MASTER THESIS

Literature Review:

How does Climate Change interrupt Defense Response Signalling Between and Within Plants?

Submitted by

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<u>Declaration</u>

I declare, that this paper is my own original scientific work and is in accordance with the principles of the Institute of Forest Ecology, within the University of Natural Resources and Applied Life Sciences for the publication of a Master thesis.

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Signature:

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Contents

Abstract

The defense response spreads quickly through a plant and triggers a protective response due to molecular signalling pathways. Volatile and below-ground defensive signals can also be perceived by neighbouring plants which activate their defenses in preparation for a potential threat, and volatile defense signals can attract predators of herbivorous insects within the ecosystem. Thus these defense-related molecular signalling pathways play a role in maintaining ecosystem resilience and functionality. The impact of climate change on ecosystem functionality has usually been in terms of macroecology and not molecular biology. An important question in forest ecology is; 'how will climate change effect the defense response in plants and therefore ecosystem functionality?'. To answer this question, defense related molecular signalling pathways must be invstigated. In this thesis I will review current knowledge about molecular signalling in the defense response within and between plants, and combine this information with the effects of climate change on defense related molecular signalling pathways and discuss the implications for ecosystem resilience and functionality.

Keywords: defense response; climate change; plant molecular biology; plant communication;

Abstract in German

Zusammenfassung

Die Abwehrreaktion breitet sich schnell innerhalb einer Pflanze aus und löst aufgrund molekularer Signalwege eine protektive Antwort aus. Flüchtige und unterirdische Abwehrsignale können auch von benachbarten Pflanzen wahrgenommen werden, die daraufhin ihre Abwehrkräfte in Vorbereitung auf eine mögliche Bedrohung aktivieren. Darüber hinaus können flüchtige Abwehrsignale Antagonisten von pflanzenfressenden Insekten innerhalb des Ökosystems anlocken. Daher spielen diese verteidigungsbezogenen molekularen Signalwege eine Rolle bei der Aufrechterhaltung der Widerstandsfähigkeit und Funktionalität des Ökosystems. Die Auswirkungen des Klimawandels auf die Ökosystemfunktionalität wurden in der Regel in der Makroökologie und nicht in der Molekularbiologie untersucht. Eine wichtige Frage in der Waldökologie ist: "Wie wird der Klimawandel die Abwehrreaktion der Pflanzen und damit die Ökosystemfunktionalität beeinflussen?". Um diese Frage zu beantworten, müssen Verteidigungs-bezogene molekulare Signalwege untersucht werden. In dieser Masterarbeit wird das aktuelle Wissen über molekulare Signale in der Abwehrreaktion innerhalb und zwischen Pflanzen untersucht und diese Informationen mit den Auswirkungen des Klimawandels auf verteidigungsbezogene molekulare Signalwege kombiniert. Außerdem werden Implikationen für die Resilienz und Funktionalität von Ökosystemen diskutiert.

Schlagwörter: Abwehrreaktion; Klimawandel; Pflanzen-Molekularbiologie; Anlagenkommunikation;

Abbreviations

SAR – Systemic acquired resistance

SAA – Systemic acquired acclimation

MeSA – Methyl salicylate

JA – Jasmonic acid

AP – Action potential

SWP – Slow wave potential

WP – Wound potential

SP – System potential

ROS – Reactive oxygen species

RBOHD – Respiratory burst oxidase homolog D

H_2O_2 – hydrogen peroxide

SA – Salicylic acid

ABA – Abscisic acid

NO – nitric oxide

TPC1 – Two pore channel 1

GLR – Glutamate like receptor

PAMPs – Pathogen activated molecular patterns

ALD1 – AGD2- like. Defence response protein 1

FMO1 – Flavin- dependent-monooxygenase1

NPR1 – Non-expressor of pathogenesis-related protein

SnRK1 – Sucrose-non-fermentation-related protein kinase 1

ERF – Ethylene response factor

MYC – Basic helix-loop-helix leucine zipper transcription factor

LSD1 – Lesion simulating disease 1

Pip – Pipecolic acid

AzA – Azelaic acid

TOR – Target of rapamycin

GLV – Green leaf volatile

HIPV – Herbivore induced plant volatile

VOC – Volatile organic compound

MN – Mycorrhizal Network

AMF – Arbuscular mycorrhizal fungi

EMF – Ectomycorrhizal fungi

JAZ – Jasmonate-zim domain

Introduction

Plants are able to perceive and respond to environmental stimuli rapidly due to signalling pathways which travel from the point of stress to trigger the accumulation of defence compounds throughout the plant and convey defence against a specific intensity and character of stress (Huber & Bauerle 2016). Reviewing the research undertaken in the molecular signalling pathways of plant defence, there is evidence that it is possible for defence signals to pass between plants, and activate defense genes (Gorzelak et al. 2015; Ton et al. 2006a). This would give plants the ability to 'sense' the defence response of a neighbouring plant, by perceiving molecular defense compounds transferred through the air as a volatile signal or through a mycorrhizal connection underground. Generally, evidence suggests that upon perception of defence signals from another plant, defence genes are partially activated, this conveys a priming effect; a basal level of resistance and a stronger and faster accumulation of defense compounds upon attack (Martinez-Medina et al. 2016). From the evidence so far it appears that several families of defence compounds, receptors and ion transporters are conserved across many plant species, and sometimes also animal species.

The existence of conserved signalling pathways, and the physical proximity of plants within forest ecosystems imply that interplant 'sensing' of the defence response could function as a level of molecular plant interconnection which conveys community resilience. It is well known that from a single point of stress, defense signalling propagates throughout an entire plant within minutes or hours, this effect is termed 'systemic' defence signalling (Shah 2009) because the entire plant system is activated for defense. Recently, accumulated evidence is beginning to indicate that a similar phenomenon could function on a plant community level,

whereby a defence response can be perceived and the priming effect activated in the plants surrounding an area of forest which is under attack.
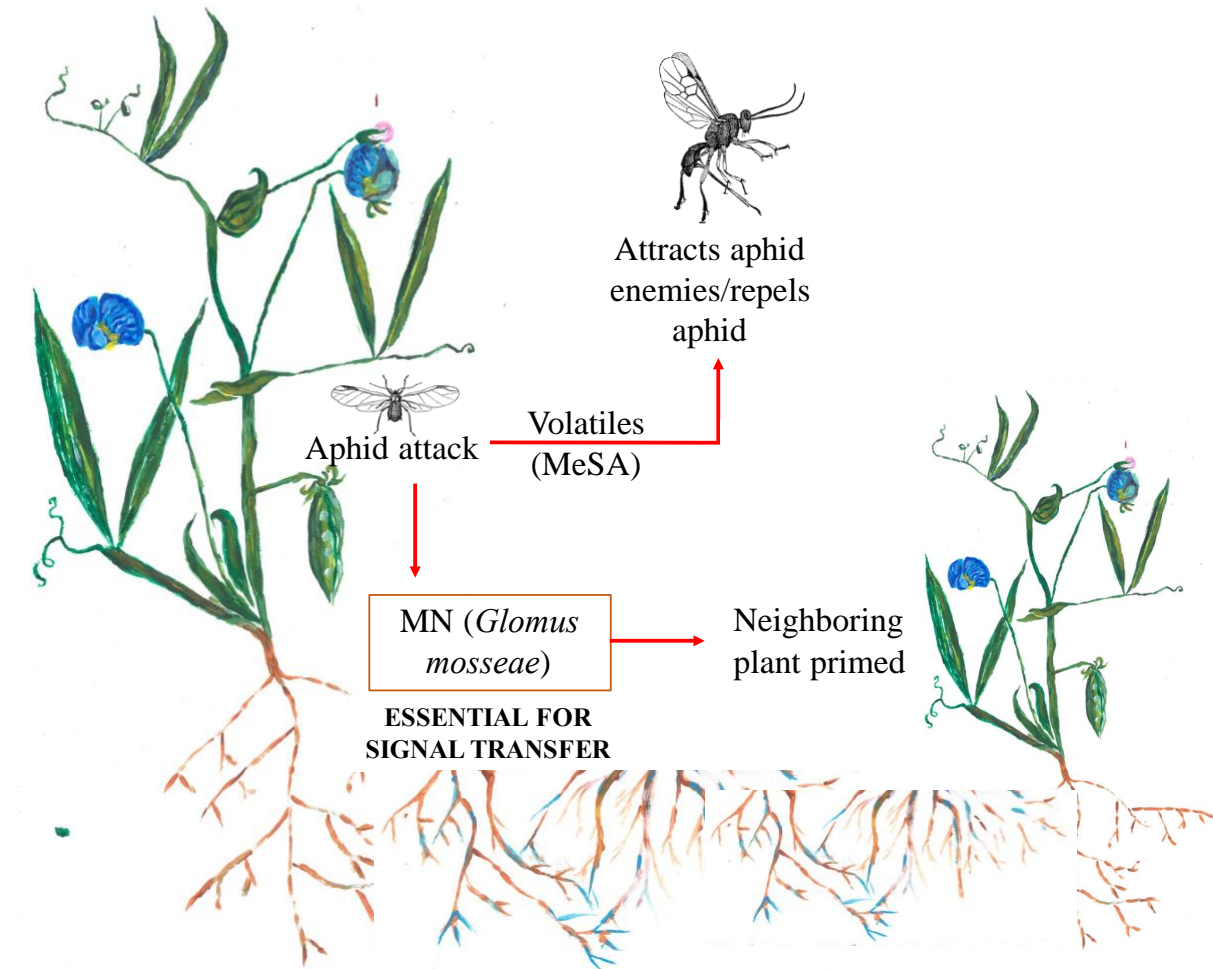
Figure 1: Graphic representing the defense response of *Vicia faba* against aphid attack and the integration of volatile and below ground signals. Mycorrhizal signal (red box) via the mycorrhizal network (MN) is essential for defense signal transfer to neighbouring plants (Babikova et al. 2013).

A good example interconnecting the levels of air borne and underground signalling between plants is described in bean plants (*Vicia faba)* under aphid (*A.pisum*) attack (figure 1), systemic defence is triggered resulting in the release of volatile compounds including methyl salicylate, which are repellent to aphids but attract parasitoid wasps (*A.ervi),* which are aphid predators (Snoeren et al. 2010). This volatile signal can then be mimicked by neighbouring unattacked *V.faba* plants, but only in the presence of an arbuscular mycorrhizal network. The defense

signal could not be transmitted between plants when the fungal hyphal connections between plants were blocked (Babikova et al. 2013). Plant 'communication' could therefore be visualised as three layers of molecular signalling which allow the defence response to pass between plants; above ground as volatile compounds, within plant, and below ground via mycorrhizal connections. These pathways are interconnected and co-dependent, they are seperated here for clarity, but in reality the defense response within a single plant extends to the surrounding environment and is always perceived by plants in the nearby vicinity.

These interactions provide a degree of plant community resilience by activating the defense response of neighbouring plants and providing a buffer against drought and nutrient defficiency and enhancing seedling success (Brunner et al. 2015; Pickles et al. 2017), thus these layers of signalling are important for maintaining ecosystem functionality. The impact of climate change on ecosystem functionality has been widely adressed, however this has usually been in terms of macroecology and not molecular biology. An important question in forest ecology is; 'how will climate change effect the defense response in plants and therefore ecosystem resilience?'. To answer this question, defense related molecular signalling pathways must be looked at more closely. Investigations into the effects of climate change on plant molecular signalling pathways and plant defense are becoming more frequent, but often only address one aspect of the question, for example the affect of elevated carbon dioxide on plant volatiles (Yuan et al. 2009) or the effect of nitrate deposition on mycorrhizal fungi (Bahr et al. 2013). These all add an important piece of the puzzle, but to attain a clearer picture, research on the effects of climate change on defense related molecular signalling pathways within and between plants should be reviewed.

   i.   *Aims and Purpose*

In this thesis I will review current knowledge about the within plant, above and below ground layers of molecular signalling in the defense response, and the importance of signal transfer between plants for plant community resilience. I will also link internal and external defense signalling and discuss the importance of defense-related plant-plant and plant-insect interactions for ecosystem functionality and resilience. I will then put these layers of signalling in the context of climate change by reviewing investigations into impacts such as elevated carbon dioxide, temperature and ozone and their effect on plant signalling. Finally I aim to combine this information with the molecular mechanisms of the plant defense response and to identify the implications for plant community resilience against climate change.

Chapter 1: Within-plant 'Systemic' Defence

The 'systemic' plant response describes the process of defense gene activation throughout the entire plant system in response to stress at a single point, for example burning or insect attack of a single leaf is perceived by the entire plant system. Systemic defense involves rapid, long-distance signalling which can include hydraulic, electrical and chemical components (Huber & Bauerle 2016). Stressors which elicit defence signalling include abiotic stimuli such as water, salt, light, heat or cold, and biotic stimuli such as herbivore or pathogen attack. Two branches of plant systemic response have been characterized; 'systemic acquired resistance' (SAR) describes the response to biotic stressors, initiated by pathogen perception, and access to an immune 'memory' which enables the plant to 'remember' pathogen-conserved molecular patterns (Henry et al. 2014). 'Systemic acquired acclimation' (SAA) is elicited in response to abiotic stimuli and involves the triggering of rapid wave-like signalling, probably via hydraulic, osmotic, temperature and redox sensors which monitor changes in light intensity, temperature, humidity, salinity and turgor (Mittler & Blumwald 2015a; Winter et al. 2014).

In nature, a plant encounters different combinations and intensities of stressors simultaneously, systemic defense is incredibly sophisticated in its ability to communicate information concerning the stressor identity and strength. This maximises efficiency and conserves resources in a multi-stress environment due to a systemic network of hydraulic, electric and chemical signals (Hedrich et al. 2017; Hlaváčková & Naus 2007; Christmann et al. 2013). Long distance signalling is thought to be mainly electrical and hydraulic; chemical signals are essential for defence gene activation, however, in general evidence suggests that chemical defense compounds are biosynthesised systemically in response to rapid long distance signals rather than transported from the point of damage via plant vasculature, which would be far slower than hydraulic or electrical signal transmission (Huber & Bauerle 2016). The crosstalk between several long and short distance signals can be interpreted by master regulators of the defense response which activate defence protein synthesis (Balderas-Hernandez et al. 2013).

Defense signals appear to be highly conserved in response to different genres of stressor, the type and intensity of stress is encoded in the pattern or 'signature' of signalling, therefor master regulators play an important role in reading these signalling signatures and eliciting the correct response (Balderas-Hernandez et al. 2013; Truman et al. 2007).

The same signals which enable systemic plant defense, also appear to enable the transfer of defense relating signalling between plants (Song et al. 2010; Babikova et al. 2013). This could be interpreted as an unintentional consequence of individual defense strategies but nevertheless provides some extent of collective plant community resilience against threats. Volatile defence chemicals such as methyl salicylate (MeSA) attract the predators of predating insects and are also perceived by neighbouring plants, priming them for the defense response (Snoeren et al.

2010). The defence chemical jasmonic acid (JA) triggers defense gene activation during systemic defense, and additionally enables the transfer of defence signals between plants via mycorrhizal connections (Song, Ye, et al. 2015).

In this section, pathways and mechanisms of the systemic stress response in plants including rapid long distance electrical and hydraulic signals and slower chemical signals are described. The branches of biotic and abiotic systemic stress response are explained, and the below and above ground extension of defense signalling, and their importance for plant community resilience are discussed.

1.1 Rapid long-distance defense signalling

Electrical and hydraulic signals have been identified as the fastest systemic response to stress, and are often the initial stress response signals (Huber & Bauerle 2016). Hydraulic signals, which could be elicited due to pressure changes caused by wounding or drought in some cases trigger cell depolarisation and electrical signals which are able to instruct cells throughout the whole plant to biosynthesise chemical defense signals (Karpinsky et al. 2013). However, different stresses elicit different types of hydraulic and electrical signal, which is important for instructing the correct downstream signals to be biosynthesised.

Four different types of electrical signal have been characterised (figure 2); action potentials (APs), slow wave potentials (SWPs), wound potentials (WPs) and systemic potentials (SPs) (Hedrich et al. 2017). They are classified as distinct from one another due to their different ionic mechanisms, propagation properties and triggers, SWPs and WPs are dependent on hydraulic induced depolarisation (Vodeneev et al. 2015a).

Action potentials (APs) are elicited in response to abiotic and mechanical stimuli, they are self-propagating and travel with a constant velocity and amplitude in all directions within the plant via the plasmodesmata and the phloem (Yan et al. 2009). A certain threshold of stimulus intensity must be reached to generate an AP, but the AP amplitude does not alter in response to different intensities of the trigger; an all or nothing response (Pietruszka et al. 1997). The mechanism of propagation begins with cell depolarisation which activates voltage gated calcium channels enabling an influx of Ca^+ ions, further depolarising the cell and activating calcium or voltage gated chloride channels enabling an efflux of Cl^- ions. The membrane potential is then restored to the resting potential due to the activation of voltage gated potassium channels and an efflux of K^+ ions (Pietruszka et al. 1997).
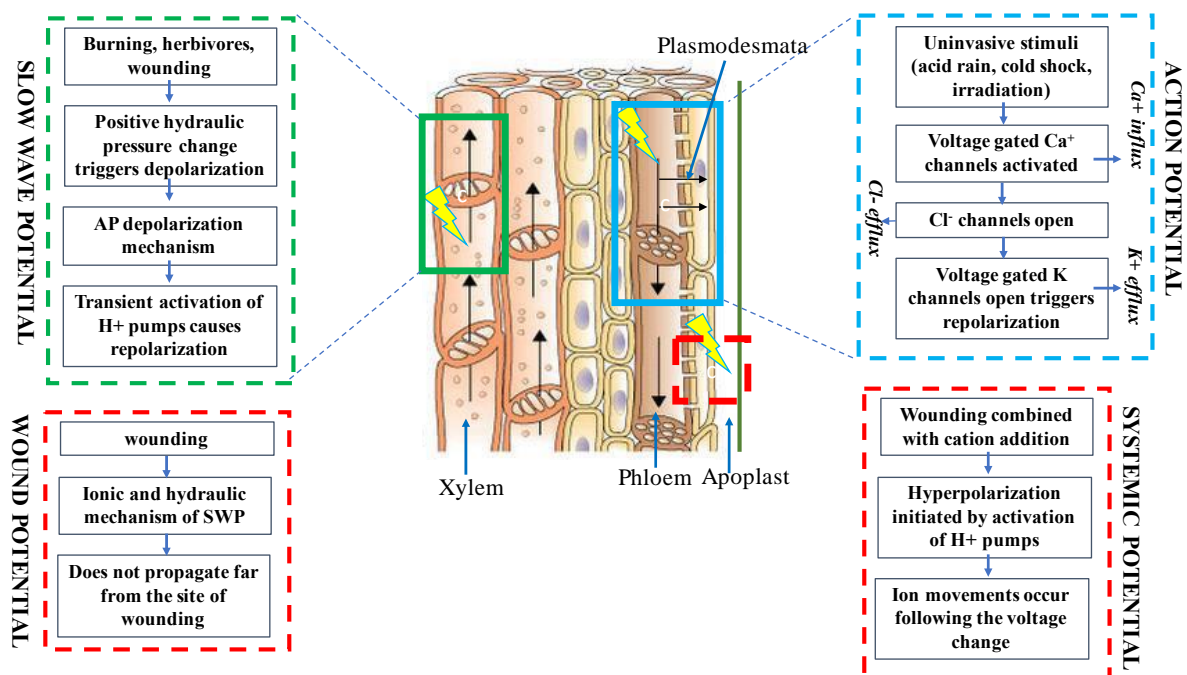
Figure 2: The mechanisms for triggering the four types of electrical signal are outlined in the boxes, and the component of vascular bundle through which they propagate is highlighted. Slow wave potential is in green, action potential in blue and wound and systemic potentials in red. The lightning symbol represents the electrical signal. Figure inspired by review of electrical signalling by (Hedrich et al. 2017).

Slow wave potentials (SWPs) are always preceded by a hydraulic pressure signal in response to wounding which triggers depolarization in response to pressure fluctuations, and propagates

via the xylem. The ionic mechanism of depolarization is the same as for APs, however the repolarization phase appears to be due to the transient activation of H^+ ATPase proton pumps and is much slower than that of APs (Stahlberg & Cosgrove 1996). The hydraulic signal which precedes SWPs attenuates with distance, and therefore so does the electrical signal, this means that SWPs vary with intensity and the signature of the signal can convey information concerning distance from the point of injury (Vodeneev et al. 2015a).

For wound potentials (WPs), the mechanism of initiation is similar to SWPs. The mechanism is elicited by broken tissue which results in hydrostatic pressure variations, believed to be perceived by mechano-sensors which cause the membrane potential to change and initiate WPs (Fromm & Lautner 2007). However, this signal has only been recorded close to the point of injury, and there is no evidence of long distance propagation (Hedrich et al. 2017).

System potentials (SPs) occur when the membrane potential moves away from its resting value due to wounding together with a chemical stimulus. It is the only signal characterised by an initial hyperpolarisation phase and that is not initiated by calcium signalling, initiation of the SP is thought to be through sustained activation of the ATPase H^+ proton pump, and the electrical signal is followed rather than preceded by ionic signalling. SP strength also varies and therefore can convey information about the severity of wounding (Zimmermann et al. 2009).

Hydraulic signals regulate cell expansion rates through cell turgor pressure changes and are initiated in response to evaporative demand, soil water fluctuations, wounding or herbivore feeding (Christmann et al. 2013). In the case of electrical slow wave potentials and system potentials, hydraulic signals are essential for propagation because they initiate depolarisation

(Vodeneev et al. 2015b; Zimmermann et al. 2009). It has been suggested that a hydraulic wave of altered pressure could trigger mechano-sensitive elements which trigger a calcium influx to cells in the phloem sieve tubes or xylem vessels (Huber & Bauerle 2016). Calcium influx induced depolarisation could then trigger an electrical signal.

Electrical signalling is able to propagate through an entire plant very rapidly via vascular bundles and the plasmodesmata (Vodeneev et al. 2016). APs travel in the phloem where sieve tubes are interconnected by plate pores, SWPs travel through the xylem following hydraulic signal propagation, and system potentials propagate in the apoplast. From vascular bundles, plasmodesmata connections to companion cells are important for the propagation of systemic signalling to all plant tissue (Hedrich et al. 2017). Wound induced pressure in the phloem is theorized to trigger mechanical sensors which initiate wave like activity via ion fluxes through mechanically/voltage gated Ca channels (Hlaváčková & Naus 2007). The transmission of calcium ions between wounded and unwounded tissue can occur via calcium channels clustered at sieve plates (Carpaneto et al. 2007; Gilroy et al. 2016). Action potentials function in an all-or-nothing manner, indicating that they can act as a stress perception signal, but probably do not convey detailed information about the character and intensity of stress. On the other hand, SWPs, and SPs give a varying signature for different intensities/types of stress (Zimmermann et al. 2009) (Stahlberg & Cosgrove 1996).

   i.   *The electrical, reactive oxygen species and calcium 'waves'*

Long-distance electrical signals spread transiently from the point of stress throughout the entire plant very quickly and activate each cell they pass through for defense in a transient wavelike manner, therefore the 'electrical wave' is described as an important aspect of the defense

response (Gilroy et al. 2014). The electrical wave generally triggers the synthesis of defense chemicals which upregulate defense genes. For example in *Arabidopsis thaliana* under insect attack, a study using accumulation rate analysis showed that electrical signalling is the primary stress response signal, followed by the systemic synthesis of the defense compound jasmonic acid (Glauser et al. 2009).

Electrical and hydraulic signals appear to be the main elicitors of rapid long-distance defense signalling, however there is also emerging evidence that chemical signalling can rapidly trigger systemic defense in plants via so-called 'waves' of calcium or reactive oxygen species (ROS) (Gilroy et al. 2014). These waves are distinct from chemical transport within the transpiration stream or phloem because they are far more rapid and appear to be linked to the systemic electrical signalling wave (Choi et al. 2016). The transient cell by cell elevation of ROS and calcium has been visualised in plants under stress using bio-tagging (Evans et al. 2016; Kudla et al. 2010). The electric, calcium and ROS waves appear to activate cells for a specific response such as defensive compound synthesis or defensive volatile release, but do not involve the passive transport of a certain compound from one cell to another, rather voltage/ligand gated channels or enzymes are rapidly activated in each cell the signal reaches (Gilroy et al. 2016). Evidence shows that several enzymes and ion channels are conserved in the mechanisms of the three signalling waves (Bonaventure et al. 2007; Forde & Roberts 2014), and that they are highly interlinked (Gilroy et al. 2014). From reviewing the evidence, it could be suggested that the ROS and calcium waves are merely components of the electrical wave.

ii.   The Reactive Oxygen Species (ROS) wave

The ROS wave can be clearly visualised using *Arabidopsis* plants expressing ROS inducible bioluminescent reporter luciferase; the transient production of ROS was visualised as a wave of luminescence spreading rapidly throughout the plant in response to wounding, high light, salinity, cold and heat stress (Miller et al. 2009). This 'wave' of ROS production is the self-propagating cell-by-cell production of ROS due to the transient activation of Respiratory Burst Oxidase Homolog D (RBOHD) in each cell in turn, generating hydrogen peroxide (H_2O_2), which is the signature of the ROS wave in plants (Baxter et al. 2014). Studies investigating the role of the ROS wave in defence have found that it is essential for the 'systemic acquired acclimation' (SAA) response (the abiotic stress response), and also that ROS trigger the synthesis of the defense compound salicylic acid (SA) which is a key defense chemical (Gilroy et al. 2014; Herrera-Vásquez et al. 2015). However, evidence suggests that the ROS wave alone indicates stress perception in a fairly vague manner. Crosstalk with other signals appear to
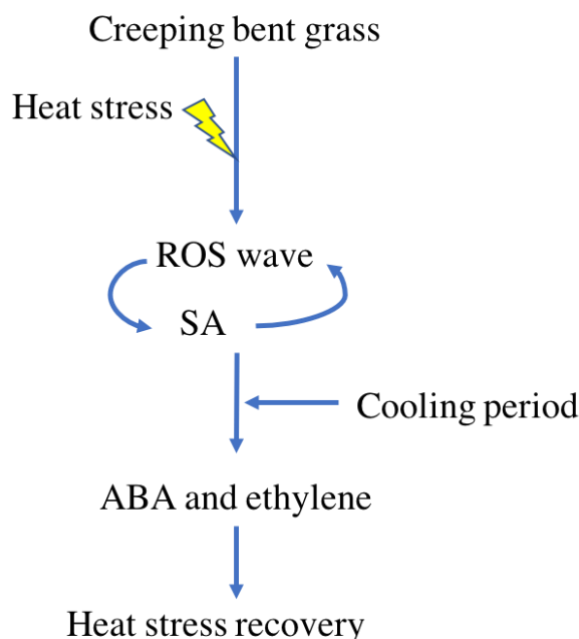
Figure 3: The sequence of signalling following heat stress in creeping bent grass. The ROS wave is the initial signal, and triggers salicylic acid accumulation in a positive feedback loop. This is followed by ABA and ethylene elevation during the cooling period, indicating their role in recovery and thermotolerance. Figure based on research conducted by (Larkindale & Huang 2005).

specify the defense response required (Gilroy et al. 2014; Suzuki et al. 2011; Baxter et al. 2014).

A study in creeping bentgrass (*Agrostis)* investigated the role of several defense related compounds in response to heat stress and identified the ROS wave as the initial stress perception signal, followed by systemic salicylic acid synthesis within an hour, whereas abscisic acid (ABA) and ethylene concentrations rose during the cooling period (figure 3) (Larkindale & Huang 2005). The conclusions drawn from this study were that rapid ROS signalling is the initial response to heat stress, and trigger salicylic acid (SA) accumulation in a positive feedback loop. The signature of ROS and SA accumulation is then thought to convey a heat stress specific signal resulting in ABA and ethylene production, defense chemicals which enable thermotolerance (Larkindale & Huang 2005). The ROS wave was also found to be the initial rapid response in plants following high light stress, and triggers defensive photorespiratory amino acid accumulation in systemic tissue (Suzuki et al. 2013).

In addition to abiotic stress, ROS functions in the biotic stress response during insect and pathogen attack. Deficiency in RBOHD was shown to result in a slower systemic accumulation of azelaic acid and glycerol-3-phosphate in *Arabidopsis thaliana*, both compounds convey resistance against insects (Mandal et al. 2011; Shah 2009). Furthermore many studies have found interdependent signalling between ROS and nitric oxide (NO), which is known to be involved in pathogen defense (Romero-Puertas et al. 2004); plants with low levels of NO display a far lower systematic ROS accumulation which compromises their defence response (El-Shetehy et al. 2015). In compliance with this, studies in *Arabidopsis* have shown that upregulation of RBOHD is dependent on NO activity and that pathogen elicited accumulation of NO depends on RBOHD activity (Miller et al. 2009; El-Shetehy et al. 2015). This suggests that NO is a regulator of ROS signalling.

Together the SA and ROS temporal-spatial signatures trigger activity from specific protective genes depending on the stressor (Miura & Tada 2014). Table 1 gives some examples of biotic and abiotic stress defense genes which can be triggered by SA and ROS interplay.

Table 1: Examples of defense genes triggered by SA and ROS signalling during abiotic or biotic stress. Data taken from the referenced articles, and the paper by (Miura & Tada 2014).

Gene	Function
LESION SIMULATING DISEASE 1	Limits boundaries of cell death response during pathogen infection and prevents unchecked lesions under light exposure (Mateo et al. 2004).
ENHANCED DISEASE SUSCEPTIBILITY 1	Triggers pathogen defence mechanisms (Zhang et al. 2015).
ETHYLENE INSENSITIVE 2	Involved in the regulation of high ozone, high salt and disease resistance (Cao et al. 2009).
MITOGEN-ACTIVATED PROTEIN KINASE 4	Involved in the regulation of defense responses against bacteria (Witoń et al. 2016).
PHOTOSYSTEM II SUBUNIT	Provides defence against high light stress through dissipation and quenching of excess light (Järvi et al. 2016).

iii.   *The Calcium Wave*

The 'calcium wave' is characterised by a systemic elevation in cytosolic Ca^{2+} which triggers signalling cascades throughout the plant. Transmission of the calcium wave in response to salt stress was first identified in Arabidopsis roots (figure 4), in which calcium signalling rapidly propagates via the cortical and endodermal root cell layers, negotiating several cells per second and triggering defense gene activation in systemic tissue (Choi et al. 2014). Wound induced transient Ca^{2+} elevation is different from the salt stress triggered calcium wave; wounding induces rapid calcium fluxes as a component of electrical signalling and propagates through the vasculature at a faster rate (Carpaneto et al. 2007; Ma & Berkowitz 2007). However, wound and salt stress induced calcium signalling appear to be interconnected. The slow vacuolar channel Two Pore Channel 1 (TPC1) was found to be important for maintaining the speed of both wound induced electrical wave and salt induced calcium wave propagation (Bonaventure et al. 2007).

Calcium channels and transporters in the plasma membrane which are activated by ROS have been identified and calcium-dependent protein kinases (CPK) can phosphorylate RBOHs and trigger ROS production (Gilroy et al. 2016; Suzuki et al. 2011). This indicates a connection between the ROS and calcium signalling waves. Several mechanisms have been proposed for Ca^{2+} and ROS interacting in a positive feedback loop during defense signalling (Gilroy et al. 2016; Suzuki et al. 2011; Mittler & Blumwald 2015a).

iv.   *Integrating the rapid signalling waves*

In simple terms, there are several rapid long distance signalling waves in the plant stress response; the ROS and electrical waves propagate via the vasculature very rapidly whereas calcium wave propagation appears to be restricted to the cortex and endodermis and moves

more slowly (figure 4) (Gilroy et al. 2016). The hydraulic signalling wave induces the electrical wave in response to wounding, insect feeding or soil water deficit, the ROS wave is triggered by abiotic stress such as wounding, high light, salinity, cold and heat stress (Christmann et al. 2013; Fromm et al. 2013; Miller et al. 2009). The calcium wave is induced by salt stress and wounding (Choi et al. 2016).

There is evidence that electric, calcium and ROS waves are interlinked and inter-regulatory (Evans et al. 2016; Suzuki et al. 2011). Calcium channels in the plasma membrane which are activated by ROS have been identified and ROS production is known to be modulated by calcium signalling (Baxter et al. 2014). Calcium permeable glutamate-like receptor (GLR) channels within the plasma membrane have been found to be essential for wound induced electrical signalling (Forde & Roberts 2014). A study in *Arabidopsis thaliana* demonstrates that fluxes of ROS are associated with electrical system potentials (Gilroy et al. 2014). It has also been found that systemic electrical activity generates a wave like change in ROS (Pavlovič & Mancuso 2011), furthermore in the absence of RBOHD, electrical signalling is diminished (Gilroy et al. 2014). The slow vacuolar channel TPC1 was found to be important for both wound induced electrical signalling and for the salt stress induced calcium wave (Bonaventure et al. 2007).

Identification of components such as the TPC1 channel, and kinetic analyses of signalling velocities give insight into the mechanisms which coordinate long-distance signalling waves, and give a basis for modelling the relationship between the hydraulic, ROS, electrical and calcium waves in response to stress. The molecular mechanisms which link calcium, ROS and electrical wave transmission are still largely unknown, however several models have been
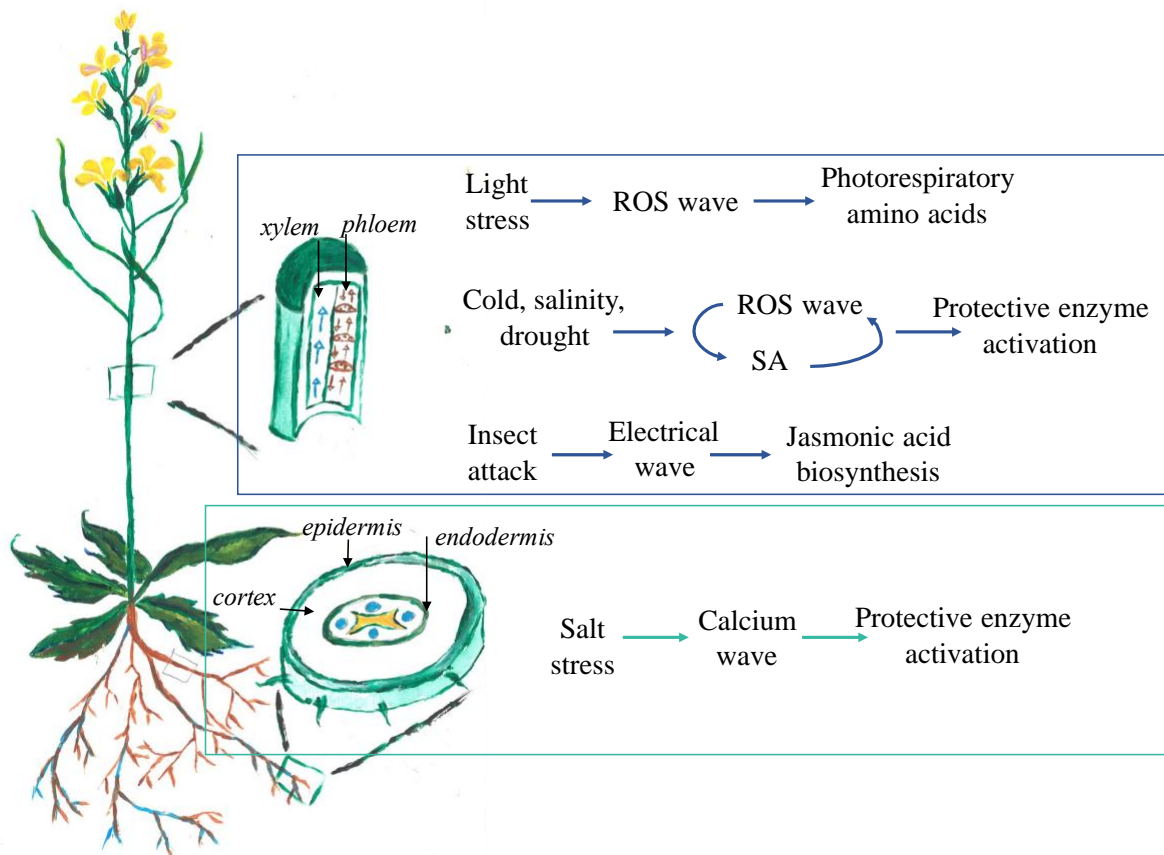
Figure 4: Rapid ROS, electrical and calcium signalling waves in *Arabidopsis thaliana* occur in response to a wide range of stressors including abiotic and biotic stimuli, and result in systemic synthesis of defence compounds such as jasmonic acid, trigger defense signalling cascades, and active defense genes to provide resistance (Pospíšil 2016; Herrera-Vásquez et al. 2015; Evans et al. 2016; Hlaváčková & Naus 2007).

proposed based on the current lines of evidence (Gilroy et al. 2016; Notaguchi & Okamoto 2015; Huber & Bauerle 2016). Disruption of the vacuolar TPC1 channel leads to a much slower propagation of both the wound-induced electrical wave and the salt-stress induced calcium wave (Evans et al. 2016). The TPC1 channel is thought to either directly release calcium into the cell, or to regulate the opening of other calcium channels, and is itself voltage-gated, therefore calcium ion induced voltage change would lead to TPC1 activation (Bonaventure et al. 2007). However, analysis of the kinetics of the velocity of salt stress induced calcium wave propagation shows that calcium (released via TPC1 in the preceding cell) diffusion induced activation of TPC1 in the next cell is not sufficient to account for the speed of calcium wave propagation (Evans et al. 2016). They investigated ROS involvement and found that blocking

ROS production led to a reduced speed of the salt stress induced calcium wave, further investigation revealed a systemic ROS flux in response to salt stress which is dependent on both RBOHD and TPC, but travels at a much higher velocity than the calcium wave (Evans et al. 2016). They developed a model in which Ca^{2+} activates RBOHD and triggers ROS production, and ROS gated calcium channels within the plasma membrane are therefore activated (figure 5). In this model, calcium would enter the cell from the apoplectic pool through plasma membrane channels, and from the vacuolar pool, leading to a faster accumulation of Ca^{2+} and TPC1 activation, and accounting for the velocity of the calcium wave (Evans et al. 2016).

In summary, the ROS and electrical waves both propagate via the vasculature at a similar velocity and are co-dependent for the maintenance of signalling velocity (Gilroy et al. 2014). The calcium wave appears to be different as it travels at a slower velocity and moves through the cortex and endodermis, however both calcium and electrical wave velocity are diminished in ROS deficient plants (Baxter et al. 2014). The TPC1 channel enables calcium, ROS and electrical wave transmission and is voltage gated. It is postulated that ROS indirectly activates TPC1 by triggering calcium ion influx into the cell, leading to rapid depolarisation which opens the TPC1 channel (figure 5) (Evans et al. 2016). The rapidity of calcium and ROS waves are dependent on voltage gated channels and the accumulation of depolarising calcium ions, thus both the ROS and calcium waves could be seen as key components of long distance electrical signalling.
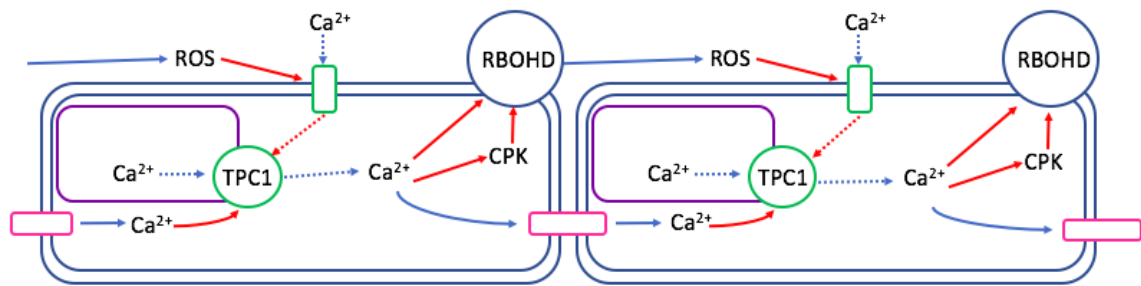
Figure 5: Model linking ROS and calcium signalling waves in response to salt stress targeting the roots. The purple box represents the vacuole, green boxes represent calcium channels, the pink box represents plasmodesmata and RBOHD is depicted as a blue circle. The dotted lines represent theorised pathways of ion transport; red arrows represent channel activation and blue arrows represent compound movement. Calcium enters the cell through ROS activated ion channels in the plasma membrane, and through the plasmodesmata from the previous cell. The calcium activated vacuolar channel TPC1 is then activated due to calcium accumulation, and RBOHD is directly and indirectly activated by calcium to produce ROS. The indirect pathway involves calcium dependent protein kinases (CPK). Figure made based on the model proposed by (Evans et al. 2016).

1.2 Chemical signals in Defense

Chemical defense compound transport via the phloem occurs in the source-sink direction and with the transpiration stream in the xylem, relatively slowly. When a defense chemical accumulates throughout the plant system very quickly, as in the systemic induction of the defense compound jasmonic acid following wounding then it is likely to have been evoked by long distance electrical signalling (Carvalhais et al. 2013). There is not much evidence for rapid long distance signalling by defense chemicals, nevertheless they are vital for defense gene activation through short distance signalling (Mittler & Blumwald 2015b; Hlavácková & Naus 2007; Kudla et al. 2010). The sequence of signalling in plants in response to a stressor is specific to the intensity and character of the stressor, and alters upon the simultaneous perception of multiple stimuli (Huber & Bauerle 2016). Defense chemicals appear to be conserved between many plant species, some of the best studied chemical plant signals include jasmonic acid, salicylic acid, ethylene, pipecolic acid, abscisic acid and auxin (Blande &

Glinwood 2016). These compounds interact in a temporally and spatially specific manner to trigger appropriate defense gene activation. Defense chemical crosstalk is integrated by molecular 'master regulators' which are able to read multiple signals, and respond by negatively or positively regulating gene transcription (Balderas-Hernandez et al. 2013). Defense signalling pathways can be divided into two branches; systemic acquired resistance (SAR) which is the response to biotic stimuli, and systemic acquired acclimatization (SAA) which is the response to abiotic stimuli (Singh et al. 2017; Karpinsky et al. 2013).

The same defense mechanisms and chemical signals can be elicited during different genres of biotic and abiotic stress. Master regulators are therefore highly important for understanding signalling patterns to elicit the correct response (Balderas-Hernandez et al. 2013). This is practical because it conserves resources and because plants are often under multiple stressors in nature.

Table 2: Defense chemicals involved in systemic acquired resistance in response to biotic stress. Data sourced from the papers referenced.

Defense Compound	Function
Salicylic acid	Central to the biotic defence response and accumulates in phloem feeding insects and biotrophic pathogens (Peng et al. 2004).
Jasmonic acid	Central to wound induced defence, accumulates in response to chewing insects and necrotrophic pathogens (Kazan & Manners 2008).
Ethylene	Acts in concert with jasmonic acid, is thought to be a regulator of defence response amplification, and is linked to volatile production (Broekgaarden et al. 2015).

Auxin	Involved in plant development and defence regulation, tends to negatively regulate SA and act in synergy with JA (Kazan & Manners 2009).
Abscisic acid	Mediates defense and tolerance of abiotic conditions, and usually plays a negative role in biotic stress defence (Mittler & Blumwald 2015b).
Pipecolic acid	Essential for SAR, interacts with Ald1 and amplifies the defence response (Bernsdorff et al. 2016).

1.3 Systemic Acquired Resistance (SAR)

Systemic acquired resistance conveys defense against biotic threats such as insects and pathogens. Certain pathogen-associated molecular patterns (PAMPs) are recognised by specific plant receptors and trigger defense-related gene expression in the systemic acquired resistance (SAR) response which involves recall from the plant 'immune memory' (Henry et al. 2014). Several chemicals and hormones have been identified as important for facilitating SAR; salicylic acid (SA), jasmonic acid (JA), ethylene, pipecolic acid and abscisic acid are widely acknowledged as integral SAR defense chemicals (table 2) (Hlaváčková & Naus 2007; Lu 2009; Broekgaarden et al. 2015).

There is generally a divide in the response to biotic stress into the SA signalling branch and the jasmonic acid (JA) signalling branch (figure 6). Phloem feeding insects such as aphids induce SA dependent responses, while wounding and tissue damage caused by chewing insects or

necrotrophic pathogens is associated with Jasmonic acid (JA) accumulation (Carvalhais et al. 2013; Lu 2009).

In the SA branch, upstream signalling is required for systemic SA biosynthesis. During SAR establishment, there are changes in concentrations of free amino acids, one of these was identified as pipecolic acid (Bernsdorff et al. 2016). The ALD1 (ABERRANT GROWTH AND DEATH-LIKE DEFENCE RESPONSE PROTEIN 1) and FMO1 (FLAVIN-DEPENDENT MONOOXYGENASE 1) proteins both act centrally to SAR, they are essential for salicylic acid (SA) biosynthesis, and without them SAR cannot be established (Chaturvedi et al. 2012). It appears that mobile pipecolic acid (Pip) accumulates through interaction with ALD1 in a feedback loop and activates FMO1 (Lu 2009). Evidence suggests that pipecolic acid is produced at the site of infection and is transported long distances via the vasculature, indicating a role in long distance systemic signalling (Bernsdorff et al. 2016).

The regulation of the SA branch of SAR is complex but certain regulatory chemical signals have been identified including reactive oxygen species (ROS) and azelaic acid (AzA) (El-Shetehy et al. 2015; Jung et al. 2009). AzA appears to regulate the accumulation of SA upon biotic stress perception, although in an unstressed scenario Aza does not have an effect on SA synthesis, indicating specific regulation of the SA branch of systemic defense (Jung et al. 2009).
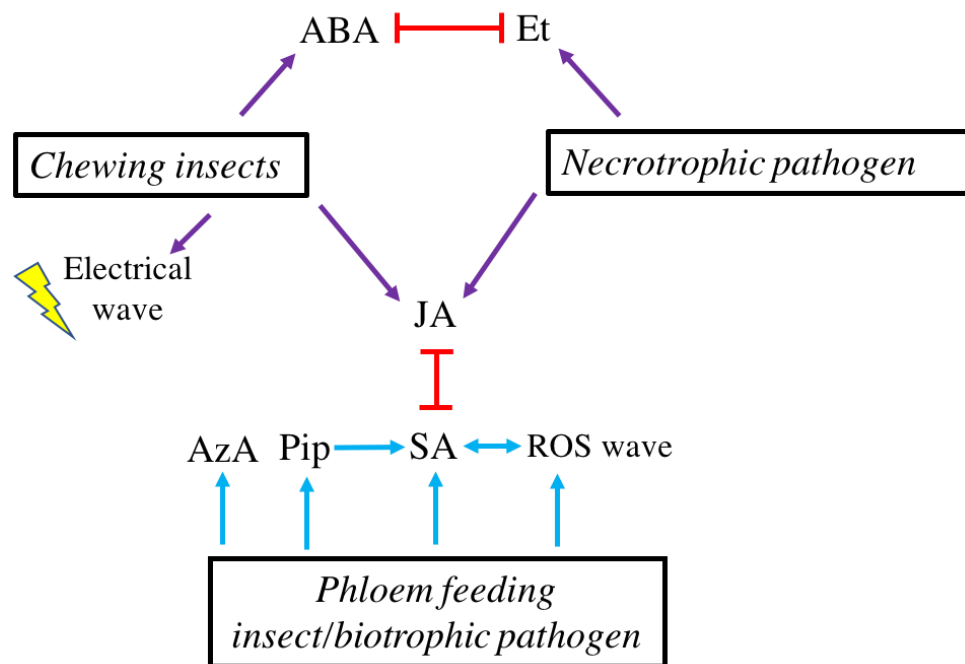
Figure 6: The salicylic acid (SA) and jasmonic acid (JA) branches of biotic stress defense, and associated chemical signals. Phloem feeding insects and biotrophic pathogens induce SA production which requires pipecolic acid (Pip) for synthesis and is regulated by azelaic acid (AzA). The JA branch is triggered by both chewing insects and necrotrophic pathogens. Ethylene (Et) is involved in the necrotrophic pathogen response while abscisic acid (ABA) regulates defense against chewing insects (Kazan & Manners 2008; Lu 2009).

In RBOHD deficient *Arabidopsis* plants, there was a lower accumulation of AzA during the SAR response, indicating that the production of ROS are likely to be involved in triggering/enhancing Aza production and in SA regulation (Mittler & Blumwald 2015a). Furthermore, RBOHD deficient Arabidopsis could not synthesise the defense chemical nitrogen oxide (NO) in response to pathogen attack (El-Shetehy et al. 2015). NO triggers plant resistance to pathogens by activating cell death and defence gene activation, and triggers SA accumulation (Romero-Puertas et al. 2004), it is theorised that NO and ROS may interact to regulate gene expression and modify the strength of the defense response (Leister 2012).

In short, salicylic acid is biosynthesised throughout the plant in response to stress, this is triggered by a long-distance systemic signal such as the ROS, electric or calcium signalling waves or the transport of small molecules from the site of injury, such as pipecolic acid (Heil & Ton 2008). Accumulation of SA is regulated by several compounds including ROS, NO and Aza, the crosstalk between these signals appear to determine the specific defense genes activated (Lu 2009).

The jasmonic acid (JA) branch of biotic stress response is also under the control of several regulatory mechanisms. The accumulation of JA upon insect wounding has been linked to the vacuolar channel TWO PORE CHANNEL1 (TPC1) which is also associated with calcium wave, wound induced-ROS wave and wound induced-electrical wave propagation (figure 5) (Gilroy et al. 2014). Evidence suggests that TPC1 is involved in JA biosynthesis in response to wounding, indicating that the regulation of JA synthesis may include calcium ion fluxes (Bonaventure et al. 2007). In support of this, it is well known that mechanical stimuli induced by insects such as wounding triggers both JA accumulation and electrical signalling (Fromm & Lautner 2007). The first identification of electrical activity in plants came from investigation of the fast leaf movements in response to insect movements in higher plants. In *Dionaea* (Venus flytrap) electrical signals are triggered in response to touch, when an insect touches the trigger hairs, mechanosensors generate an action potential (AP) (Volkov et al. 2009). Two APs in quick succession, as would be elicited by a moving insect, are required to shut the Dionaea trap and also stimulate the jasmonic acid signalling pathway (Fromm & Lautner 2007; Yan et al. 2009). Once the prey is inside the trap it continues to move, repeatedly touching the trigger hairs, more than three APs trigger the secretion of digestive hydrolases (Volkov et al. 2009; Bohm et al. 2016).

To add a further layer of complexity to SAR, the jasmonic acid signalling branch can also be divided into two. The chewing insect-elicited JA response is upregulated by abscisic acid (ABA), and the necrotrophic pathogen-elicited JA response is upregulated by ethylene (Et), furthermore, the two responses are mutually antagonistic (Broekgaarden et al. 2015; Chen et al. 2012) This double sided aspect of the JA signalling branch can be explained by the transcription factors ethylene response factor (ERF) and basic helix-loop-helix leucine zipper transcription factor (MYC) which negatively regulate each other (Boter et al. 2004; Huang et al. 2016). The ERF transcription factor is responsible for regulation of defensive gene transcription in response to JA and ethylene signalling and is essential for necrotrophic pathogen resistance (Huang et al. 2016), whereas MYC regulates the response to chewing insects through JA and ABA signalling (Boter et al. 2004).

The SA and JA branches of biotic stress defense are mutually antagonistic, ethylene appears to regulate SA-JA crosstalk, and causes resource distribution to the JA branch over the SA branch in multi-stress situations (Broekgaarden et al. 2015). MYCs have also been found to mediate JA/SA antagonism (Zhang et al. 2015), however this antagonistic relationship is complicated and is likely to have many regulators.

In summary, systemic long distance ROS, electric and calcium waves are closely associated with JA signalling (Kazan & Manners 2008). SA signalling may also be triggered by these rapid signalling waves, particularly the ROS wave, but is also induced by the slower long-distance transport of pipecolic acid from the site of injury (Bernsdorff et al. 2016). The JA branch of defense is further divided into Et regulated pathogen defense and ABA regulated insect defense, which are antagonistic in the case of multiple stressors (Chen et al. 2012). The coordination of these branches of defense within SAR is managed by master regulators and

transcription factors, to maximise resource efficiency and survival (Balderas-Hernandez et al. 2013; Boter et al. 2004).

1.4 Systemic Acquired Acclimation (SAA*)*

Systemic Acquired Acclimation (SAA) is the systemic defense response against abiotic stress, less is known about this branch of defense in comparison to SAR. SAA appears to be strongly associated with the rapid ROS, calcium and electrical waves (Choi et al. 2016), similarly to the wound induced jasmonic acid branch of SAR, which may be because wounding can be caused by biotic or abiotic stimuli. There is evidence that the ROS wave is required for the SAA response, but interactions with other hormones/signals specify the defence genes activated (Baxter et al. 2014). For example, ABA and ROS were found to interact in a positive feedback loop which regulates stomatal function and gene expression during drought stress (Mittler & Blumwald 2015a). Electrical activity is specific to abiotic and biotic mechanical stimuli and wounding and elicits jasmonic acid synthesis, a compound which triggers defense and recovery from tissue damage (Hlaváčková & Naus 2007).

There are many examples of abiotic stress response in model plants such as *Arabidopsis thaliana* via the rapid ROS, calcium and electrical signalling waves (figure 4). Evidence suggests that rapid long distance signalling is followed by short distance chemical signalling which then upregulate defense genes, for example ROS signalling triggers salicylic acid (SA) synthesis (Herrera-Vásquez et al. 2015). SA is a well-known defense chemical which is synthesised systemically in response to stress and triggers defense during SAA and SAR through the regulation of gene activation, cell death and stomata activity (Lu 2009).

1.5 Defense Trade-offs and Master Regulators

In nature, plants are often under simultaneous abiotic and biotic stress, there is a trade-off in resource allocation to prioritise one branch of defense response over the other and to maximise energy efficiency. This is particularly relevant in the context of climate change, for example it has been shown that tobacco plants (*Nicotiana*) under simultaneous high temperature and pathogen stress have an increased susceptibility to disease (Király et al. 2008). Stress induced electrical signalling has been found to reduce photosynthesis (Fromm & Lautner 2007), this is probably a trade-off based on the diversion of resources required for electrical signalling (Pavlovič & Mancuso 2011).

Co-regulation of abiotic and biotic stress defense has been linked to various regulatory hubs, for example LESION SIMULATING DISEASE 1 (LSD1) is a putative transcription factor which regulates both PAMP related innate immune SAR and light acclimation SAA (Mateo et al. 2004). In innate immunity, the 'hypersensitive response' follows the recognition of pathogen-associated molecular patterns (PAMPs) and is characterised by rapid cell-death to prevent the spread of infection (Alvarez 2000). Cell death is driven by extracellular ROS and runaway cell death is prevented by LSD1, in addition LSD1 is a negative regulator of cell death triggered by excess excitation energy under conditions of high light stress (Dietrich et al. 1994). This indicates that the branches of abiotic and biotic stress response share some defense mechanisms, and can be regulated by the same transcription factors.

Transcription factors play an important role in coordinating the sequence of signalling events between stress perception and physiological response. Generally, in response to a stressor, the initial step is rapid long distance systemic signalling which enables the entire plant to register

stress, the next step is the production of short distance defense chemicals such as SA and JA and their regulators. Master regulators simultaneously perceive numerous defense chemicals, and in response upregulate the appropriate transcription factors. Transcription factors then activate defense genes and trigger the physiological response (figure 7) (Balderas-Hernandez et al. 2013).
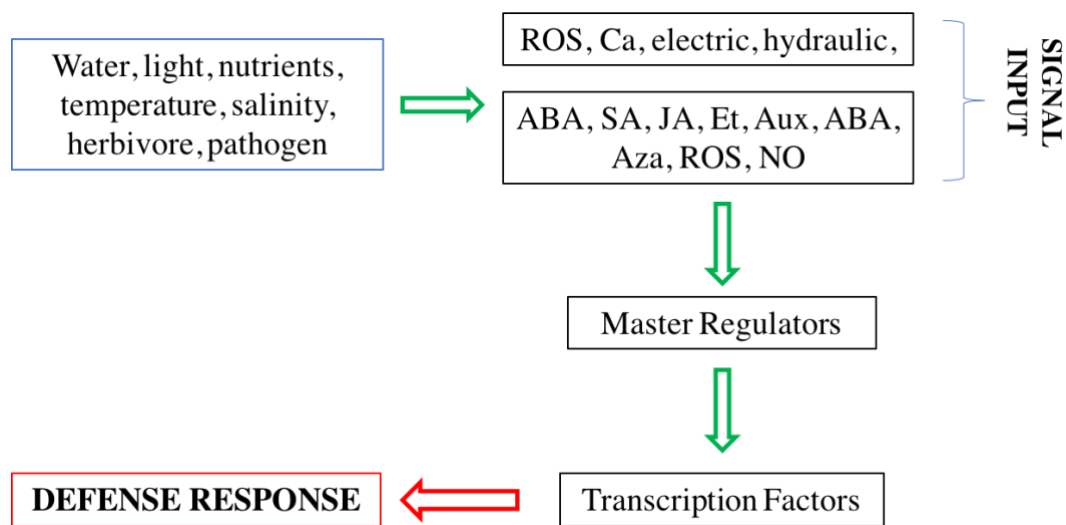

Figure 7: The step by step stress response inspired by the review by (Balderas-Hernandez et al. 2013). Stress is perceived using rapid long distance signals, which trigger short distance defense chemicals perceived by master regulators which activate transcription factors triggering the physiological response.

Master regulators control gene expression by either direct interaction with the promotor region of genes, or by transcription factor or repressor activation and coordinate biotic and abiotic stress signalling. Some of the best-known master regulators are also highly conserved between plant species. In *Arabidopsis Thaliana*, a regulatory model of the genome identified the most important master regulators as; Mediator, non-expressor of pathogenesis-related protein (NPR1), sucrose-non-fermentation-related protein kinase 1(SnRK1) and target of rapamycin (TOR) (table 3) (Balderas-Hernandez et al. 2013).

Table 3: Most important master regulators of stress defense in Arabidopsis. Data sourced from the papers referenced and the review by (Balderas-Hernandez et al. 2013).

Master regulator	Function
Mediator	Implicated in a mixture of abiotic and biotic stresses; cold, drought, osmotic stress and UV-C irradiation tolerance, as well as jasmonate-dependent and necrotrophic fungal pathogen defense gene expression and is associated with JA and ABA cascades (Chen et al. 2012).
Sucrose-non-fermentation-related protein kinase 1(SnRK1)	SnRK1 regulates ABA and auxin signals in response to energy deprivation associated stressors such as oxygen hypoxia due to flooding, drought, extreme hot or cold, and pathogen attack (Radchuk et al. 2010).
Non-expressor of pathogenesis-related protein (NPR1)	NPR1 is involved with antagonistic interactions between salicylic acid and jasmonic acid, and the trade-off between the two branches of JA or SA related biotic stress. NPR1 acts in response to salicylic acid as a transcriptional regulator of genes in response to various biotic stresses, and controls the suppression of jasmonic acid, while ethylene modulates the role of NPR1 during SA-JA interactions (Zhang et al. 2015).

target of rapamycin (TOR)	TOR is a regulator of cell growth, and integrates signals for energy, osmotic stress and nutrient deficiency, and allocates resources to growth or stress response accordingly (Pu et al. 2017).

1.6 Systemic defence signalling in plant communities

Collectively, this gives a view of defense signalling in plants which is highly complex involving the temporal-spatial coordination of multiple signalling mechanisms and compounds. Biotic and abiotic stressors are associated with initial rapid long distance signalling via hydraulic, electrical, ROS and calcium waves (Gilroy et al. 2016). During abiotic stress, rapid signalling waves trigger the synthesis of short distance chemical signals such as ABA, SA, JA and auxin which are coordinated by master regulators SnRK1and TOR1 (Pu et al. 2017; Radchuk et al. 2010).

During biotic stress, long distance signalling may also be conveyed via mobile chemicals such as pipecolic acid in the case of SA synthesis (Bernsdorff et al. 2016), SA accumulation is also regulated by ROS and NO (Mittler & Blumwald 2015b). The JA branch of biotic stress defence is linked to the electrical signalling wave and works in concert with abscisic acid in response to chewing insects and with ethylene in response to necrotrophic pathogens (Kazan & Manners 2008). The ABA/JA branch is mutually antagonistic with the Et/JA branch which is controlled by antagonism between the ERF and MYC transcription factors (figure 8). SA and JA are

antagonistic due to regulation by the master regulator NPR1 and by ethylene (Zhang et al. 2015). Abiotic and biotic defense branches are also mutually antagonistic (Huber & Bauerle 2016). This demonstrates the sophisticated integration of signalling pathways in plants in response to different stressors to maximise resource efficiency.

Interestingly, the JA branch of signalling is also associated with volatile defense compound production, and enabling of defense signalling via mycorrhizal connections (Johnson & Gilbert 2015; Ton et al. 2006a). Therefore, JA mediated defense signals are not exclusively processed within the plant but may be released into the surrounding environment. In herbivore stressed plants jasmonic acid signalling was found to be essential for the upregulation of defense genes in neighbouring plants via mycorrhizal connections (Song et al. 2014). Furthermore, jasmonic acid signalling results in the release of several volatile compounds in response to pathogen attack, which are potent antifungal and antibacterial agents (Tanaka et al. 2014). Evidence suggests that ethylene positively regulates the accumulation of volatile defense compounds, probably in synergy with JA (Huang et al. 2016).

On a community level, the below and above ground transmission of defense signals to neighbouring plants can result in partial defense gene activation in surrounding unattacked plants (Martinez-Medina et al. 2016), conveying a base level of defense, and probably enhancing ecosystem resilience against stressors. Volatile signals are regulated by JA, ethylene and the ERF transcription factor (figure 8) (Broekgaarden et al. 2015). Signalling via mycorrhizal networks has been shown to be associated with jasmonic acid and possibly salicylic acid signalling (Song, Ye, et al. 2015). Volatile and mycorrhizal signals are produced as a part of the systemic defence response of a single plant, and are released into the surrounding environment. It appears that mechanisms and compounds conveying defense are

widely conserved between plants, therefore in a forest ecosystem it is inevitable that neighbouring plants will perceive stress signals released in close proximity, and evidence shows that they respond by weakly activating their own defences (Jung et al. 2009). This extension of systemic defense may have evolved due to a community resilience effect, or may just be an unintended consequence of molecular defense signalling.
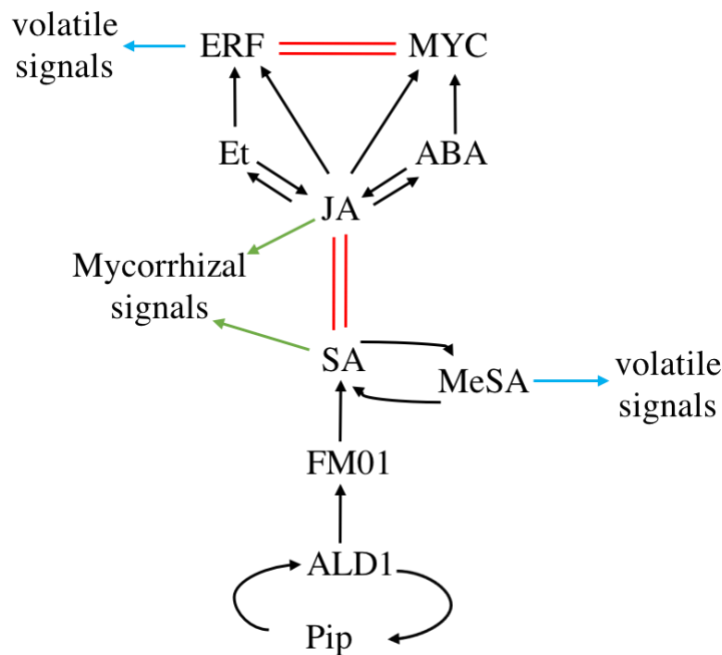

Figure 8: Illustration of the JA and SA branches of the defense response including the pathways leading to volatile and below ground signalling. Red lines represent antagonism, green arrows represent mycorrhizal signals, blue arrows represents volatile signals.

Chapter 2: Volatile Defence Signalling

2.1 Characterisation of plant volatiles

The downstream effects of systemic defence activation in plants include the synthesis of volatile compounds which act as a part of the abiotic and biotic defense response (War et al. 2011). Volatiles often induce defense gene regulation in other parts of the plant rapidly, and when they reach neighbouring unattacked plants can warn them of a potential threat (Tanaka

et al. 2014). When volatile signals are perceived by neighbouring plants, studies have found a reactive partial activation of defense genes, conveying a basal level of resistance and much faster activation of the full defense response in the event of attack, this phenomenon of partial defense response activation appears to act as an energy efficient precaution and is referred to as 'priming' (Ton et al. 2006b). Plants produce hundreds of volatile compounds in complex combinations in different stress situations, however only a few are well characterised, table 4 contains the major groups of volatiles which have so far been identified in plant defense.

Terpenoids are the largest group of volatiles emitted by plants and have been found to elicit defence against both biotic and abiotic stress (Mumm et al. 2008). Interestingly, the enzyme responsible for terpene synthesis, terpene synthase, is strongly effected by minor changes in residue availability and can create many different variations of compounds depending on the most abundant residues available (Köllner et al. 2004). This has implications for the increasingly serious human impact on ecosystems which is rapidly altering the composition of the air, water and soil.

Table 4: Major groups of volatile defense compounds, and mechanisms of synthesis and main function. Data sourced from referenced papers.

Volatile Compound	Synthesis and Function
Green Leaf Volatiles (GLVs)	Synthesised through the lipoxygenase pathway and convey defence against herbivores and pathogens, and can prime neighbouring plants for defense. Released immediately after insect damage (ul Hassan et al. 2015).
Methyl salicylate and Methyl jasmonate	Methylated products of salicylic acid and jasmonic acid, and can active SA and JA signalling in neighbouring plants,

	inducing defence related gene expression (Tang et al. 2015; (Tanaka et al. 2014).
Herbivore-induced plant volatiles (HIPVs)	Low molecular weight compounds including GLVs and terpenoids. Involved in interactions with natural enemies of insect herbivores, neighbouring plants and distal regions of the same plant (War et al. 2011).
Terpenoids	Synthesis triggered by jasmonic acid and precursors. Terpenoids comprise the largest and most diverse set of volatiles released by plants, they play multiple roles in resistance to abiotic and biotic stress (Mumm et al. 2008).
Amino-acid derivatives	Derived from amino acids such as valine, leucine, isoleucine and methionine. Many play an important role in recruiting the natural enemies of the herbivore (War et al. 2011).

Defense signals central to systemic defence have been found to trigger resistance pathways resulting in the production of volatile compounds in specific stress situations. For example, jasmonic acid is able to activate both the terpenoid production pathway, and the lipoxygenase pathway, which results in the production of green leaf volatiles (GLVs) (Tanaka et al. 2014). Healthy plant tissue always contains low levels of GLVs which accumulate upon insect attack or wounding, an increase in free fatty acids released by tissue damage together with jasmonic acid signalling are required for GLV synthesis (Matsui et al. 2006).

In maize (*Zea Mays*) challenged by *Spodoptera littoralis*, GLVs trigger defense gene activation in distal areas of the same plant, and in neighbouring plants. Volatiles also attracted the

parasitic wasp, a predator of *Spodoptera* (figure 9) (Ton et al. 2006a). In the same plant, leaf hopper attack results in the production of a different blend of volatile compounds which is repellent to the leaf hopper (Oluwafemi et al. 2013). This demonstrates the diversity and plasticity of the volatile defense response.
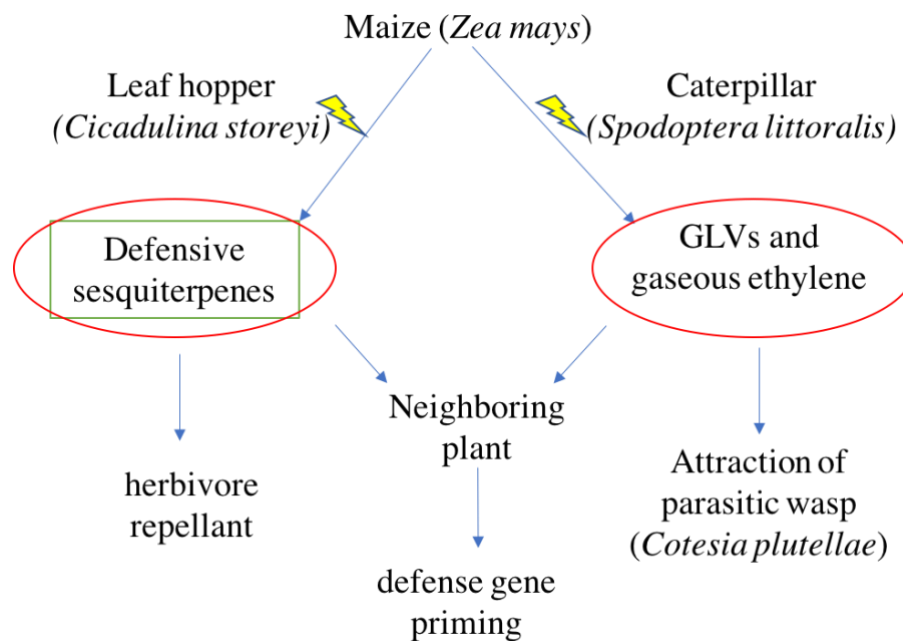

Figure 9: Graphic representing insect attack on maize and the diverse volatile compounds which can be produced depending on the predating insect, and their effects including defense priming of neighbouring plants (Ton et al. 2006b; Oluwafemi et al. 2013). Red circles represent volatiles which could be effected by elevated carbon dioxide, and green square represents volatiles potentially effected by changed residue availability (climate change section).

An alternate insect defense mechanism was characterised in Lima bean (*Phaseolus lunatus*) and involves the production of extra-floral nectar when under attack from spider mites, to provide a temporary non-essential food source (figure 10) (Choh et al. 2006). Volatile signals also provide defence against abiotic stress; the terpenoids monoterpene and isoprene elicit plant adaptation to heat and light stress (Loreto et al. 1998; Sharkey et al. 2001). Isoprene fumigation increased recovery of *phaseolus vulgaris* leaves from short term heat stress by 20-40% by enabling leaf cell membranes to change their properties very rapidly and thereby protecting them from damage (Sharkey et al. 2001).

Lima bean
(*Phaseolus lunatus*)

Spider mite
(*Phytoseiulus persimilis*)

HIPVs

Extra-floral nectar
production (alternative
mite food source)
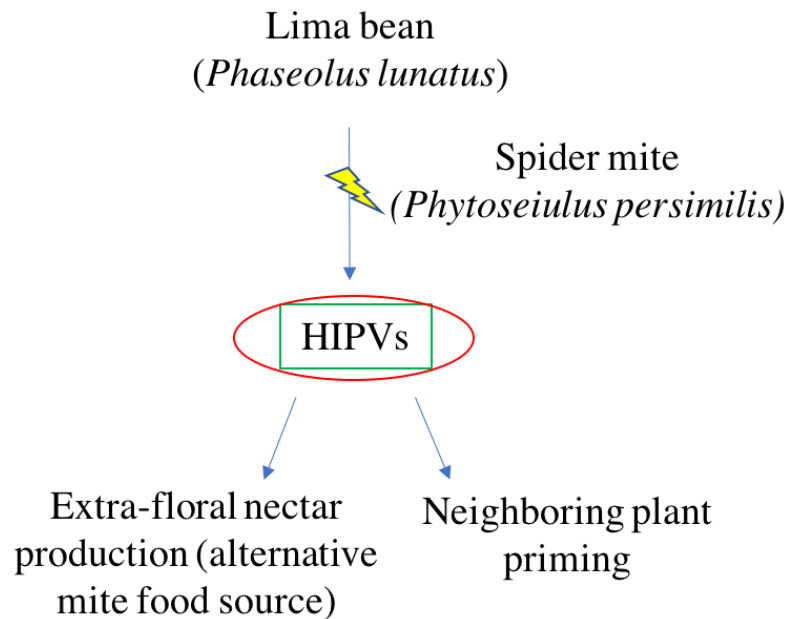
Neighboring plant
priming

Figure 10: Graphic representing lima bean attack by spider mite and effects of herbivore induced plant volatiles (HIPVs) in neighbouring plant defense priming and extra-floral nectar production as alternative mite food source (Choh et al. 2006). Red circles represent volatiles which could be effected by elevated carbon dioxide, and green square represents volatiles potentially effected

2.2 Defense Priming

Methyl salicylate and methyl jasmonate are important in priming systemic defence in neighbouring plants (Heil & Ton 2008; Tang et al. 2015). During defense priming, the information from the stimulus is stored until exposure to the triggering stimulus (such as an insect) which induces a faster, stronger and more sustained defense response (Ton et al. 2006a). Therefore priming is an immune response memory based low-cost method of defense via plant-plant signalling (Martinez-Medina et al. 2016). However, the reliability of studies investigating plant-plant communication via volatiles has been questioned because often glass vials containing unnaturally high concentrations of the signalling volatile were used (Paschold et al. 2006).

These claims provoked counter studies, some of which proved that low concentrations of volatiles could indeed activate defence genes (Oluwafemi et al. 2013), however there remains some controversy in this area. Scientists supporting the volatile mediated inter-plant defense

priming hypothesis have pointed out that volatiles such as GLVs are denser than the composition of atmospheric air and therefor remain close to the ground with little diffusion, and additionally the leaf boundary layer provides a potentially beneficial microenvironment for the accumulation of high concentrations of volatile substances (Matsui et al. 2006).

Although difficult to prove under experimental conditions, the evidence of the priming effect conveyed by low levels of volatile substances under close to natural conditions is convincing (Oluwafemi et al. 2013). Interplant communication via VOC stress signals appears to be an unavoidable consequence of individual defence strategies, providing an evolved extension of within plant signalling, which nevertheless conveys a collective advantage within plant communities due to a faster and stronger immune response (Gorzelak et al. 2015).

Chapter 3: Mycorrhizal Network Defence Signalling

Systemic defense signalling not only extends into the surrounding environment through volatile signalling, but also below ground via mycorrhizal networks (MNs). The basis for mycorrhizal symbiosis is considered to be the acquisition of soil derived nutrients extracted by fungal hyphae, in exchange for plant derived photosynthate containing the organic carbon required for fungal growth and reproduction (Editor & Caldwell 2015). In addition to this mutualistic exchange of nutrients, mycorrhizal networks are also able to alter plant responses and influence defense signalling and resource distribution between plants within a community (Smith et al. 2008a; Song et al. 2010; Gorzelak et al. 2015; Merckx et al. 2010).

3.1 Mycorrhizal Network Structure

In plant communities, nutrient acquisition and defence against pathogens are enhanced by MNs and survival is enhanced by symbiosis with mycorrhizal fungi (Smith et al. 2008a). The importance of mycorrhizal networks (MNs) for plant community establishment is generally accepted; evidence suggests that primitive rootless plants were dependent on a symbiotic association with fungi for early plant community establishment (Adam et al. 2013).

There are many clades of fungi but in this review only arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) (Smith & Read 2008; Toju et al. 2014), will be discussed. AMF and EMF interact with plant roots in different ways, arbuscular hyphae penetrate root cells whereas ectomycorrhizal fungi forms a sheaf enclosing the root (Yamamoto et al. 2014; Smith et al. 2008b). Evidence from studies using high throughput sequencing analyses have shown that a single plant may be simultaneously infected by both arbuscular and ectomycorrhizal fungi, and that the plant species determines the nature of the mycorrhizal interaction (Toju et al. 2014; Toju et al. 2015; Smith & Read 2008). MNs connect multiple plant and fungal species in the same network, and interactions can be mutualistic, antagonistic or parasitic within the same network, therefore there is high complexity in the interactions and signalling within MNs in forest ecosystems (Fortuna et al. 2010; Simard et al. 2015).

A study by Toju et al investigated the architecture of a large-scale mycorrhizal network using next-generation sequencing technology to analyse a temperate forest in Japan, it was found that the mycorrhizal network structure was characterised by high anti-nestedness, (Toju et al. 2014; Toju et al. 2015; Yamamoto et al. 2014). Anti-nestedness implies a network in which a few species are 'specialists' and engage in few interactions with each other and different trees, while most species are 'generalists' and are highly connected to many other species (Fortuna et al. 2010). Some studies theorise that anti-nestedness may enable resilience in a community

where antagonistic as well as mutualistic interactions exist (Thébault & Fontaine 2010; Mougi & Kondoh 2012; Toju et al. 2015) which would make sense in the context of fungal-plant interactions which may be more beneficial to the fungi or the plant depending on environmental conditions.

The plasticity of fungi (ability to interact with many different species simultaneously) was probably caused by natural selection for fungal species able to interact with a wide range of species, enabling resilience in the case of forest ecosystem disturbances and resulting in anti-nestedness (Baluška & Mancuso 2013). In the context of climate change, this is an advantage, however increasing monodominance in forests weakens resilience, furthermore it can be expected that anthropogenic impacts on soil, air and water chemistry may lead to an altered ecosystem structure. It has been found that different fungal clades benefit from CO_2 elevation depending on soil type (Procter et al. 2017).

3.2 Fungi vs Plants for Symbiotic Control

There is some controversy regarding whether the fungal or the plant partner exerts control within mycorrhizal symbiosis, and which partner benefits the most (Walder et al. 2012; van der Heijden & Horton 2009). From a phyto-centric point of view, evolutionary reasons for a plant to support a fungal symbiont which takes photosynthate and transfers it to another plant could be that if seed dispersal from the parent is limited, as in forests, then there would be a high degree of relatedness between nearby parent trees and seedlings, thus enhancing species success (van der Heijden et al. 2015).

From studies in douglas fir mycorrhizal resource transfer, it has been shown that significantly larger quantities of micronutrient and carbon is transferred from douglas fir to nearby kin than to unrelated neighbours (Pickles et al. 2017), thereby increasing the fitness of the evolving genotype. Plant root exudates communicate information about the presence and genetic identity of neighbours and in some cases appear to limit competitive mechanisms such as thievery of soil resources in the presence of closely related kin, which can effect community structure and function (Semchenko et al. 2014). However, it is challenging to empirically compare kin vs stranger competition in plant communities, and evolved traits such as avoidance of selfing and higher resilience in biodiverse environments suggest that kin altruism may be limited (Dudley et al. 2013).

Another line of evidence supporting a phyto-centric view is that when soil fertility is high or when light intensity/ C availability is low then plant roots often display reduced fungal colonisation, which suggests that plants possess the ability to some extent to regulate symbiosis depending on resource availability (Smith & Smith 2011; van der Heijden et al. 2015).

From the fungal point of view, the gain of excess carbon from host plants could be used to supply other plants in need, insuring against the potential loss of a host and ensuring that the network contains multiple plants species, increasing the resilience of the plant community and therefore the fitness of fungal species in a variable environment (Toju et al. 2014). Furthermore, there is evidence that fungal exudates are able to manipulate the systems of plant defense and development (Boivin et al. 2016; Garcia et al. 2015).
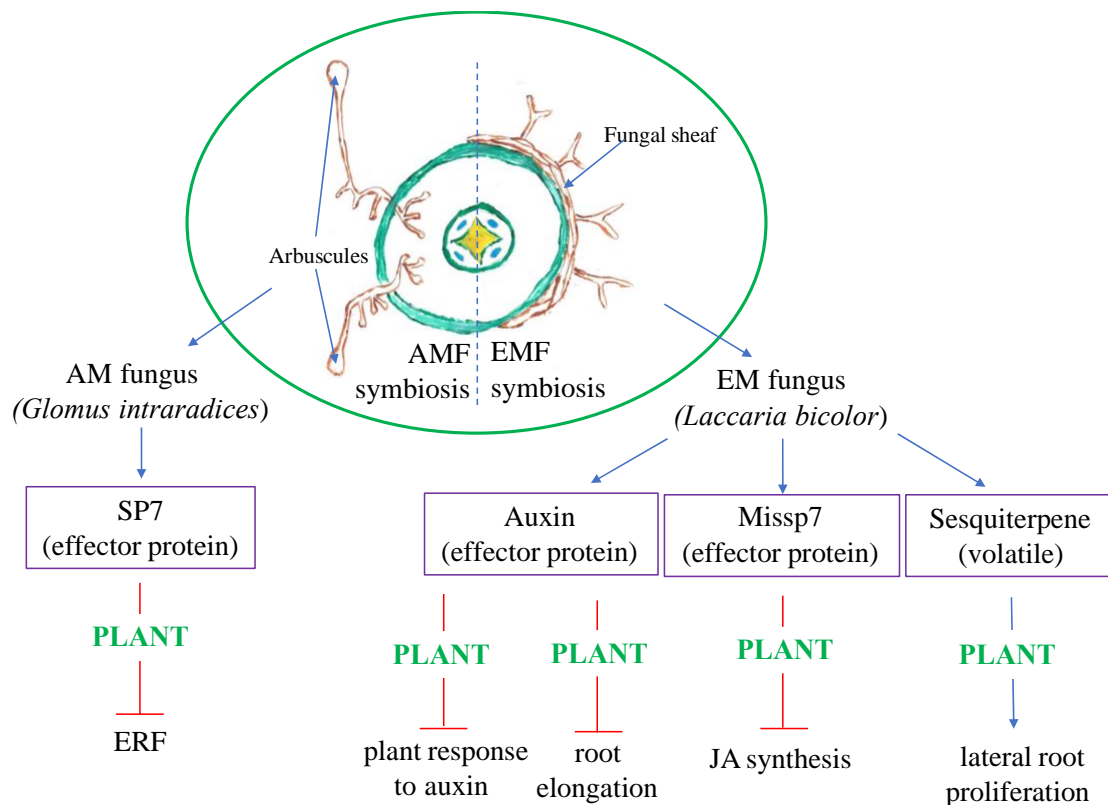
Figure 11: Effector proteins released by fungi which manipulate the plant growth and defense response. Effectors are in the purple boxes, downstream effects after effectors have reached plant receptors are displayed under the green 'plant' label (Kazan & Manners 2009; Boivin et al. 2016; Garcia et al. 2015; Pozo et al. 2015). EMF and AMF symbiosis are illustrated.

During the establishment of symbiosis, several plant defense mechanisms are controlled by fungal effector proteins, which can bind to plant receptors, and control the plant defense system (figure 11) (Garcia et al. 2015). These can target transcription factors such as ERF (ethylene response factor) and JAZ (jasmonate-zim domain) which regulate the jasmonate and ethylene signalling pathways, inducing jasmonic acid signalling (Pozo et al. 2015). In addition, ectomycorrhizal fungi can produce auxin which binds to the plant auxin receptor and permanently decreases plant response to auxin which appears to effect root growth to favour colonisation and provide symbiosis beneficial conditions (Kazan & Manners 2009). Investigations into the effects of defense compounds on symbiosis demonstrate that jasmonic acid and auxin induce fungal colonisation, which explains the release of fungal proteins which

induce JA and auxin during symbiosis (Pozo et al. 2015) The sesquiterpene volatile is also released by fungi and effects plant root growth (Li et al. 2016). Overall, the ability of fungal partners in symbiosis to monitor and control the plant defense response indicates that they may have more control over symbiosis than plants, however there is also evidence for the production of plant root exudates which exert control over fungi (figure 12) (Steinkellner et al. 2007).
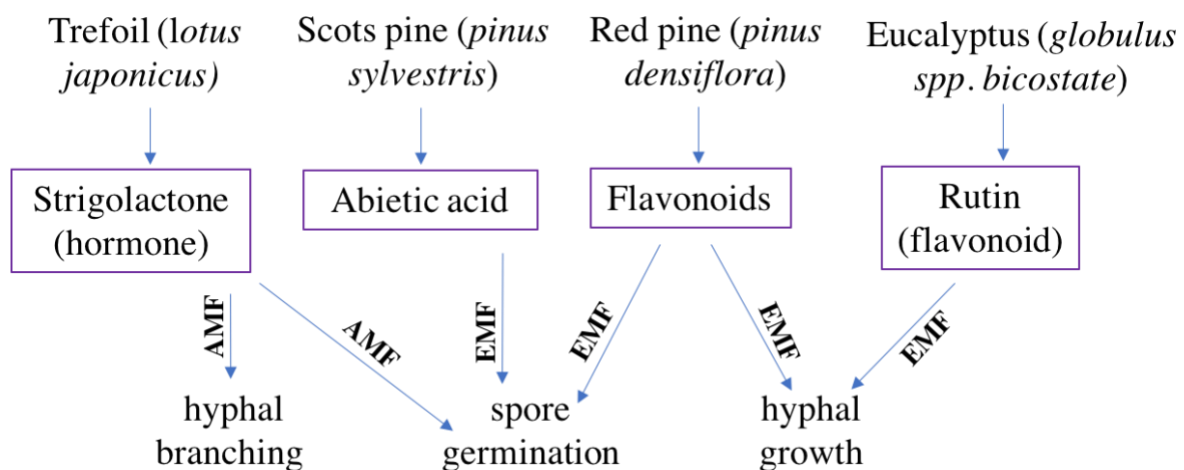

Figure 12: The effects of flavonoids and other plant derived signals (in purple boxes) on fungal processes. The labels 'AMF' and 'EMF' denote whether the interaction occurred during the establishment of arbuscular mycorrhizal or ectomycorrhizal fungal networks (Steinkellner et al. 2007).

Root exudates flavonoids and strigolactones, (a group of sesquiterpene lactones) are known to be important for fungal-plant interactions (Steinkellner et al. 2007). Evidence shows that strigolactones released by *lotus japonicus* induce hyphal branching and spore germination during symbiosis with AMF. Abietic acid released by Scots pine (*Pinus sylvestris*) appears to enhance spore germination in EMF, and flavonoids released by red pine and eucalyptus have been found to trigger fungal hyphae growth, and spore germination (figure 12) (Steinkellner et al. 2007).

In legumes, flavonoids attract rhizobial fungi, and induce the fungal program for symbiosis which involves the synthesis of nodulation (nod) factors, which are fungal lipo-chitin signals that induce the expression of the plant's 'symbiotic program' genes (figure 13) (Garcia et al. 2015). A burst of calcium signalling generally accompanies symbiotic establishment, similarly to the calcium wave triggered upon pathogen perception, but with a different oscillation pattern (Kosuta et al. 2008). This could be indicative of the triggering of the plant defense system in response to fungal colonisation, and indicates the possibility that calcium signalling could be involved in defense signal transmission via the MN.
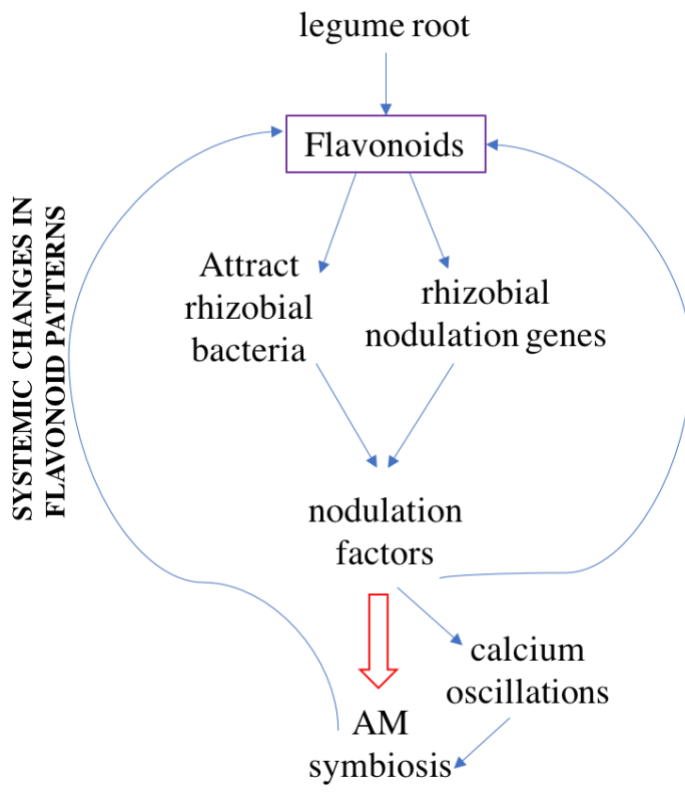

Figure 13: The effects of flavonoid release from legume roots on rhizobial bacteria. Following symbiosis, flavonoid expression patterns are permanently altered (Steinkellner et al. 2007; Kosuta et al. 2008).

In summary, there is still much controversy regarding the identity of the 'controlling partner' as plant or fungi in MN symbiosis, as both antagonistic and mutualistic interactions occur. A fungal species can have mutualistic interactions with one plant while simultaneously exploiting another plant and mycoheterotrophic plants acquire all the carbon required to survive and grow from the MN (Adam et al. 2013). Such interactions constitute parasitism, although there could be an advantage for fungi because they allow MN colonization over a larger area (Thébault &

Fontaine 2010). From the evidence, it appears that mycorrhizal symbiosis generally offers a community resilience effect to plants and fungal networks, although individuals may engage in antagonistic or parasitic interactions.

3.3 Defence signal transfer via Mycorrhizal Networks

Evidence indicates that the transfer of signalling compounds via MNs can convey stress signals from connected plants and consequently activate defence genes in unaffected neighbouring plants, in an extension of SAA and SAR (Gorzelak et al. 2015; Song et al. 2010; Barto et al. 2011). Although the exact mechanism of defense signal transport is unknown, there are several lines of evidence which cast light on mycorrhizal defense signal transfer. Jasmonic acid signalling has been associated with the secretion of flavonoids from the plant roots, enhancing root disease resistance in SAR (Carvalhais et al. 2013; Pozo et al. 2015; Steinkellner et al. 2007). Furthermore, studies investigating the mechanism by which defense signals are conveyed via mycorrhizal connections indicate the importance of salicylic acid (SA) and jasmonic acid (JA) (Song et al. 2010), both compounds are well acknowledged as important in systemic plant signalling (Larrieu & Vernoux 2016; Lu 2009). There are several examples of JA involvement in MN signal transmittance; the herbivore-induced plant volatile methyl salicylate which is repellent to aphids but attractive to aphid enemies is released by *Vicia faba* in response to aphid herbivory. The production of methyl salicylate can subsequently occur in neighbouring unaffected plants, but only when they are linked via a MN (Babikova et al. 2013), this implies that a chemical, electrical or hydraulic signal triggering SA synthesis can be transmitted via the MN.

Attack of tomato plants by necrotrophic fungus triggers SA and JA signalling in the defense response of the stressed plant, and activates defense genes in plants connected in the MN (figure 14) (Song et al. 2010). A further study in tomato plants, showed that attack by the *Spodoptera litura* caterpillar resulted in defence related gene activation in uninfected neighbours but only when they were linked via the MN and could not occur when the jasmonic acid signalling pathway was blocked (figure 14) (Song et al. 2010; Song, Ye, et al. 2015). This indicates that jasmonic acid signalling can directly or indirectly trigger the transport of defense signalling via the MN.
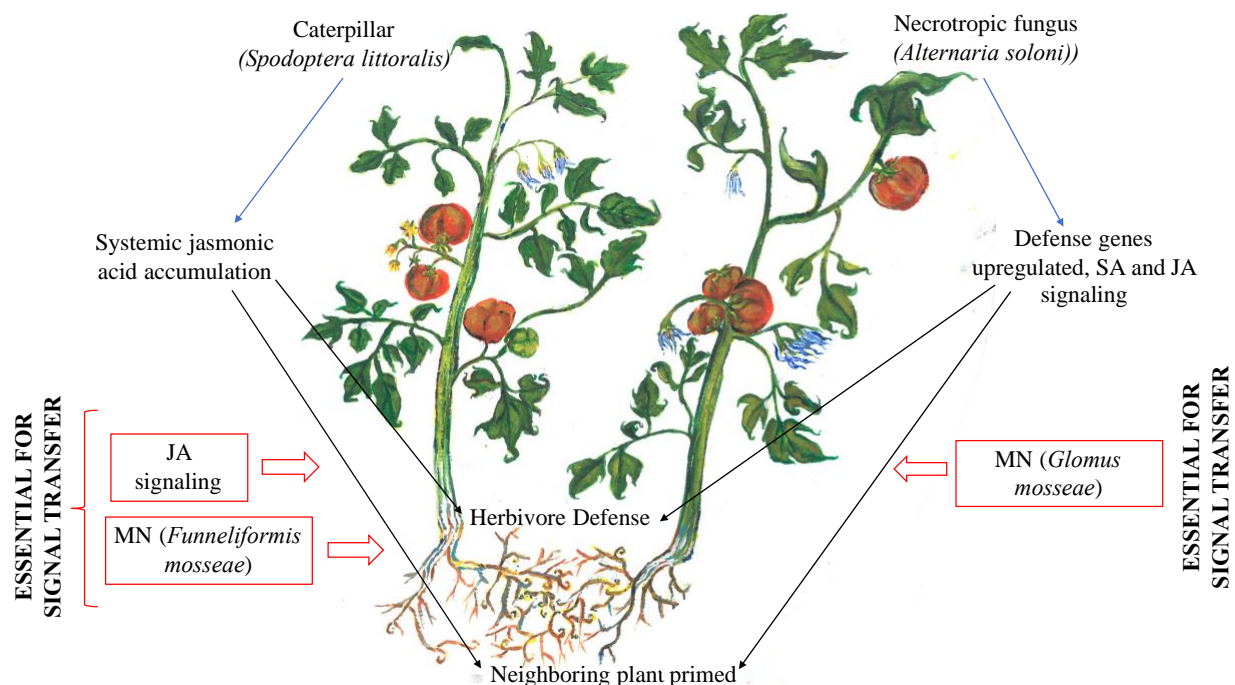

Figure 14: Graphic representing defense signalling in tomato plants in response to insect and pathogen attack. The lightning strike represents the stressor, red boxes represent components found to be essential for defense signal transfer to neighbouring plants (Song et al. 2010; Song, Ye, et al. 2015).

Given the evidence for mycorrhizal network involvement in defence signal transfer between plants, the next obvious question is how defence compounds may be transported via the plant-mycelia-plant pathway. From the evidence so far, it appears the most likely that defence compounds travel within MNs via cytoplasmic streaming within hyphae or electrical signalling (Johnson & Gilbert 2015). There is evidence for action potential and calcium signalling during

MN symbiosis (Johnson & Gilbert 2015; Kosuta et al. 2008) which indicates that the calcium, electrical and ROS waves could be involved in mycorrhizal processes. The interaction of fungal derived compounds with master regulators of the plant defence hormone network permanently alters the systemic plant hormone system (Kazan & Manners 2009; Boivin et al. 2016; Pozo et al. 2015). This indicates that mycorrhizal fungi may be able to monitor and react to the plant's defence response to an extent that it becomes integrated with a plant's defence system.

3.4 Resource transfer via Mycorrhizal Networks

Interplant resource transfer occurs through the MN in response to stressors such as drought. Fluxes include carbon, water, nitrogen, phosphorus, micro nutrients and stress signalling compounds (figure 15) (S Simard et al. 2015). MNs also support the transfer of allelochemicals from supplier to target plant, and facilitate allelopathy by which compounds produced by one plant limit the growth of surrounding plants, enhancing competition (Barto et al. 2011).
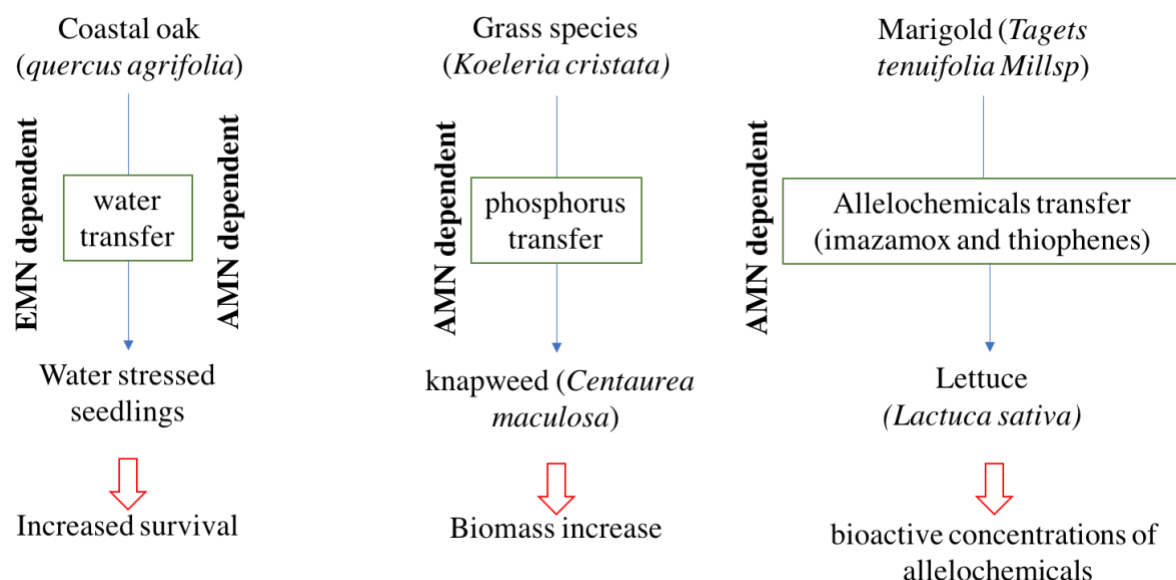

Figure 15: Graphic representing resource transfer via MNs (in green box) and effect (red arrow) (S Simard et al. 2015).

However the importance of below ground nutrient exchange for forest ecosystem stability is still debated, it is difficult to control all factors in investigations into MN dynamics due to confusing factors such as the potential influence of varying ages of plants, differences between plant-host species interactions and soil fertility (Selosse et al. 2006). Nevertheless, evidence indicates that MN connections improve plant community resilience to abiotic and biotic stresses, and may well provide a buffer for maintaining ecosystem functionality under changing climatic conditions (Smith & Smith 2011).

Evidence is variable in how evenly resources are distributed between the different species of fungi and plants which comprise mycorrhizal networks. Arbuscular fungi species which contribute a higher level of nutrients in an MN are supplied with a higher quantity of carbon by species such as the legume *Medicago truncatula*, suggesting that mutualism is equal in some cases (Kiers et al. 2011). However the evidence is unclear and there are also many examples of unequal symbiotic exchange, for example in a community of flax mixed with sorghum the flax contributes very little carbon and yet receive the majority of nutrients, while sorghum invests a lot of carbon but receives very little in return (Walder et al. 2012; Suzanne Simard et al. 2015; Perry et al. 1989). Plants grown together are often more productive than when grown in monoculture. Confusingly, this beneficial effect was found in communities of paper birch mixed with douglas-fir, both species displayed increased productivity and resistance from disease, even though douglas fir benefits from an uneven transfer of carbon from paper birch (Smith et al. 2008c). This indicates that the overall effect of symbiosis is positive, but possibly we do not yet fully understand why.
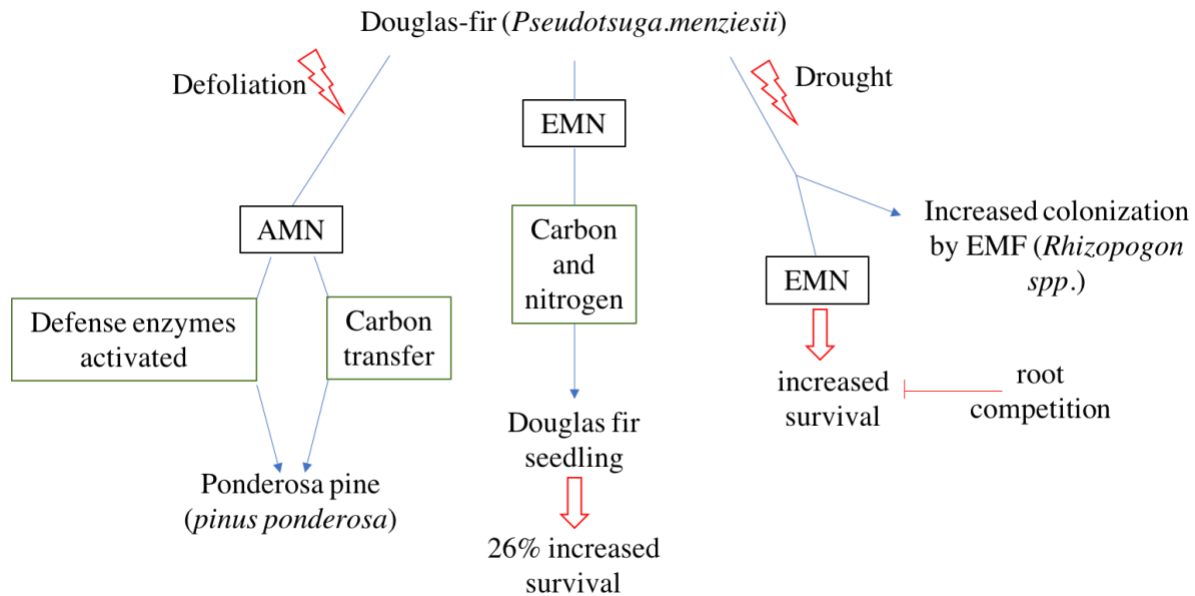
Figure 16: Graphic representing resource transfer from douglas fir via MNs in different situations (in green box) and effect (red arrow) (Song, Simard, et al. 2015). Recipients of resources are the species at the bottom of the graphic and Douglas-fir is the donator. The resources are in the green boxes, the red arrows show the effects of resource transfer.

Seedlings within a plant community particularly benefit from the interplant exchange of nutrients mediated by mycorrhizal networks. Studies have shown that access to a MN significantly lowers seedling mortality rates, and increases growth and leaf number in forests (S Simard et al. 2015). It is proposed that small quantities of nutrients such as nitrogen transferred from the residual roots of mature trees and conveyed by an MN enables seedling establishment following disturbances in natural forest conditions (van der Heijden et al. 2015).

Furthermore, forest MNs have been shown to mediate the transfer of resources from older trees to regenerating seedlings, associated with rapid increases in photosynthesis and growth, this effect appears to be conserved across various regions and climates (Suzanne Simard et al. 2015). It was found that defence signals and carbon are transferred to *Pinus ponderosa* via the MN when the donor Douglas pine undergoes defoliation, this is because defoliation results in

the transfer of carbon into the roots as a survival mechanism, and carbon transfer occurs due to the source-sink effect of resource transfer, which appears to be function even between different species (figure 16) (Song, Simard, et al. 2015).

These examples of symbiotic resource transfer could be perceived as a method for the fungus to maintain a community of healthy hosts, but also highlights the importance of MNs in forest resilience. MN mediated recovery from disturbances, drought resistance and a quicker defence response to pests could all be important in changing climatic conditions, however, it is probable that there is a limit to the extent of such resilience, and over a certain threshold these mechanisms would not be sufficient to ensure stress resistance.

3.5 Resource Transport Mechanism

Long-distance transport of carbon and other nutrients is facilitated via mass flow driven by the source-sink gradient generated by interplant nutrient differences (Suzanne Simard et al. 2015). Compounds are transferred within the central medulla which contains hollow vessel hyphae (Elmore & Coaker 2011). Sucrose is delivered by the plant at the plant-fungal interface and is cleaved into glucose and fructose and then converted into fungal compounds (S Simard et al. 2015). Carbon and nitrogen travel through MNs as basic amino acids which are able to pass across the membrane between fungal hyphae and plant cells (Editor & Caldwell 2015). The water potential gradients due to plant transpiration cause water to move from the soil to hyphae to roots and into other plant tissues (Simard & Durall 2004).

Plant sink and source strength governs the magnitude of resource transfer; rapidly growing EMF saplings with high transpiration rates, or plants under water stress, receive larger amounts

of carbon and water from MNs (Teste et al. 2009). When douglas fir trees undergo above ground mechanical damage they generally transfer quantities of labile carbon to their roots as a survival mechanism, these deposits are strong sources of labile carbon and can be transferred from the roots of injured seedlings to healthy neighbours due to the source-sink effect, and nitrogen is generally transferred from N_2 fixing plants to non-N_2 fixing plants (Gorzelak et al. 2015; He et al. 2009).

In mycorrhizal structures, the fungal hyphae contain transporters which allow a flow of soil nutrients into the fungus (S Simard et al. 2015). The presence of symbiosis triggers the expression of certain nutrient transporters in the plant which appear to be stimulated by the presence of carbon, indicating the importance of reciprocal carbon exchange for the acquisition of fungal nutrients (Garcia et al. 2015). There are several examples of species specific nutrient transporters, which are induced by symbiosis and carbon allocation. In the legume *Medicago Truncatula*, the presence of an AMF network activates a phosphate transporter which is essential for acquisition of fungal derived phosphate upregulated by the simultaneous transfer of carbon derived sugar. It was found that the presence of the phosphate transporter is essential for the maintenance of symbiosis (figure 17) (Javot et al. 2007). Nitrate transporters have also been found to be expressed by fungi in response to symbiosis and an external sugar source (figure 17) (Anon 2014).
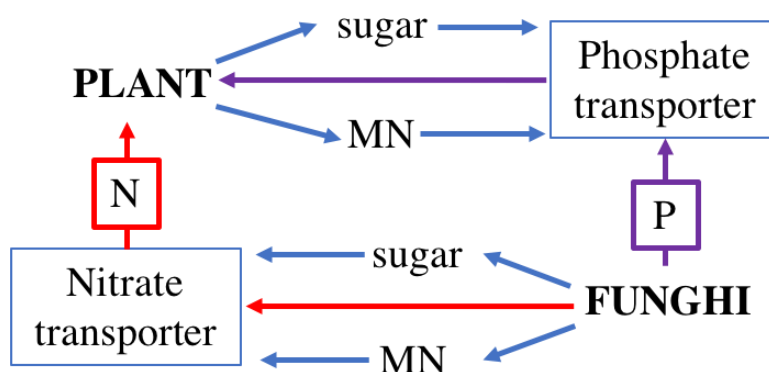

Figure 17: Graphic representing the activation and upregulation of nutrient transporters in plant and fungus reliant on the presence of symbiosis (Javot et al. 2007; Anon 2014). The purple arrow represents phosphate movement, the red arrow represents nitrate movement, and the blue arrows show the elements required for transporter expression

Chapter 4: Climate Change and Plant Defense Response

Altered environmental conditions caused by climate change are predicted to disrupt plant phenology due to elevated temperatures, changed atmospheric gas composition and longer summers. Ecologically, climate change can generate mismatches between plants and insect pollinators. In addition, a potential increase in the number of insect generations and a change in leaf nutrient density may cause some herbivores to consume larger quantities of leaves to fulfil their nutritional needs (DeLucia et al. 2012). Furthermore elevated CO_2 can alter herbivore preference for host species/genotype (Agrell et al. 2006) and human impacts are altering the composition of soil and water chemistry, as well as forest structure and biodiversity. Plants are continually evolving to optimise their performance under specific environmental conditions, but there is a limit on how quickly adaptation can happen in response to unnaturally rapid human induced climate change.

4.1 Climate Change and mycorrhizal networks

Interactions within mycorrhizal networks can be beneficial or unfavourable for plants, and often internal and external conditions define mycorrhiza-plant cost/benefit dynamics (Morgan et al. 2005). Therefore, the nature of interaction between fungi and plants, and the extent of the benefits gained through the mutualism is difficult to predict, especially under changing climatic conditions (Adam et al. 2013; Editor & Caldwell 2015). Furthermore, interactions and signalling within MNs are sensitive to anthropogenic alterations in air and soil composition, reduction in microbial and plant biodiversity, and temperature fluctuations, indicating the potential impact of climate change (Compant et al. 2010; Brunner et al. 2015).

The links between salicylic acid (SA) and jasmonic acid (JA) with inter-plant defense signal transfer (Song et al. 2010) are relevant in the context of elevated levels of CO_2 which result in suppression of JA and stimulation of SA (Gray & Brady 2016). This indicates that plant-plant communication via MNs could be compromised by anthropogenic pressure, leading to potentially less resilient plant communities. In addition, the effects of elevated temperature and carbon dioxide on central phytohormones such as JA and SA (Gray & Brady 2016) may also affect the process of mycorrhizal symbiosis due to the involvement of JA, SA, Et and auxin in symbiosis initiation (Pozo et al. 2015).

Agriculture, air pollution and water contamination often leads to the deposition of chemicals such as nitrate and phosphate in the soil. In consequence, the availability of different compounds in the soil may be altered which could to a variation in root exudate composition (Compant et al. 2010), in addition elevated temperature and drought may also effect exudates. This could affect the concentration or composition of flavonoids and other signalling compounds which may alter the symbiosis formation process and alter MN structure (Brunner et al. 2015). Furthermore, nitrate is known to reduce EMF growth, therefore elevated nitrate levels could significantly alter MN structure and viability (Bahr et al. 2013).

It is clear that integration within a MN enhances seedling survival and forest regeneration capacity (Teste et al. 2009), drought survival (Brunner et al. 2015) and increasing ecosystem resilience through defense signal transfer (Pozo et al. 2015). Therefore, collectively MNs could enhance ecosystem resilience in response to challenging conditions, however if boundaries are pushed too far by human pressures it is possible that the mechanism of symbiosis establishment and maintenance may not be able to cope. Climate change mediated disruption in the function

of central signalling compounds such as SA and JA (Gray & Brady 2016) and changed patterns of root exudates and fungal survival due to chemical deposition within the soil (Bahr et al. 2013) causes interrupted communication within the ecosystem, and thus is likely to weaken ecosystem resilience.

4.2 Climate change and plant volatiles

The plant species, and the genre of stress inducer as well as physical conditions such as water and nutrient status and atmospheric gas composition all effect VOC production (Tanaka et al. 2014). Potentially plant fertility, biotic and abiotic stress tolerance and herbivore predator success could be effected by disrupted plant volatile emissions (DeLucia et al. 2012). Anthropogenic deposition of chemicals such as nitrate and phosphate, and air pollution can cause a significant change in plant VOC composition; in the case of the terpene synthase gene family, minimal changes in residue availability can lead to the production of new compound
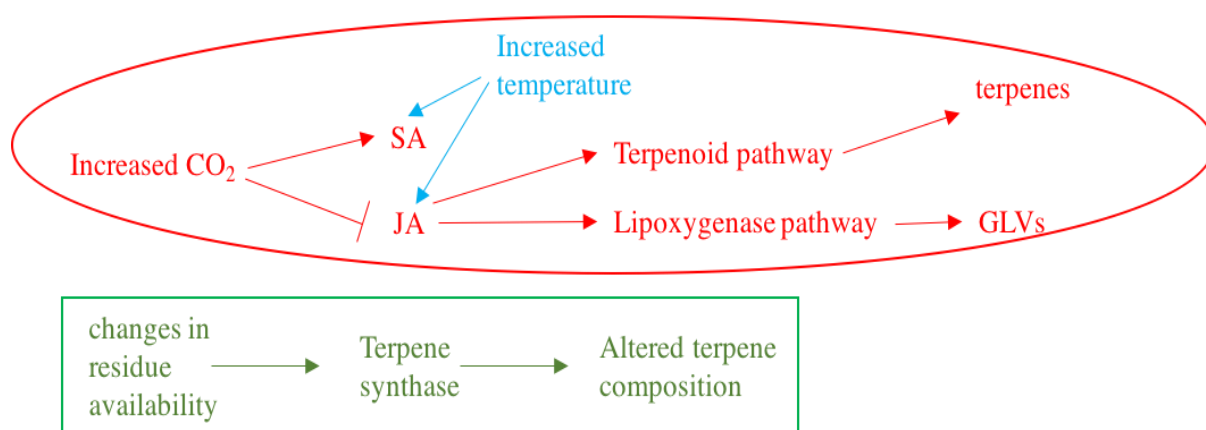

Figure 18: The effects of increased carbon dioxide (red), temperature (blue) on jasmonic and salicylic acid signalling pathways, including the downstream effects on volatile compound synthesis (in the red circle). Changes in environmental biochemical residue availability and effects on terpene synthesis are displayed in the green square. Figure based on the review from DeLucia (2012).

sequences (Yuan et al. 2009). Ozone (O_3) degrades some classes of VOCs including terpenoids and green leaf volatiles (GLVs) (Šimpraga et al. 2016). If plant volatile-sensing species within ecosystems cannot evolve quickly enough to react to new compositions and concentrations volatile signals, then ecosystem function could be seriously disrupted.

Climate change also has a more indirect effect on plant volatiles, by altering central signalling pathways which mediate defense pathways and volatile synthesis. It was found that elevated CO_2 levels suppress synthesis of jasmonic acid (JA) while stimulating the synthesis of salicylic acid (SA) (figure 18) (Gray & Brady 2016; Guo et al. 2012). These changes could potentially increase susceptibility to chewing insects and necrotrophic pathogens by weakening the JA branch of biotic defense, and enhance resistance to biotrophic pathogens and phloem drinking insects by strengthening SA-associated biotic defense. In accordance with this, increased susceptibility of soybean to Japanese beetle and corn rootworm due to down regulated JA and ET was found in conditions of elevated carbon dioxide (Zavala et al. 2008). However, an increased production of antioxidants in soybeans was also reported under conditions of elevated carbon dioxide, indicating an enhanced oxidative stress tolerance which could be caused by enhanced SA signalling, which is known to play a role in oxidative stress resistance (Shiow Y. Wang et al. 2003; Gillespie et al. 2012; Belkadhi et al. 2014).
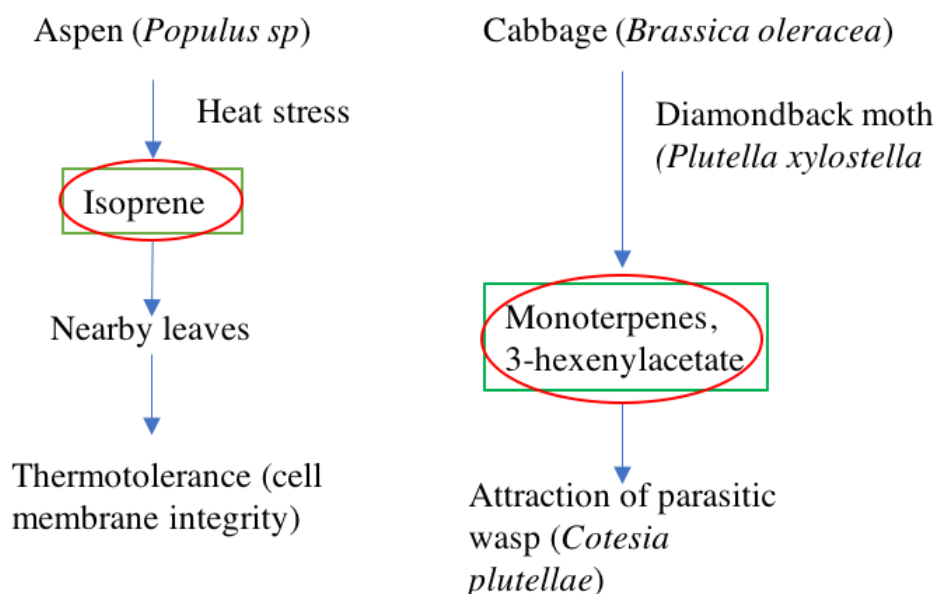
Figure 19: The defense response to heat stress in aspen and moth attack of brassica. The red circle and green box indicate that elevated carbon dioxide and changed residue availability could alter the production of volatiles (see figure 18) (Sharkey et al. 2001; Vuorinen et al. 2004).

It has been shown that a rise in CO_2 can result in minor changes in certain VOC concentrations, probably due to disruption of the volatile synthesis pathways, these changes are generally very small but nevertheless have significant effects when they enable interactions at higher trophic levels in the ecosystem. In *Brassica oleracea*, small changes in volatile signal emissions are amplified at higher trophic levels, it was found that only a minor reduction in VOC emissions fail to attract the enemies of the herbivorous diamondback moth (figure 18) (Vuorinen et al. 2004). This shows that altered climatic conditions could result in an ineffective defense response, and potentially disrupt ecosystem structure due to altered plant volatile emission.

The evergreen oak *quercus ilex* produces lower levels of monoterpenes under higher CO_2 conditions, however in the same species another terpene, limonene was produced in elevated quantities due to enhanced limonene synthase activity (Loreto et al. 2001). Terpenes constitute over 90% of the total VOC emissions in many plant species, and changes in resource

availability indicate altered signal composition and therefore altered ecological interactions (Köllner et al. 2004). A reduction in heat stress terpenoids such as monoterpenes and isoprene could result in compromised heat stress tolerance, in Aspen isoprene is important for increased cell membrane integrity and therefore thermotolerance of leaves under heat stress (figure 19) (Sharkey et al. 2001). This is especially relevant under climate change associated conditions of elevated temperature.

Increased temperature was found to stimulate jasmonic acid, ethylene and salicylic acid production (figure 18) (DeLucia et al. 2012) which indicates that the plant defense response may be effected, but does not give a clear picture. It is possible that this effect would counteract the higher susceptibility of plants to herbivore attack caused by CO_2 alone, due to the effect of ethylene in reducing SA antagonism of JA, however it seems likely that if carbon dioxide levels rise high enough to effect SA and JA there will be significant consequences on the plant defense system and ecosystem resilience (Niziolek 2012, (DeLucia et al. 2012). Table 5 illustrates the general trends found in conditions of elevated temperature, ozone and CO_2 on plant signalling.

Table 5: Trends in effects of climate change related impacts on plant volatiles, data taken from referenced papers.

Elevated CO_2	Induces salicylic acid and reduces jasmonic acid signalling (Yuan et al. 2009; DeLucia et al. 2012).
	Increases antioxidant accumulation (Shiow Y. Wang et al. 2003; Gillespie et al. 2012).
Higher temperature	Increased jasmonic acid, ethylene and salicylic acid signalling (Gray & Brady 2016; DeLucia et al. 2012).

	Higher volatile synthesis and volatility (DeLucia et al. 2012).
Higher ozone	Volatile degradation (Peñuelas & Staudt 2010).

In general, it is unclear how the defense response could be altered in a changed climate, it is very difficult to predict how far anthropogenic pressures could alter environmental conditions, and it is equally difficult to control experimental conditions to mimic the natural forest ecosystem. However, although the findings so far are unclear as the exact effects of climate change conditions on plant volatile release, from the evidence it appears that volatile signal composition and production are indeed effected by elevated carbon dioxide, temperature and ozone, and could significantly impact plant defense pathways and ecosystem resilience.

In summary, the disruption of molecular signalling-mediated ecosystem interactions has important implications for ecosystem functionality (figure 20). Volatile compounds can be altered in their composition and concentration due to ozone degradation, disturbed soil chemical composition and the impact of altered SA and JA signalling on volatile synthesis. This results in the disruption of defense related plant-insect and plant-plant interactions. The mycorrhizal network can also be affected by altered SA and JA signalling, as JA appears to play a key role in transmitting defense signals via the MN, and both signalling pathways are involved in plant-fungi interactions. Chemical deposition, drought and temperature can affect the viability of mycorrhizal fungi and could lead to significant changes in mycorrhizal network structure and therefore function. Furthermore, the presence of multiple stressors can
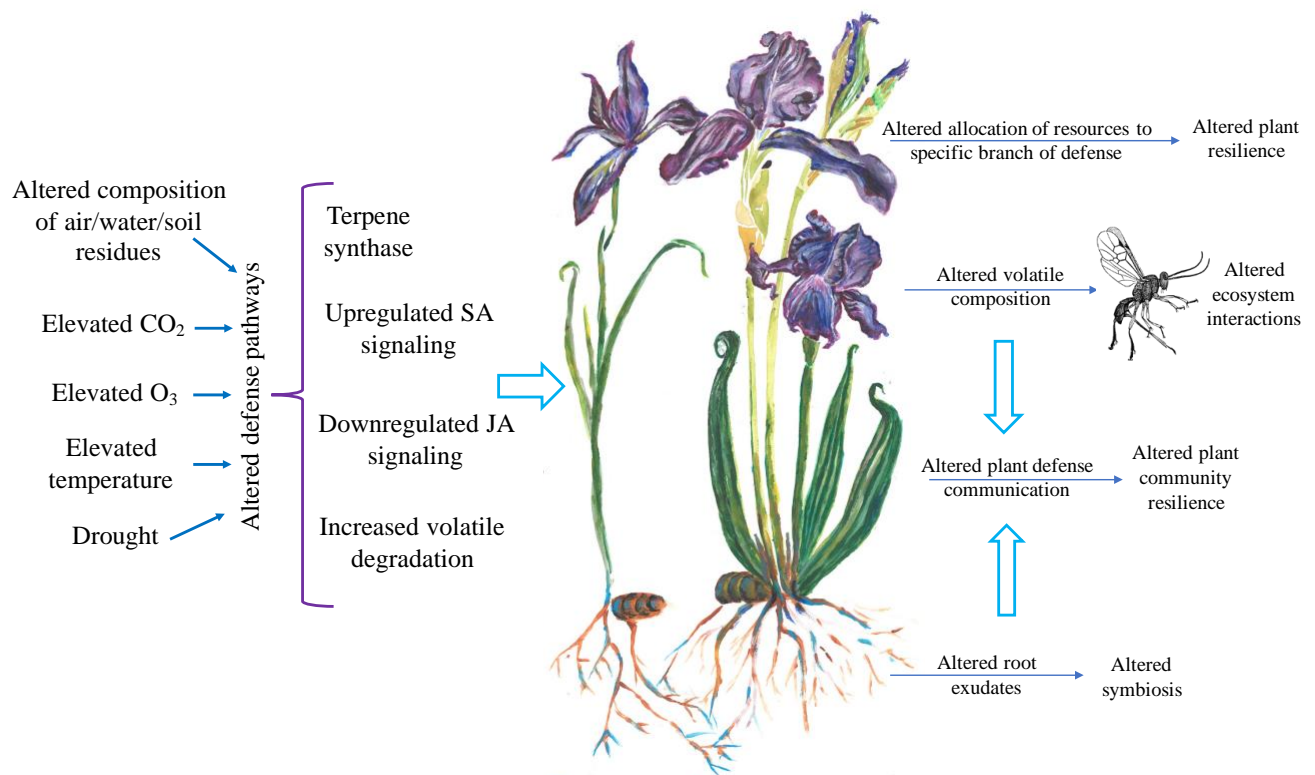
Figure 20: Overall implications for plant community defense due climate change impacts. The column furthest to the left represents the effects of climate change, the next column represents the molecular pathways disturbed, the right-hand column represents the resulting impacts on plant defense and ecosystem function ((Yuan et al. 2009; Compant et al. 2010; Gray & Brady 2016).

cause trade-offs between different branches of defense which could lead to a compromised biotic stress response in plants under long-term heat or drought stress (Balderas-Hernandez et al. 2013). Collectively this demonstrates that the effects of climate change can disturb plant molecular pathways with the consequence that plant defense signalling could become defective.

Conclusion

In conclusion, the evidence reviewed here indicates that the molecular pathways enabling plant-plant and plant-insect defense signalling and systemic plant defense could be seriously affected by climate change. The defense signalling pathways within plants are highly

sophisticated, and extend into the surrounding environment, allowing plants to communicate with different entities within an ecosystem very rapidly and using a molecular language which can be understood by other species of plant and insects. The evidence reviewed here shows that effects of climate change, such as the soil contamination, elevated carbon dioxide, elevated ozone. More extreme temperatures, and drought can disrupt defense related plant molecular signalling pathways (figure 20). This means that the ability for different entities within an ecosystem to communicate could be lost and if environmental conditions are pushed too far and too fast by anthropogenic pressure then there could be a severe loss in plant community resilience and ecosystem functionality.

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