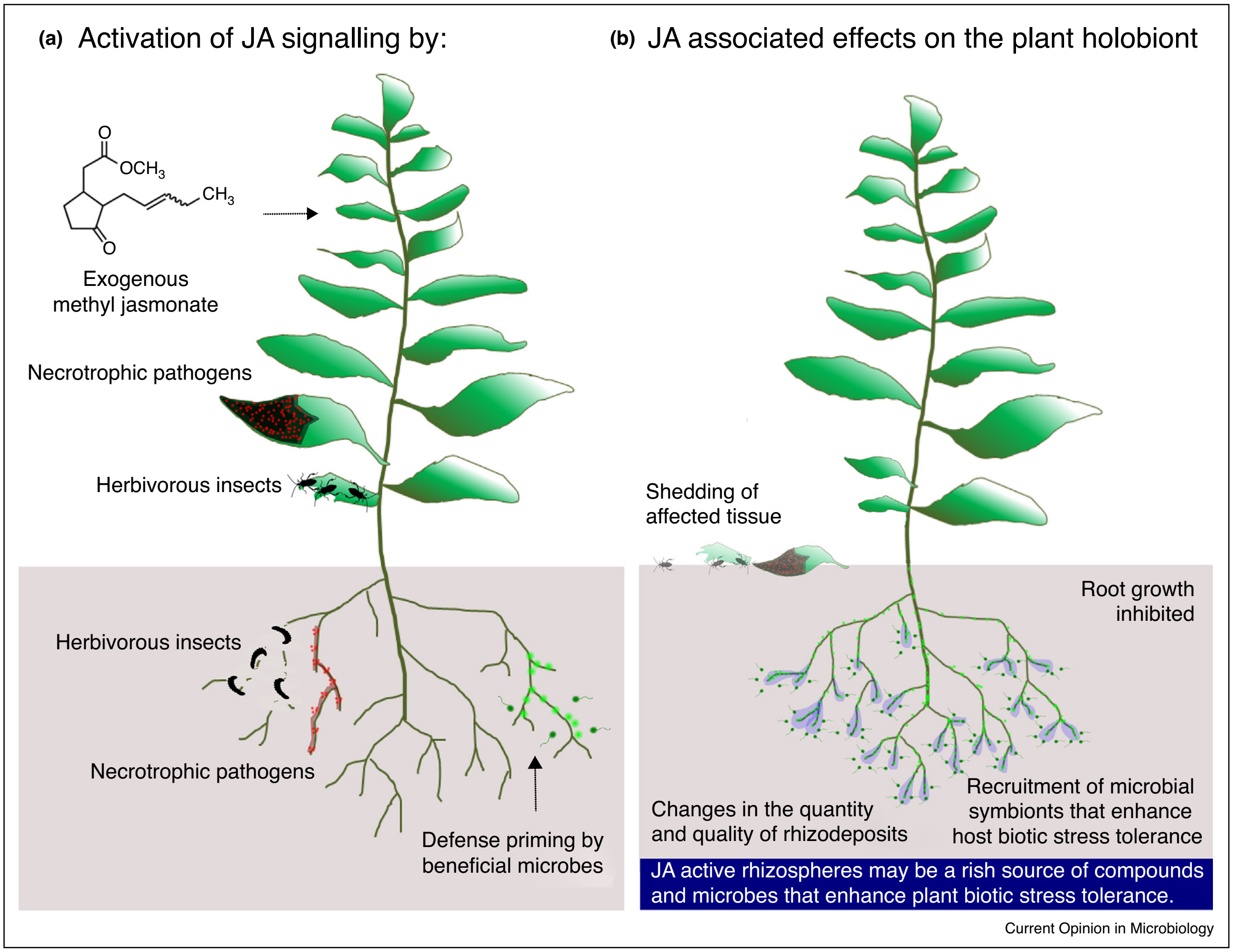
Potential mechanisms underpinning JA-mediated changes in the plant microbiome

Plant roots release c. 25% of photosynthetically-fixed carbon into soil and in return reap a wide-range of chemically and biologically mediated benefits [27,28]. Changes in the quantity and composition of organic compounds released from roots elicit changes in the root-associated microbiome [29,30••]. In response to abiotic and biotic stresses, these changes often promote interactions with organisms that enhance plant stress tolerance [31]. When exposed to nitrogen deficiency, for example, leguminous plants release flavonoids that attract symbiotic N-fixing bacteria [32]. In addition, under nutrient-limiting conditions, many plant species release larger quantities of strigolactones, which attract arbuscular mycorrhizal fungi that enhance nutrient supply to the plant (notably P) [33]. Likewise, when exposed to the leaf pathogen *Pseudomonas syringae*, *Arabidopsis* release large quantities of malate, which attracts *Bacillus subtilis* strain FB17 that suppresses infection [34]. The secretion of antimicrobial compounds by roots can also contribute to the recruitment of plant growth promoting bacteria (PGPR) which are insensitive to them. For instance, benzoxazinoids released by maize attract the insensitive

PGPR *Pseudomonas putida* KT2440 [35]. Moreover, exudates released by roots exposed to different nutrient deficiencies have been shown to also affect the transcriptome of PGPR, for example up-regulation of genes associated to motility and an ABC transporter for bacterial siderophores under P and Fe deficiencies, respectively [36].

Exposure of *Arabidopsis* roots to either methyl jasmonate (MeJA), SA or NO led to distinct exuded metabolomes compared to the control, with MeJA being the treatment that elicited the highest increase in exudation rates [37]. The release of several phenolic compounds was induced by all three signals, but kaempferol-3-*O*-β-D-glucopyranoside-7-*O*-α-l-rhamnoside was exclusively exuded by MeJA-treated roots [37]. This indicates that during JA signalling there is chemical communication between plant roots and soil microbes, with phenolics being suitable candidates as plant-derived signals. We have previously reported a highly significant correlation of similarities between *Arabidopsis* mutants and wild-type based on root exudate profiles and the rhizosphere microbiome [30••]. These mutants have impaired JA signalling in distinct branches of the pathway: *myc2* has enhanced gene expression associated to defence against biotrophic and hemibiotrophic pathogens but reduced responses to wound and herbivory; *med25* exhibits decreased responses to JA-mediated pathogen defence as well as wound and herbivory [30••]. The relative abundances of particular populations of bacteria and Archaea were distinct among the mutants and the wild-type. Some of these populations were correlated with specific exudates differentially released from the different genotypes [30••]. These observations suggest that exudates released during

Figure 2



Schematic overview of the hypothesis that JA signalling recruit biocontrol agents via changes in exudation patterns.

defence signalling are important factors driving changes in relative abundance of root-associated microbial populations.

JA signalling as a tool to engineer plant microbiomes

The goal of engineering root microbial communities is to manipulate their composition towards 'net' beneficial effects to the plant, such as increased nutrient acquisition, enhanced yield and abiotic and biotic stress tolerance [38••]. Current approaches include (1) application of microbial inoculants, (2) alteration of plant exudation profiles through breeding or genetic engineering, and (3) land management (*e.g.* pH amendment and tillage) [38••,39,40]. These approaches, however, have a range of problems that currently limit their effectiveness. For example, inoculants often fail due to competition with native organisms [41]. In addition, modifying plant exudation profiles is extremely challenging because it is not clear how to increase exudation of one compound without altering levels of others [39]. Furthermore most microbes inhabit basal regions of roots, whereas most exudates are released from root apices [27,28]. It is difficult therefore to deliver exudates where they are needed [28]. Lastly, management approaches are not at all targeted [39]. Targeting mechanisms that may have naturally evolved to select for mutualistic symbioses that enhance holobiont fitness may provide new strategies to select beneficial microbiomes. In this regard, JA-mediated microbiome engineering may be advantageous as it may exploit a co-evolved mechanism to recruit microorganisms that confer enhanced biotic stress tolerance.

Conclusions

At present the hypothesis that JA signalling leads to changes in root exudation that help plants recruit microbes that confer enhanced tolerance to biotic stress remains untested (Figure 2). It is also not known whether the microbiome of other plant species is influenced by activation of the JA pathway, and whether these effects, if any, are also apparent in endophytic compartments of the host. Considerable work should be performed in this regard. Function-based approaches such as metagenomics, metatranscriptomics and metaproteomics using rhizosphere soil or tissues from plants that have the JA signalling pathway activated could provide new insights into the mechanisms associated with the recruitment and the responses elicited in plant-associated microbial communities. New opportunities exist to increase plant yields by (1) understanding how JA signalling can be better used to attract and maintain beneficial microbes, (2) breeding microbe-optimised plants, and (3) breeding specific plant-optimised microbiomes that may serve as powerful inoculants.

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