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Plant mediator

Mediating the jasmonate response

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Jasmonate (JA) signaling plays an important role in regulating both plant defense and development. We have recently reported that the *PHYTOCHROME AND FLOWERING TIME1* (*PFT1*) gene, which encodes the MEDIATOR25 subunit of the plant Mediator complex, is a key regulator of JA regulated transcription. We showed that the *pft1* mutant had attenuated expression of a wide range of JA responsive genes and altered resistance to fungal pathogens. Here we examine the position of PFT1/MED25 within the JA pathway and discuss its role in "mediating" the JA response.

Key words: jasmonate, JAZ, mediator, transcription, defense, PFT1, *Fusarium oxysporum*

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The plant hormone jasmonate (JA), and its conjugates, regulate a wide range of plant responses. These include defense against insects and plant pathogens, protection against abiotic stresses and also developmental processes such as reproductive development and senescence.[1] Research on understanding jasmonate signaling has made significant progress in recent years with the discovery of the *JASMONATE ZIM DOMAIN* (*JAZ*) gene family.[2-4]

Together with the isoleucine conjugate of JA, the JAZ proteins have been shown to bind to the F-box protein, COI1 (CORONATINE INSENSITIVE1), where they are tagged with ubiquitin and subsequently degraded by the 26S proteasome.[3,5,6] It has been proposed that the JAZ proteins act as repressors of JA associated transcription factors (TFs).[2,3] Indeed, the majority of the JAZ proteins have been shown to interact with MYC2,[6,7] an important TF involved in the regulation of diverse JA responses.[8,9]

These findings provide a potential mechanism for the activation of JA responses through degradation of the JAZ proteins and the release of transcriptional repression. However, the sequence of events that occur directly after JAZ degradation have not been fully elucidated and at present, MYC2 is the only TF to have been shown to interact with a JAZ protein. As *myc2* mutants do not possess the full spectrum of JA-dependent phenotypes, it is likely that the JAZ proteins repress other TFs in order to control JA signaling.

Previous research on JA signaling has identified a number of TFs important for JA regulation. In addition to MYC2, the AP2/ERFs (APETALA2/ETHYLENE RESPONSE FACTORs) such as ERF1, ERF2, ERF4 and ORA59 (OCTADECANOID RESPONSIVE ARABIDOPSIS AP2/ERF 59), have been shown to be important in regulating JA responses.[10-13] These transcription factors can act either synergistically or antagonistically on JA responsive genes. For example, MYC2 and ERF4 are known to repress pathogen responsive defense genes such as *PDF1.2* (*PLANT DEFENSIN 1.2*)[8,12] whereas both ERF1, ERF2 and ORA59 induce the expression of *PDF1.2*.[10,11,13,14]

In order to control transcription, the sum of the regulatory information provided by TFs must be integrated into a signal for the RNA Polymerase II (RNA Pol II) machinery to act. The correct processing of the signal is compounded by the sheer number of transcription factors encoded in the plant genome, but also by the possibility of multiple TFs influencing the transcription of a single gene under different conditions, tissue types

or developmental stages. To process this information, eukaryotes have evolved a protein complex called "Mediator" which bridges the gap between transcription factors and RNA Pol II. The Mediator complex in plants was found to comprise 27 subunits, 21 of which were conserved between plants and other eukaryotes.[15] Upon interaction with RNA Pol II, the Mediator complex forms a crescent shaped structure that surrounds RNA Pol II and provides a surface for the interaction with adjacent TFs.[16,17] Recognition of a positive signal would then trigger RNA Pol II to initiate transcription. Therefore, identifying which of the Mediator subunits receives JA-associated signals could help improve our understanding of how JA-associated gene expression is controlled.

Through investigating the *PFT1* gene, which encodes the MED25 subunit of Mediator, we were able to identify an important role of PFT1/MED25 in regulating JA responses. Initially, we have identified a significant reduction in basal transcript levels of JA-dependent defense gene expression in the *pft1* mutant and later showed that *pft1* is unable to activate JA-dependent defense genes in response to JA treatment. As a result, *pft1* plants display increased susceptibility to the leaf infecting necrotrophs, *Alternaria brassicicola* and *Botrytis cinerea*.[18]

Interestingly, we found that *pft1* plants also display increased resistance to the root infecting hemibiotroph, *Fusarium oxysporum*.[18] *F. oxysporum* has been shown to hijack JA responses to induce disease symptoms as the *myc2* and *coi1* mutants which are impaired in jasmonate signaling, are both resistant to this pathogen.[19,20] Using a microarray experiment we demonstrated that *F. oxysporum* was indeed able to induce JA-responsive genes in wild type plants and that the expression of these genes was significantly attenuated in *pft1*. These results, together with the increased resistance of *myc2* and *coi1* suggest an important role for JA in *F. oxysporum*-induced disease progression. One explanation for the role of JA in *F. oxysporum*-induced disease progression may be that the pathogen is utilising jasmonate-dependent senescence programs to induce chlorosis or lesion development and may be incapable of activating these programs in the JA signaling mutants.[20]

The Role of PFT1/MED25 in the JA Pathway

An important question arising from these findings is just how important is PFT1/MED25 in regulating the JA pathway. We were able to identify a number of JA genes that had attenuated expression in *pft1*, such as the JA-associated transcription factors, *MYC2* and *ERF4*, defense genes such as *PDF1.2* and *CHI B*, wound genes such as *VSP* and *ESP* and JA biosynthetic genes such as *LOX2* and *JMT*.

A reduction in the expression of such a wide range of JA associated genes in *pft1* plants suggests a key role in regulating JA-dependent transcription. However unlike *coi1* which has abolished JA responses, *pft1* has only attenuated JA responses and retains male fertility. This suggests that PFT1/MED25 is not the only subunit of the Mediator complex that carries out JA-dependent transcription and that others may also be involved. It is also possible that PFT1/MED25 and Mediator act as a gain control quantitatively regulating transcriptional rates once jasmonate signaling is initiated. Further investigation into the other Mediator subunits may reveal additional subunits that are required for JA regulation.

The results from this study as well as other publications on the Mediator complex in plants,[21,22] hint at the information that can be gained from studying this essential complex. The specificity of PFT1/MED25 in regulating JA-dependent gene expression has revealed an additional level of regulation in JA signaling. Future experiments should identify which transcription factor(s) are involved in integrating upstream signals to PFT1/MED25 during activation of JA-responsive gene expression. The other challenge is to unravel the function of the remaining Mediator subunits. The result of such endeavours will not only reveal more about eukaryotic transcription, but may provide significant insight into the control of diverse plant processes.

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