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Fungal pathogen: A game changer for insect herbivore in sequential attack on tomato

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ABSTRACT

Plants have several means of coping with biotic stress, which involves physiological, cellular and molecular mechanisms. The interplay of two principal phytohormonal pathways, Jasmonic acid (JA) and Salicylic acid (SA) play a crucial role in transmitting stress-induced signals throughout the plant. However, the interplay of these hormonal pathways is not clear when plants encounter biotic agents that trigger antagonistic hormonal signals. To address this, we conducted biochemical and gene expression studies on tomato, *Solanum lycopersicum* plants, exposed to insect alone (IA), fungus alone (FA), or sequential dual stress with fungi followed by insect (FI) and insect followed by fungi (IF), with untreated control. We also assessed the performance of late-arriving conspecific herbivore on these plant sets. The total phenol, and non-tannin phenols content in IF and FI plants showed similar increase or decrease as FA and IA plants, respectively. Gene expression analysis revealed that JA-related genes (*MYC2*) were dominant in FI plants, while SA-related genes (*PR1*) were upregulated in IF plants. Moreover, late-arriving herbivores showed significantly decreased relative growth rate, efficiency of conversion of ingested food (ECI) and digested food (ECD) when feeding on FA and IF plants, indicating that sequential treatments substantially induce plant responses. However, herbivory did not affect the late-arriving conspecific herbivore. Thus, biochemical responses and hormonal interplay of the plant are influenced by both sequence as well as the duration of the biotic stress. Furthermore, while the late-arriving conspecific herbivore is negatively affected by the presence of a pathogen, it remains unaffected by previous herbivory.

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1. Introduction

In their natural environment, plants encounter a diverse array of biotic stressors, such as insect herbivores and pathogens. These stressors can occur on the plant simultaneously or sequentially, resulting in positive or negative influences on each other (van Dijk et al., 2020; Zandalinas and Mittler, 2022). To defend against these challenges, plants deploy a variety of mechanisms, constituting changes in morphological, physiological, biochemical and molecular responses. Several factors determine the nature of these induced responses. These include type of attack such as pathogen (biotrophic, hemibiotrophic or necrotrophic) or herbivore (sap-sucking or chewing insects), location of attack (aboveground or belowground), and timing of induction (Mathur et al., 2011; Ponzio et al., 2013; Martínez-Medina et al., 2021; He et al., 2022; McCombe et al., 2022). To combat these different stressors, a finely tuned defence system ensures that plants are capable of effectively responding to the threat in a targeted and efficient manner. However, the order of attacker arrival and spatial competitiveness plays an important role in either rendering the plant vulnerable to the subsequent attack or strengthening its defences against future threats (Mathur et al., 2013a; Fragata et al., 2022). The majority of the existing literature focuses on the effect of a single biotic agent or simultaneous attack of two stressors on the plant at a certain time point (Agrawal et al., 2006; Poelman et al., 2010; Mathur et al., 2013b; Stam et al., 2018; Ekholm et al., 2020). However, very few studies have determined the plant's response to subsequent attacks following a prior encounter with a con- or heterospecific (members of same or different species respectively) insect or pathogen (Moreira et al., 2018; Kroes et al., 2016).

In response to biotic stress, plants activate specific stress-associated phytohormonal signalling pathways, primarily salicylic acid (SA), jasmonic acid (JA) and ethylene (ET), to transmit the signals between the site of attack and non-attacked tissues. Induction of phytohormones signalling leads to changes in induction of biochemical,

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