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CROSSTALK SIGNALLING IN PLANTS: AN ADAPTIVE MECHANISM

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Abstract

Crosstalk is generally defined as a communication or the exchange of messages between two or more individuals. Biological crosstalk refers to "instances in which one or more components of one signal transduction pathway affect another". Crosstalk is also observed between the plants or trees through which the message signals are passed to neighbour plants for better adaptation to severe climatic or environmental conditions (Hussain *et al.*, 2018). Due to plant's immobile existence, they have developed morphological and metabolic adaptability, enabling colonization in diverse habitats. Plant cells utilize parallel information processing to combine external inputs with internal signals to adapt their metabolism to ambient conditions (Genoud and Metraux, 1999). Several instances of detecting stimuli, including hormone, heat, light, salt, or pathogen awareness, have been described as signal transduction and amplification (Taylor and McAinsh, 2004). A paradigm of separate cascade events has been used to portray the sequences of the biochemical reactions that started following perception.

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Introduction

In plants, crosstalk can occur between different signaling pathways such as hormonal and environmental signaling pathways. In hormonal signaling, different plant hormones, such as auxin, cytokinin, gibberellin, abscisic acid, and ethylene, can interact with each other to regulate plant growth and development (Jogawat *et al.*, 2021). For example, auxin and cytokinin interact to control cell division and differentiation during organ development (Chinnusamy *et al.*, 2004). Additionally, abscisic acid (ABA) and gibberellins (GA) can act antagonistically to regulate seed germination and dormancy (Salvi *et al.*, 2021; Nejat and Mantri, 2017).

Symbiotic relationships between trees and other organisms, such as mycorrhizal fungi and nitrogen-fixing bacteria, involve several mechanisms of crosstalk. Trees and their symbiotic partners communicate through chemical signals such as plant hormones, secondary metabolites, and volatile organic compounds (Sharifi *et al.*, 2022; Vazquez-Gonzalez *et al.*,

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2022; Yu *et al.,* 2022). These signals can activate or inhibit specific signaling pathways in both the tree and the symbiont, leading to coordinated responses that benefit both organisms.The physical interaction between the tree roots and the mycorrhizal fungi or nitrogen-fixing bacteria can also lead to crosstalk (Pantigoso*et al.,* 2022). For example, the formation of specialized structures called arbuscules in the tree roots during mycorrhizal symbiosis can allow a direct exchange of nutrients and signaling molecules between the tree and the fungi (Ding *et al*., 2022).The exchange of nutrients between the tree and the symbiotic partner can also involve crosstalk between signaling pathways (Bag*et al.,* 2022; Boyno and Demir, 2022). For example, the transfer of carbohydrates from the tree to the mycorrhizal fungi can activate specific signaling pathways in the fungi that lead to increased nutrient uptake by the tree.

Overall, symbiotic relationships between trees and other organisms involve complex mechanisms of crosstalk that allow the organisms to communicate and coordinate their responses. These relationships are crucial for the growth and survival of trees and are essential components of forest ecosystems. Crosstalk allows plants to adapt to changing environmental conditions and optimize their growth and survival.

Various Types of Plant Cross-Talks

Crosstalk mechanisms within plants involve hormonal crosstalk, crosstalk between light, stress, and nutrient signaling pathways (Aerts *et al.,* 2021), while crosstalk among plants is facilitated through secondary metabolites production and root association with soil micro-fauna.(Fig.1).

Signaling Crosstalk within Plants / Signal Transduction

In hormonal signaling, crosstalk occurs when two or more hormones interact with each other to regulate plant enzymatic activities (Jogawat *et al.,* 2021). Trees produce several hormones, including auxin, cytokinin, gibberellin, abscisic acid, and ethylene, which interact with each other to control various aspects of tree physiology. Crosstalk can also occur between hormonal signalling's and environmental signaling pathways, such as responses to light or stress. For instance, the hormone ethylene interacts with light signaling pathways to regulate plant growth and development in response to changes in light conditions. Abscisic acid (ABA) involves in regulating plant responses to environmental stresses (Li *et al.,* 2019; Salvi *et al.,* 2021). ABA interacts with other signaling pathways such as the reactive oxygen species (ROS) pathway to regulate stress-responsive genes and activate protein kinases that regulate the tolerance and adaptive mechanism of trees (Lian *et al.,* 2018). Moreover, crosstalk can occur between signaling pathways involved in plant defense mechanism against pathogens. Plants have a complex defense system that involves the activation of different signaling pathways such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) (Fig. 2). These pathways can interact with each other to coordinate the defense response and provide resistance against pathogens (Aftab and Roychoudhury, 2021). Many studies (Hussain *et al.,* 2022; Kim *et al.,* 2022; Singh *et al.,* 2011; Taylor and McAinsh, 2004) have noted the crosstalk between hormones in trees for regulating various morphological and physiological functions. Auxin and cytokinin interact to regulate cell division and differentiation during tree growth. Auxin promotes cell elongation, while cytokinin stimulates cell division. The balance between these two hormones determines the growth pattern of the tree, such as the ratio of shoot-to-root growth. Gibberellin and abscisic acid have opposite effects on tree growth. Gibberellin promotes stem elongation and cell division, while abscisic acid inhibits these processes. The balance between these two hormones regulates tree growth in response to environmental factors such as light and temperature. The photoperiod, or the length of the day and night, affects tree growth and development by regulating hormone synthesis and signaling. The photoperiod influences the synthesis and transport of the hormone auxin, which plays a critical role in controlling tree growth and development.

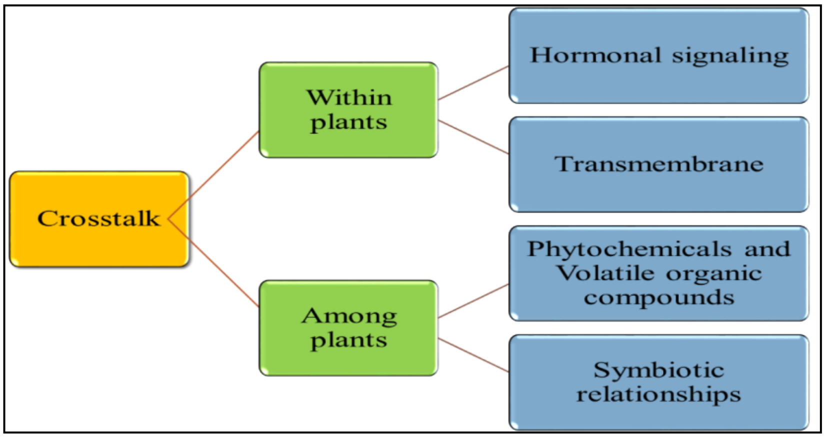

Fig.-1. Intra and Inter crosstalk signaling in plants

Trees can respond to abiotic stresses such as drought, heat, and cold through the activation of signaling pathways that lead to changes in gene expression and protein synthesis. For example, the stress hormone abscisic acid (ABA) can induce the expression of stress-responsive genes and activate protein kinases that regulate tree growth and development. Abscisic acid and ethylene interact to regulate tree responses to environmental stresses such as drought and high salinity. Abscisic acid induces stomatal closure, while ethylene promotes stomatal opening. The balance between these two hormones determines the tree's response to stress. Crosstalk is generally studied by understanding the physiological, and biochemical mechanisms, which are now advanced and coupled with recent 'omics' techniques. The most commonly identified gene families in model crops (*i.e.*, *Arabidopsis*, *Oryza*) are WRKY, RLK, RLCK, CBF, NAC, *etc* (Nejat and Mantri, 2017).

Signalling Crosstalk among Plants

Crosstalk among plants refers to the complex network of signaling interactions and communication that occurs between different signaling pathways between different plants. This communication can involve various biochemical, physiological, and molecular processes and is crucial for plants to respond effectively to environmental stimuli, stress conditions, and developmental cues. Plants release chemicals into the environment that affect the growth and development of neighbouring plants. These chemicals inhibit or stimulate germination, root growth, and overall plant health. Plants emit VOCs as signals to communicate with other plants. For example, when a plant is attacked by herbivores, it releases VOCs to warn neighboring plants, which then activate their own defense mechanisms. Symbiotic relationships between trees and other microorganisms (such as mycorrhizal fungi and nitrogen-fixing bacteria) and the production of secondary compounds involve crosstalk signaling among plants (Song *et al.*, 2014; Song *et al.*, 2015). Crosstalk enables plants to integrate multiple signals and mount appropriate responses to

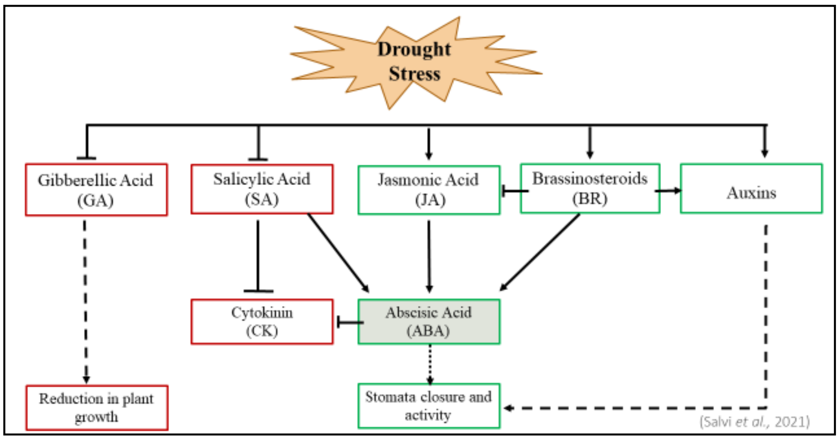

Fig.-2. Crosstalk between different phytohormones for mediating drought stress complex environmental conditions, such as drought, salinity, and pathogen attack. By effectively responding to biotic and abiotic stresses through signaling crosstalk, plants can enhance their survival and reproductive success (Barker *et al.*, 2013). Proper development of plants, including processes like germination, flowering, and fruiting, relies on the integration of hormonal and environmental signals through crosstalk.

Mycorrhiza-tree-herbivore interactions involve complex relationships between plants, fungi, and herbivores, influencing plant health, growth, and defense mechanisms. Mycorrhizal fungi form a mutually beneficial relationship with trees, in which the fungi colonize the tree roots and help the tree absorb nutrients such as phosphorus and nitrogen from the soil. In return, the tree provides the fungi with carbohydrates produced through photosynthesis (Fraser *et al.*, 2006).The mycorrhizal fungi can activate signaling pathways in the tree roots that lead to pass-on messages from tree to tree through 'Wood Wide Web' network (Fig. 03). This relationship involves crosstalk between the signaling pathways of the fungi and the tree, as well as between the fungal and bacterial communities in the soil (Wang *et al.*, 2012). Nitrogen-fixing bacteria can also form symbiotic relationships with trees, in which the bacteria convert atmospheric nitrogen into a form that can be used by the tree. The compatibilities between donor and receiver plants along with the symbionts decide the intensity of the material/message flow (Rasheed *et al.*, 2022). The neighbors receiving these messages could potentially then modify their behaviour through altered morphology, physiology, or biochemistry, thus reducing the stress damage and improving fitness. Mycorrhizal trees may better tolerate herbivory due to improved nutrient status and overall health, allowing them to recover more quickly from damage.Herbivory can change the composition of root exudates, potentially affecting mycorrhizal colonization and function.

Trees emit VOCs in response to herbivore attack, which attract predators of the herbivores or signal neighboring plants to enhance their defenses. Mycorrhizal associations modifies the VOC profile, influencing these interactions(Padmanaban *et al.*, 2022).Jasmonic Acid and Salicylic Acid Pathwaysare involved in plant defense against herbivores and pathogens (Wasternack and Hause, 2013). Mycorrhizal fungiinfluences the regulation of these pathways, enhancing the plant's defensive response. Mycorrhizal trees may allocate more carbon to roots and fungal partners, potentially influencing the plant's ability to allocate resources to herbivore defense (Cameron *et al.*, 2013).The presence of mycorrhizae affects the distribution of nutrients within the plant, potentially enhancing the production of defensive compounds in response to herbivory.

Mycorrhizal associations contribute to the biodiversity and stability of forest ecosystems by enhancing tree health and resilience to herbivores. Determining and understanding of these interactions can assist in forest management practices aimed at maintaining healthy and resilient forests. Investigating the molecular and biochemical mechanisms underlying mycorrhiza-tree-herbivore interactions can provide deeper insights into these complex relationships. Long-term field studies are essential to understand how these interactions proceed in natural and agricultural ecosystems over time. Developing practical applications, such as mycorrhizal inoculants, can help to harness the benefits of these interactions for sustainable agriculture and forestry.

Conclusion and Future Perspective

Overall, crosstalk allows trees to respond to environmental stimuli (Loreto and D'Auria, 2022). Although plants have an innate defensive system to withstand uncertain environmental fluctuations and the effectiveness of that defense mechanism depends mainly on the genetic makeup of the plant, the stage at which stress is recognized, as well as the length and intensity of stress. Many studies have highlighted several molecular characteristics

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of stress, and even the phytohormonal syndicate has been linked to a key role in cellular homeostasis. Due to their inter-crosstalk response, phytohormones' adaptive signaling modules also support a convoluted cascade (Koornneef and Pieterse, 2008). The well-established roles and regulations are given a new dimension by the knowledge of phytohormonal interaction. The precise knowledge of the molecular interactions between these phytohormones is largely unexplored, though.In order to reduce the effects of stressors on plant growth, development, and production and to increase plant longevity, knowledge of the intricacies of defense systems and stress signaling is essential. The complexity and high degree of signaling crosstalk in plant immune responses have recently been shown on individual and combined biotic and abiotic stresses (Bag *et al.*, 2022). Despite remarkable advancements in high-throughput sequencing technologies and potent bioinformatics tools for genome-wide study, transcriptome, and proteome analysis, our understanding of signalling between components of the plant defense pathways under combined stress conditions is still limited (Ashwath *et al.*, 2023). Recent research has shown that the immune system's shared mechanisms for responding to biotic and abiotic challenges, including the creation of ROS, MAP-kinase cascades, and hormone signaling, are non-specifically activated by both biotic and abiotic environmental stimuli (Cavaco *et al.*, 2021). Moreover, identifying both general and unique elements of signaling crosstalk in plants will enable the creation of brand-new instruments to resist the mix of biotic and abiotic challenges that are often present in field situations (Yu *et al.*, 2022). Hence, finding the genes involved in both biotic and abiotic stress resistance as well as multifunctional genes may hasten the production of resistant agricultural plants by careful genome editing.

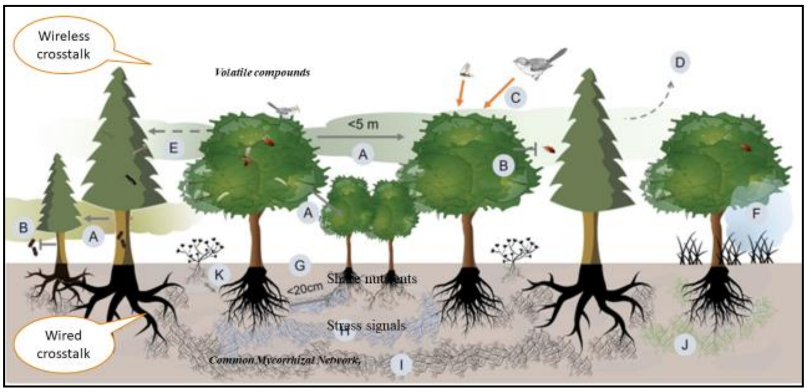

Fig.-3. Schematic representationof Wired (through mycorrhizalnetworks) and wireless crosstalks (through VOCs

Several plant species have provided solid evidence of plant-plant interactions that take place above and below ground. The ecological interactions mediated by volatiles and soil microorganisms are a very complicated system (Pantigoso *et al.*, 2022). It is now obvious that plants can communicate with their communities and receive information from them, but still much knowledge is unearthed in this aspect. Thus, a variety of biological, chemical, and physical variables can have an impact on production, dispersion, and biological consequences. Researchers can better examine and comprehend each component of a complicated issue by breaking it down into manageable components. To comprehend the complexities in reality, however, requires putting the jigsaw pieces together. It is appropriate to plan studies to observe biological interactions mediated by volatiles in real-time utilizing non-destructive techniques. Prior to constructing an experiment, it is also essential to consider the scientific context. The evolutionary history of volatile-mediated plant-microbe interactions will be made clear through studies of volatile communication between early plants and bacteria (Ding *et al.*, 2022).Unfortunately, data from actual forest ecosystems are few, and it can be challenging to distinguish between processes that occur above and below ground. Stress signals are transferred through the common mycorrhizal networks (CMNs) built up between the neighboring plants. Studies on underground communication mediated by mycorrhizae have addressed the majority of questions concentrating on kin recognition among trees (Sharifi *et al.*, 2022). For instance, it has been shown that trees have stronger mycorrhizal connections among relatives. The older trees supply nutrients that help conspecific younger trees to develop and survive. Research has to be scaled up to incorporate older trees and reactions in all areas of the canopy in order to better understand plant communication in forest ecosystems. A mature forest with towering trees makes it difficult to perform precisely controlled tests, but technology for climbing up into canopies and reaching below to root tip to gather measurements and samples would advance this field.

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