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Salicylic Acid-Centred Defence Signalling and Hormonal Crosstalk under Natural Farming Systems: Mechanisms of Disease and Insect Suppression

Chena Panchal [a++], K. V. Chaudhary [a#], Y. A. Tamboli [b#*], B. L. Raghunadan [a†] and G. D. Vadodariya [a‡]

[a] *Gujarat Natural Farming Science University, Halol, Gujarat, India.*
[b] *School of Agricultural Sciences, Jaipur National University, Jaipur, Rajasthan, India.*

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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Abstract

Salicylic acid (SA) occupies a central and integrative role in plant immunity, mediating systemic acquired resistance against biotrophic and hemibiotrophic pathogens whilst engaging in extensive crosstalk with jasmonic acid, ethylene, and abscisic acid signalling pathways. Under natural farming systems — encompassing organic cultivation, agroecological management, and related low-input approaches — the chemical milieu and microbial architecture of the rhizosphere undergo substantial restructuring in ways that carry consequential effects on plant hormone physiology and defence capacity. This review critically examines the molecular basis of SA biosynthesis, receptor-mediated signal perception, and systemic

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[++] *Assistant Research Scientist;* [#] *Assistant Professor;* [†] *Director of Research;* [‡] *Associate Professor;*
**Corresponding author: E-mail: yasirtamboli786@gmail.com;*

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immunity, with particular attention to the antagonism between SA and jasmonic acid signalling that fundamentally shapes how plants allocate defensive resources between biotrophic pathogens and insect herbivores. The roles of beneficial rhizosphere microorganisms enriched under natural farming — including plant growth-promoting rhizobacteria, arbuscular mycorrhizal fungi, and biocontrol agents such as *Trichoderma* and *Bacillus* species — in priming SA-mediated and induced systemic resistance pathways are evaluated. The significance of organic soil amendments, including composts and vermicomposts, in modulating endogenous SA concentrations and influencing defence gene expression is also examined. Particular attention is given to the trade-offs inherent in SA–jasmonic acid hormonal antagonism, which may affect resistance to chewing herbivores in agroecosystems. The review concludes that natural farming systems, through their enhancement of rhizosphere microbial diversity and activity, create conditions broadly conducive to plant defence priming, though further field-based molecular studies are needed to translate these insights into durable management strategies.

Keywords: Salicylic acid; systemic acquired resistance; jasmonic acid; induced systemic resistance; hormonal crosstalk; natural farming; rhizosphere microbiome; defence priming; plant immunity; organic agriculture.

1. Introduction

1.1 Natural Farming Systems and Plant Protection

Growing concern about the environmental consequences of synthetic pesticide use — including disruption of soil microbiomes, surface water contamination, the development of resistance in target organisms, and adverse effects on non-target arthropods and pollinators — has intensified scientific and policy interest in alternative approaches to crop protection (Reganold & Wachter, 2016). Natural farming systems, a term covering organic agriculture, agroecological cultivation, and related low-input approaches that forgo synthetic chemical inputs, represent one prominent suite of alternatives. These systems depend fundamentally on ecological processes: the harnessing of soil biodiversity, biological control, and the intrinsic disease and pest resistance capacities of cultivated plants themselves (Lori et al., 2017). Understanding the molecular mechanisms by which such systems might enhance or modulate those capacities has therefore become a central question at the interface of plant biology and sustainable agronomy.

Plants have evolved an extraordinarily sophisticated immune system that operates without specialised immune cells, relying instead on hormone-mediated signalling networks distributed throughout the organism (Spoel & Dong, 2012). Among the phytohormones constituting this system, salicylic acid holds a particularly prominent position. First recognised as an endogenous plant signal following pathogen challenge in the late twentieth century, SA is now established as the principal mediator of systemic acquired resistance — a durable, broad-spectrum resistance state that develops after local infection and confers protection on systemically uninfected tissues against subsequent pathogen attack (Fu & Dong, 2013). The signal transduction machinery through which SA operates, from its perception by receptor proteins to the activation of hundreds of defence-related genes, has been elucidated in considerable mechanistic detail, primarily in *Arabidopsis thaliana* but increasingly in crop species as well (Peng et al., 2021).

Comparatively less attention has been paid to how the agronomic management regime under which plants grow influences the functional state of their SA-centred immunity. This is not a trivial question. The rhizosphere microbiome — arguably the primary ecological variable distinguishing naturally managed from conventionally managed soils — is a major determinant of plant hormonal tone and immune status (Berendsen et al., 2012). Plant growth-promoting rhizobacteria and beneficial fungi commonly enriched in organically managed soils can activate induced systemic resistance, a form of primed immunity that, whilst mechanistically distinct from classical systemic acquired resistance, converges on many of the same defensive outputs and in some instances potentiates SA-dependent pathways (Pieterse et al., 2014). The application of organic amendments introduces additional complex biological and biochemical signals into the rhizosphere that may influence plant hormone biology in ways not yet fully characterised. More recent field-scale evidence has also linked organic management with greater rhizosphere microbial network connectivity and fewer putative fungal pathogens, reinforcing the relevance of microbiome-mediated disease suppression in naturally managed agroecosystems (Dasgupta & Banerjee, 2025).

1.2 Salicylic Acid in the Context of Hormonal Defence Networks

Salicylic acid does not act in isolation. Plant defence is orchestrated through a network of phytohormones whose signals are integrated — sometimes synergistically, often antagonistically — to produce pathway-specific responses calibrated to the nature of the attacking organism (Glazebrook, 2005). Jasmonic acid and its bioactive conjugate jasmonoyl-isoleucine mediate resistance to necrotrophic pathogens and chewing herbivores, whereas SA is primarily effective against biotrophic and hemibiotrophic pathogens (Thaler et al., 2012). The antagonism between SA and JA signalling — in which elevated SA generally suppresses JA-responsive gene expression and vice versa — means that plants cannot simultaneously activate both pathways at full capacity, creating trade-offs that attackers may exploit and that agricultural management may inadvertently shift (Caarls et al., 2015). Ethylene modulates both SA and JA responses in a context-dependent manner, whilst abscisic acid can suppress SA-based immunity under abiotic stress conditions — a relationship of practical significance in naturally managed systems where water stress is managed differently and where abiotic and biotic defence signals frequently overlap (Broekgaarden et al., 2015; Vlot et al., 2009). Recent synthesis further emphasises that SA and JA form central, interacting nodes in plant immunity, with SA most closely associated with local and systemic resistance to biotrophic and hemibiotrophic pathogens and JA with responses to necrotrophs, herbivores, and wounding (Zhang et al., 2025).

Understanding how natural farming practices alter the state of these interconnected networks matters not merely for academic phytohormone biology but for the practical management of disease and pest pressure in agroecosystems that increasingly operate without synthetic chemistry. Despite this conceptual convergence, a clearly defined gap remains in connecting natural farming-induced rhizosphere changes with specific SA-centred signalling outcomes and their consequences for simultaneous disease and insect suppression under field-relevant conditions.

1.3 Scope and Objectives

This review critically examines current knowledge on SA biosynthesis, perception, and systemic signalling, the hormonal crosstalk that modifies SA-dependent immunity, and the influence of natural farming practices — including soil microbial enrichment, organic amendment application, and the exclusion of synthetic pesticides — on the operation of these mechanisms in relation to disease and insect suppression. Evidence is considered at multiple scales, from molecular signal transduction in model organisms through to observations in organically managed agroecosystems. The review identifies key mechanistic questions that remain unresolved and discusses the implications of current knowledge for the rational design of crop protection strategies within natural farming frameworks.

2. Methods for Literature Selection

The literature underpinning this review was identified through searches conducted across eight databases: Web of Science (Core Collection), Scopus, Google Scholar, PubMed, CAB Abstracts, AGRICOLA, BIOSIS Previews, and AGRIS. Field-specific indexing services including Biological Abstracts and the USDA National Agricultural Library's PubAg platform were also consulted to ensure comprehensive coverage of both fundamental plant biology and applied agronomic literature.

The primary search period extended from January 2012 to February 2026. The year 2012 was selected as the start date because it marks a period of major mechanistic convergence — encompassing the identification of NPR3 and NPR4 as SA receptors (Fu et al., 2012), landmark studies on rhizosphere microbiome–plant immunity interactions (Berendsen et al., 2012; Zamioudis & Pieterse, 2012), and formative work on phytohormone dynamics during herbivory (Erb et al., 2012; Thaler et al., 2012). Classic references predating this period were identified through forward and backward citation tracking of key review articles and included where they provided foundational mechanistic context on which more recent studies build. The end date of February 2026 falls 45 days before the date of finalisation, consistent with standard practice for currency verification.

Search strings were constructed around four thematic clusters. The first addressed SA biosynthesis and signalling, using terms such as "salicylic acid signalling," "systemic acquired resistance," "NPR1," "isochorismate synthase," and "N-hydroxypipecolic acid." The second covered hormonal crosstalk, with terms including "SA-JA crosstalk," "jasmonic acid antagonism," "phytohormone interaction," and "defence signalling network." The third addressed rhizosphere ecology and natural farming, using terms such as "plant growth-promoting rhizobacteria," "induced systemic resistance," "organic farming soil microbiome," "natural farming plant defence," and "compost-induced resistance." The fourth covered insect suppression and priming, using terms such as "herbivory resistance," "defence priming mechanisms," "organic agriculture insect management," and "volatile-mediated resistance."

Searches were restricted to English-language peer-reviewed journal publications. Books, grey literature, conference proceedings, trade publications, pre-prints, and patents were excluded throughout. Duplicate records arising from multi-database searches were removed through comparison of DOI strings and titles. Studies were selected on the basis of mechanistic relevance, methodological rigour, and representativeness of key findings within each thematic area. Review articles were included where they provided authoritative synthesis of primary evidence. A narrative rather than systematic methodology was adopted, which is appropriate for a multidisciplinary topic integrating molecular genetics, soil ecology, and agroecology in ways that resist uniform quantitative treatment across the full scope of questions addressed (Snyder, 2019).

3. Salicylic Acid: Biosynthesis, Accumulation, and Molecular Perception

3.1 Biosynthetic Pathways and Their Regulation

Salicylic acid is a small phenolic compound biosynthesised in plants through two principal routes: the isochorismate (IC) pathway and the phenylalanine ammonia-lyase (PAL) pathway (Vlot et al., 2009). In *Arabidopsis thaliana*, the IC pathway dominates under pathogen attack, contributing the large majority of SA produced during immune activation, whilst the PAL pathway plays a smaller but non-negligible role, particularly under basal and wound-stress conditions (Peng et al., 2021). The enzyme ISOCHORISMATE SYNTHASE 1 (ICS1), localised to the chloroplast stroma, catalyses the conversion of chorismate to isochorismate — the committed step in pathogen-induced SA biosynthesis (Wildermuth et al., 2001). For many years, the downstream enzymatic steps converting isochorismate to SA itself remained unresolved, representing a conspicuous gap in the biosynthetic roadmap.

Two studies published in 2019 substantially filled this gap. Rekhter et al. (2019) demonstrated that the cytosolic enzyme PBS3 (AVRPPHB SUSCEPTIBILITY 3), together with EPS1 (ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1), catalyses the conversion of isochorismate to SA via an isochorismate-9-glutamate intermediate, completing the pathway from chorismate to the bioactive hormone. Independently, Torrens-Spence et al. (2019) confirmed that PBS3 functions as an isochorismate-glutamate ligase and that EPS1 acts downstream to complete SA production. These findings resolved a long-standing mechanistic gap and opened new avenues for investigating how environmental signals — including those originating from the rhizosphere microbiome — might modulate specific enzymatic nodes in the SA biosynthetic pathway. SA is further subject to diverse metabolic modifications, including conjugation to glucose producing inactive storage forms, and methylation by SABATH methyltransferases to yield methyl salicylate (MeSA), a volatile and phloem-mobile derivative with important signalling functions (Park et al., 2007).

The PAL pathway proceeds through phenylalanine, trans-cinnamic acid, and benzoic acid intermediates, and its relative contribution varies across species, developmental stages, and stress contexts. Under the elevated soil organic matter conditions characteristic of naturally managed soils, altered nitrogen and carbon cycling may influence phenylalanine availability as a PAL substrate — with possible downstream consequences for PAL-derived SA accumulation in field-grown crops — though this connection has not been systematically investigated and represents a tractable open question for natural farming research.

3.2 Salicylic Acid Receptors and Downstream Signal Transduction

The identification of bona fide SA receptors was a landmark achievement in plant immunity research, clarifying how SA concentration information is converted into transcriptional output. NPR1 (NON-EXPRESSOR OF PR GENES 1) had long been recognised as a master co-regulator of SA-responsive gene expression, but its status as a direct SA receptor remained uncertain. Fu et al. (2012) provided compelling evidence that the related proteins NPR3 and NPR4, previously characterised as transcriptional repressors of defence genes, bind SA with measurable affinity and that this binding modulates their repressive capacity. A more integrated model was subsequently advanced by Ding et al. (2018), who demonstrated that NPR1 and NPR3/NPR4 play opposing roles as SA receptors: NPR1 functions as a transcriptional co-activator of SA-responsive defence genes that is stabilised and activated by SA, whilst NPR3 and NPR4 act as transcriptional repressors at low SA concentrations. The accumulation of SA following pathogen recognition effectively shifts the balance from repression to activation across this three-way receptor system, creating a finely tuned response scaled to pathogen intensity. The broader significance of this receptor architecture — how it generates a sensitive and dynamic SA response spectrum calibrated to pathogen identity and infection severity — was critically reviewed by Ding & Ding (2020).

NPR1 exerts its co-activating function primarily by interacting with TGA family bZIP transcription factors in the nucleus, facilitating expression of pathogenesis-related (PR) genes including PR-1, PR-2, and PR-5, whose protein products contribute antimicrobial activity (van Loon et al., 2006). Regulation of NPR1 through nucleo-cytoplasmic shuttling adds further complexity: under basal conditions, NPR1 is sequestered in the cytoplasm as an oligomeric complex held together by intermolecular disulphide bonds; upon SA accumulation and consequent cellular redox change, the oligomers are reduced to active monomers that translocate to the nucleus (Klessig et al., 2018). This redox-dependent mechanism positions NPR1 as an integrative sensor of both SA concentration and cellular redox state — the latter itself being influenced by the reactive oxygen species burst generated during pathogen recognition (Herrera-Vásquez et al., 2015).

WRKY transcription factors constitute a major additional layer of transcriptional control in SA-dependent immunity, with different family members serving as positive activators, negative regulators, or signal amplifiers at different stages of the immune response (Birkenbihl et al., 2017). The combinatorial flexibility conferred by WRKY factor interactions with SA-responsive promoters helps explain how a single hormone can orchestrate highly nuanced transcriptional programmes adapted to diverse pathogen types. Beyond transcription, SA-triggered immune activation also involves global reprogramming of translation that is distinct from basal transcript-level changes (Spoel & Dong, 2012).

Plant immune recognition operates through two overlapping tiers. Pattern-triggered immunity (PTI) is initiated by extracellular receptor-like kinases and receptor-like proteins that recognise conserved pathogen-associated molecular patterns, whilst effector-triggered immunity (ETI) is activated by intracellular NLR proteins upon detection of pathogen effectors (Jones & Dangl, 2006). The previously sharp conceptual boundary between these tiers was substantially eroded by Ngou et al. (2021), who demonstrated that PTI and ETI mutually potentiate each other through convergent signalling interactions that include SA accumulation — establishing SA-centred signalling as integral to both tiers of immune activation, not merely to ETI as earlier models implied.

3.3 Systemic Acquired Resistance and Long-Distance Signalling

Upon local infection, a signal must traverse the plant to establish protection in distal, uninfected tissues — the defining property of systemic acquired resistance. The identity of the mobile signal responsible for this systemic communication has been the subject of intensive investigation and considerable debate (Klessig et al., 2018). Park et al. (2007) demonstrated that MeSA, produced at the infection site by SA methyltransferases and transported through the phloem, is perceived in distant tissues where it is converted back to biologically active SA by salicylate-binding protein 2. Subsequent studies showed that MeSA is not universally required across all species or infection contexts, pointing to the existence of additional parallel signals (Durrant & Dong, 2004).

A particularly significant conceptual advance was the discovery of N-hydroxypipecolic acid (NHP) as a critical mobile signal for SAR. Hartmann et al. (2018) showed that NHP is synthesised from the amino acid lysine through a two-step enzymatic pathway involving ALD1 and the flavin monooxygenase FMO1, accumulates systemically following infection, and is alone sufficient to confer a primed resistance state. Independently, Chen et al. (2018) demonstrated that NHP is exported from infected leaves into the phloem, travels to systemic tissues, and there primes defence gene expression in a manner that amplifies SA-dependent responses. These parallel discoveries substantially expanded the molecular picture of SAR beyond SA itself, though SA accumulation remains indispensable for the full activation of systemic defence gene expression programmes (Fu & Dong, 2013). The discovery of NHP is particularly relevant for natural farming research: several rhizosphere microbial communities enriched under organic management are known to trigger amino acid-derived signalling cascades in plants, raising the possibility of intersection with the lysine-to-NHP conversion pathway — though direct evidence for this in natural farming contexts remains to be established.

Table 1 summarises the key molecular components of SA biosynthesis, perception, and systemic signalling discussed in this section.

Table 1. Key Molecular Components of the Salicylic Acid Signalling Pathway in Plants

Component	Function	Subcellular Location	Representative Reference
ICS1	Converts chorismate to isochorismate; primary SA biosynthetic enzyme under pathogen challenge	Chloroplast stroma	Wildermuth et al. (2001)
PBS3	Isochorismate-glutamate ligase; downstream IC pathway step	Cytoplasm	Rekhter et al. (2019); Torrens-Spence et al. (2019)
EPS1	Completes isochorismate-9-glutamate to SA conversion	Cytoplasm	Rekhter et al. (2019)
PAL pathway	Alternative SA biosynthesis via phenylalanine and benzoic acid	Cytoplasm	Peng et al. (2021)
NPR1	Master co-activator of SA-responsive gene expression; SA receptor at activating concentrations	Nucleus/Cytoplasm	Ding et al. (2018)
NPR3/NPR4	Transcriptional repressors; SA receptors mediating gene repression at low SA concentrations	Nucleus	Fu et al. (2012); Ding & Ding (2020)
TGA factors	bZIP transcription factors; interact with NPR1 to activate PR genes	Nucleus	van Loon et al. (2006)
WRKY transcription factors	Positive and negative transcriptional regulators in SA-dependent immunity	Nucleus	Birkenbihl et al. (2017)
MeSA	Volatile/phloem-mobile SA derivative; long-distance SAR signal	Phloem/volatile	Park et al. (2007)
N-hydroxypipecolic acid (NHP)	Lysine-derived mobile SAR signal; primes systemic immunity	Phloem-mobile	Hartmann et al. (2018); Chen et al. (2018)

Sources: Wildermuth et al. (2001); Rekhter et al. (2019); Torrens-Spence et al. (2019); Peng et al. (2021); Ding et al. (2018); Fu et al. (2012); Ding & Ding (2020); van Loon et al. (2006); Birkenbihl et al. (2017); Park et al. (2007); Hartmann et al. (2018); Chen et al. (2018)

4. Hormonal Crosstalk: SA, Jasmonic Acid, Ethylene, and Abscisic Acid

4.1 The SA–Jasmonic Acid Antagonism: Molecular Architecture

The antagonism between SA and jasmonic acid is one of the most ecologically consequential regulatory interactions in plant immunity — a trade-off that profoundly shapes how plants allocate defence resources between different classes of attacking organisms. JA and its bioactive conjugate JA-Ile are primarily effective against necrotrophic pathogens and chewing herbivores, whilst SA is effective against biotrophs and hemibiotrophs. The negative interaction between these pathways means that activating either one comes at some cost to resistance mediated by the other (Glazebrook, 2005; Thaler et al., 2012). The mechanistic underpinnings of this antagonism have been substantially elucidated in *Arabidopsis*.

At the molecular level, SA suppresses JA signalling through several converging mechanisms. Spoel et al. (2003) provided important early evidence that cytosolic NPR1 mediates SA-dependent suppression of JA-responsive gene expression, revealing a role for the SA co-regulator that is distinct from its nuclear function in PR gene activation. Subsequent work has identified multiple downstream mechanisms through which this antagonism operates, including SA-driven attenuation of JA biosynthesis and JA-Ile conjugation, as well as transcriptional interference at JA-responsive promoters (Caarls et al., 2015). The WRKY factor WRKY70, induced by SA and suppressed by JA, acts as a point of crosstalk that simultaneously upregulates SA-responsive PR genes and represses JA-responsive defence genes (Li et al., 2008). MPK4 (MITOGEN-ACTIVATED PROTEIN

KINASE 4) constitutes another regulatory node: its inactivation leads to constitutive SA signalling with attendant suppression of JA responses (Brodersen et al., 2006). More recently, Gimenez-Ibanez et al. (2017) demonstrated that JAZ proteins can interact with components of the SA signalling network in a manner that inhibits SA-responsive gene activation, revealing a reciprocal dimension to the antagonism — the architecture of SA–JA cross-suppression thus operates in both directions.

The JA signalling pathway is centrally regulated through JASMONATE ZIM-DOMAIN (JAZ) repressor proteins. Upon JA-Ile perception, JAZ proteins are ubiquitinated via the SCF^COI1 complex and degraded by the 26S proteasome, releasing repression of MYC2 and related transcription factors that drive JA-responsive gene expression (Pieterse et al., 2014). MYC2 can in turn suppress SA pathway gene expression as part of its transcriptional programme, creating a bidirectional antagonism at the level of master regulatory transcription factors. Consistent with this, studies in both tomato and *Arabidopsis* have confirmed that activating JA responses — for example by herbivore feeding — is frequently accompanied by downregulation of SA-associated PR genes (Thaler et al., 2012).

4.2 Crosstalk with Ethylene and Abscisic Acid

Ethylene intersects with both SA and JA pathways in a context-dependent manner, often acting synergistically with JA. Ethylene signalling, through the EIN3 and EIL1 transcription factors, can cooperate with MYC2 to amplify JA-responsive gene expression, particularly in responses to necrotrophic pathogens (Lorenzo et al., 2003). In the context of induced systemic resistance triggered by certain plant growth-promoting rhizobacteria, ethylene is a primary signalling hormone, and the ISR pathway depends on functional ethylene signalling in the host plant (Pieterse et al., 2014). Ethylene can also modulate SA responses in a concentration-dependent manner, enhancing SA-related PR-1 gene expression at low concentrations whilst potentially suppressing SA-dependent immunity at higher concentrations (Broekgaarden et al., 2015).

Abscisic acid occupies a particularly complex position in the hormonal crosstalk network. Under water deficit stress — commonly encountered in naturally managed systems without irrigation — ABA accumulation can suppress SA-mediated defence responses at multiple levels, including downregulation of ICS1 expression and interference with NPR1 activity (Yasuda et al., 2008). Moderate ABA concentrations may simultaneously promote callose deposition at plasmodesmata, which can restrict pathogen spread even when SA signalling is partially suppressed, creating a nuanced picture in which ABA is not simply a negative regulator of immunity (Mur et al., 2008). This interaction is further complicated by the fact that many beneficial rhizosphere microorganisms can modulate ABA sensitivity in host plants, potentially altering the outcome of SA–ABA crosstalk under field conditions.

Auxin represents an additional modulator of SA immunity, largely through negative regulation of SA signalling and promotion of bacterial virulence accommodation. Several phytopathogenic bacteria deploy auxin-mimic effectors to suppress SA-based immunity, and SA has been shown to suppress auxin signalling through stabilisation of the AXR2/IAA7 and AXR3/IAA17 repressors in *Arabidopsis* (Wang et al., 2007). Under natural farming conditions, elevated auxin production by rhizosphere microorganisms — a well-established plant growth-promoting mechanism — may have secondary effects on SA-mediated resistance that deserve closer attention, though current field evidence remains limited.

4.3 Ecological Consequences of Hormonal Crosstalk in Agroecosystems

From a crop protection standpoint, the most practically significant consequence of SA–JA antagonism is the possibility that conditions favouring elevated SA-mediated disease resistance might simultaneously reduce resistance to herbivorous insects, particularly chewing species whose management depends on JA-responsive defences (Thaler et al., 2012). This concern is not merely theoretical. Crops with elevated SA responses — whether through constitutive signalling mutations, elicitor treatment, or certain biological control interventions — have shown reduced volatile-mediated indirect defence and reduced accumulation of JA-responsive glucosinolates or protease inhibitors (Caarls et al., 2015). In naturally managed systems, where the absence of synthetic insecticides increases reliance on plant-intrinsic defences against herbivores, understanding how agricultural practices shift the SA–JA balance becomes especially pressing.

That said, the antagonism is not absolute. Certain hemibiotrophic pathogens initially trigger SA responses before shifting to necrotrophic infection strategies that induce JA, generating a temporally dynamic hormonal sequence rather than a fixed opposition (Glazebrook, 2005). Some beneficial microorganisms, including specific *Trichoderma* strains, can simultaneously prime both SA and JA pathways — a property of particular practical value in natural farming contexts where both disease and insect pressure require simultaneous management (Hermosa et al., 2012).

Table 2 summarises the key crosstalk interactions between SA and other phytohormones relevant to plant defence.

Table 2. Hormonal Crosstalk Interactions in Plant Defence Signalling

Hormone Pair	Direction of Interaction	Key Molecular Mediators	Primary Defence Target	Representative Reference
SA ↔ JA	Mutual antagonism	NPR1, WRKY70, JAZ proteins, MYC2	SA→biotrophs; JA→necrotrophs/herbivores	Caarls et al. (2015); Thaler et al. (2012)
SA ↔ ET	Context-dependent synergy/antagonism	EIN3, EIL1, NPR1	ET potentiates JA; modulates SA	Broekgaarden et al. (2015)
SA ↔ ABA	ABA generally suppresses SA	ICS1, NPR1 activity	ABA suppresses biotroph resistance	Yasuda et al. (2008)
JA ↔ ET	Synergistic (necrotrophs)	MYC2, EIN3, EIL1	Necrotrophic pathogens, insects	Lorenzo et al. (2003)
SA ↔ Auxin	Reciprocal suppression	AXR2/IAA7, AXR3/IAA17	Suppression of pathogen accommodation	Wang et al. (2007)

Sources: Caarls et al. (2015); Thaler et al. (2012); Broekgaarden et al. (2015); Yasuda et al. (2008); Lorenzo et al. (2003); Wang et al. (2007)

5. Rhizosphere Microbial Communities Under Natural Farming and Their Role in SA-Mediated Immunity

5.1 Microbial Enrichment Under Natural Farming Conditions

One of the most consistently replicated findings in comparative soil microbiology is that organic and natural farming systems support substantially greater microbial biomass, functional diversity, and taxonomic richness in the rhizosphere compared with conventionally managed soils receiving synthetic chemical inputs (Lori et al., 2017). Analyses using high-throughput 16S rRNA amplicon sequencing and shotgun metagenomics have demonstrated that organically managed soils are enriched in several bacterial phyla — particularly *Actinobacteria*, *Firmicutes*, and certain lineages within *Proteobacteria* — and in arbuscular mycorrhizal fungal taxa (Hartmann et al., 2015; Lori et al., 2017). This restructuring reflects both the removal of pesticide-associated microbiome disruption and the positive effects of organic amendments on the physical and nutritional quality of the soil habitat. It is also worth noting that the composition of rhizosphere microbial communities is itself partly shaped by plant signals and root exudates, meaning crop plants actively recruit specific microorganisms from the surrounding bulk soil — a phenomenon with important implications for how farming history propagates through microbial community assembly (Hartmann et al., 2009).

The plant growth-promoting rhizobacteria enriched in naturally managed soils include well-characterised genera such as *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Azospirillum*, *Rhizobium*, and *Streptomyces*, many of which independently demonstrate capacity to prime plant immunity through induced systemic resistance (Pieterse et al., 2014; Schlaeppi & Bulgarelli, 2015). The functional significance of rhizosphere microbial diversity for plant immunity goes beyond the effects of individual taxa, however. Emerging evidence suggests that the compositional structure and ecological connectivity of the rhizosphere community influence plant defence priming through microbiome-level interactions that cannot be reduced to the effects of single species (Berendsen et al., 2012; Durán et al., 2018).

5.2 PGPR-Triggered Induced Systemic Resistance and SA Interactions

Plant growth-promoting rhizobacteria were originally characterised as triggering induced systemic resistance through a pathway considered SA-independent, requiring instead functional JA and ethylene signalling in the host plant (Pieterse et al., 1996). This characterisation sharply distinguished ISR from SAR and was used to argue that rhizobacteria-mediated protection operated through a wholly different hormonal mechanism. Subsequent research has substantially refined this picture. Pieterse et al. (2014) reviewed evidence showing that multiple PGPR strains can activate ISR through pathways that involve SA accumulation, depending on the bacterial strain, host plant species, and soil context. Certain strains of *Pseudomonas fluorescens*, for example, trigger ISR without detectable SA accumulation in systemic tissue in *Arabidopsis* but engage SA-dependent mechanisms in tomato — underscoring how host species can fundamentally alter the hormonal identity of the protective response.

The key molecular features of ISR include epigenetic and chromatin-level priming of defence gene loci, such that SA- or JA-responsive promoters are held in a transcriptionally permissive but not yet active state until a subsequent pathogen challenge arrives (Conrath et al., 2015). This primed state involves changes in histone acetylation at PR gene loci and partial pre-activation of MAP kinase pathway components. The priming model has direct relevance to natural farming research: it predicts that soils supporting diverse and active PGPR communities continuously prime plant defence in ways that are not apparent under non-challenge conditions but manifest as accelerated and amplified PR gene expression upon pathogen attack. Van der Ent et al. (2009) demonstrated that *Pseudomonas*-triggered ISR results in primed expression of several SA-responsive genes in a pathogen challenge-dependent manner, providing direct molecular evidence for this phenomenon.

Bacillus species, which are particularly prevalent in compost-enriched and organically managed soils, produce a diverse array of lipopeptides and volatile compounds — including surfactin, iturin, and 2,3-butanediol — that trigger distinct but partially overlapping priming responses in host plants (Chowdhury et al., 2015). The volatile compound 2,3-butanediol produced by *Bacillus subtilis* GB03 was shown to enhance SA accumulation and activate PR gene expression in *Arabidopsis* in a manner requiring a functional SA biosynthetic pathway (Ryu et al., 2004). *Bacillus amyloliquefaciens* strains have been shown to activate both SA-mediated SAR and ISR responses simultaneously in several crop species, suggesting that certain PGPR can bypass the classical hormonal dichotomy between these two systemic resistance pathways (Chowdhury et al., 2015).

5.3 Arbuscular Mycorrhizal Fungi and Defence Priming

Arbuscular mycorrhizal fungi (AMF), obligate biotrophic symbionts that colonise the roots of the large majority of terrestrial plant species, exert significant effects on plant hormone balance and defence capacity through complex interactions with SA-mediated immunity (Pozo & Azcón-Aguilar, 2007). A central paradox in AMF–plant interactions is that these fungi are obligate biotrophs, yet successful AMF colonisation is not accompanied by high SA accumulation and PR gene activation. Instead, colonisation is characterised by localised and transient SA responses that are actively downregulated, allowing the symbiosis to establish (Pozo & Azcón-Aguilar, 2007; Cameron et al., 2013).

Crucially, this localised suppression of SA signalling during early colonisation does not translate into systemic susceptibility to pathogens. AMF colonisation frequently results in a primed systemic resistance state — referred to as mycorrhiza-induced resistance — characterised by faster and stronger activation of both JA-responsive and SA-responsive defence genes upon subsequent pathogen challenge (Cameron et al., 2013). The mechanism involves enhanced responsiveness to SA rather than constitutive PR gene activation, consistent with the priming model described for PGPR-triggered ISR. Since AMF are substantially more prevalent and functionally active in naturally managed soils — where synthetic phosphate fertilisers that typically suppress AMF colonisation are excluded — the contribution of AMF to systemic defence priming in organic agroecosystems deserves particular recognition (Verbruggen et al., 2010).

5.4 *Trichoderma*, *Bacillus*, and Biocontrol Agents in Natural Systems

Trichoderma species occupy a distinctive and practically significant position in the ecology of biological control within natural farming systems. They are common colonisers of organically rich soils, actively encouraged by the application of composted organic materials, and their capacity for direct antagonism of plant pathogens through mycoparasitism and antibiosis is well-established (Hermosa et al., 2012). Beyond these direct effects, multiple *Trichoderma* strains trigger whole-plant systemic defence through both SA and JA pathways, making them agents of dual-pathway priming with clear agronomic significance (Shoresh et al., 2010).

Salas-Marina et al. (2011) demonstrated that colonisation of *Arabidopsis* roots by *Trichoderma atroviride* induces systemic PR gene expression and reduces susceptibility to foliar pathogens in patterns consistent with SA-mediated systemic resistance. Hermosa et al. (2012) comprehensively reviewed evidence showing that different *Trichoderma* strains differentially modulate SA and JA pathways depending on the crop species and the nature of the pathogen challenge, with some strains effectively priming both pathways simultaneously and thereby potentially circumventing the SA–JA trade-off. The practical relevance is that systems managed with diverse composts and without fungicide application tend to support *Trichoderma* populations that provide dual-pathway priming in situ without deliberate inoculation, though quantifying this effect under field conditions across diverse crop systems remains a significant challenge (Harman, 2011).

6. Organic Soil Amendments and SA-Dependent Defence

6.1 Composts, Vermicomposts, and Endogenous SA Modulation

The application of compost and vermicompost is a defining management practice in natural farming systems, contributing not only plant nutrients but also an extraordinarily diverse range of biologically active compounds and microbial communities with demonstrated capacity to influence plant hormone biology (Bonanomi et al., 2007; Bonanomi et al., 2010). Compost-amended soils consistently suppress a broad range of soil-borne pathogens, and whilst the mechanisms involved are multiple — encompassing microbial antagonism, improved soil physical properties, and nutrient competition — growing evidence implicates SA-dependent and SA-independent systemic resistance in the whole-plant disease suppression observed in compost-treated crops (Yogev et al., 2006).

Pane et al. (2013) showed that compost extracts applied to tomato induced PR gene expression and enhanced resistance to *Botrytis cinerea* in patterns consistent with SA-mediated priming rather than constitutive activation — a distinction with meaningful implications for the metabolic cost to the plant.

Primed plants that mount elevated defence responses only upon challenge impose lower fitness costs under unchallenged conditions compared with plants that constitutively express defence genes (Conrath et al., 2015). Natural farming systems, through the provision of chronic low-level biological stimuli from diverse rhizosphere communities, appear to maintain rhizosphere-induced priming states that are energetically efficient and environmentally responsive — a meaningful potential advantage over approaches based on exogenous elicitor application.

6.2 Cover Crops, Green Manures, and Plant Hormone Interactions

The incorporation of leguminous cover crops and green manures is another common natural farming practice that introduces biological nitrogen and diverse biochemical substrates into the soil in ways that may influence SA signalling (Finney et al., 2017). Decomposing cover crop residues release a range of phenolic compounds, some structurally related to SA or convertible to SA, and these may serve as direct precursors of SA biosynthesis through the PAL pathway (Peng et al., 2021). The nitrogen released from leguminous green manures — primarily as ammonium and subsequently as nitrate — has been shown to influence the balance between plant immune responses and growth, with nitrate signalling modulating NPR1 expression in ways that may interact with SA signalling (Brtnický et al., 2019).

Cruciferous cover crops such as *Brassica* species produce glucosinolates and their breakdown products — isothiocyanates and related compounds — upon tissue decomposition, some of which have demonstrated biological activity as priming agents (Matthiessen & Kirkegaard, 2006). The direct interaction of isothiocyanates with the SA signalling pathway has not been systematically characterised, but the induction of systemic resistance by *Brassica*-derived soil amendments observed across several crop systems suggests that these compounds, or the microbial communities they stimulate, engage SA-related immunity at least in part (Omirou et al., 2011). This mechanistic connection deserves closer scrutiny in the context of natural farming system design.

6.3 Biochar and Rhizosphere Modulation of SA Signalling

Biochar, whilst not a traditional natural farming input, is increasingly incorporated into agroecological systems as a soil amendment that enhances water retention, carbon sequestration, and soil microbial diversity (Lehmann et al., 2011). Emerging evidence suggests that biochar influences plant immunity through changes in rhizosphere microbial community composition and potentially through direct chemical effects on SA metabolism. Harel et al. (2012) reported that biochar application enhanced systemic resistance in strawberry against foliar fungal pathogens, pointing to the capacity of biochar-mediated changes in the rhizosphere to translate into whole-plant defence responses. Huang et al. (2023) subsequently showed that biochar amendment altered the relative abundance of PGPR genera associated with ISR in pepper rhizospheres and was correlated with enhanced SA-responsive gene expression following pathogen challenge, though the study acknowledged that direct causal attribution to biochar-specific chemistry versus microbiome-mediated signalling remained to be resolved.

7. Defence Priming Mechanisms: Epigenetic and Molecular Dimensions

7.1 Transcriptional Priming and Chromatin Remodelling

A recurring theme in the preceding sections is that natural farming environments appear to engender a primed rather than constitutively activated state of SA-mediated defence — a distinction with fundamental molecular underpinnings. Defence priming is characterised at the molecular level by the accumulation of latent pools of defence-related signalling components and by epigenetic changes at key defence gene loci that lower the activation threshold without incurring the full cost of constitutive defence gene expression (Conrath et al., 2015). The most thoroughly characterised epigenetic mechanism of priming involves changes in histone methylation and acetylation at SA-responsive gene promoters — particularly trimethylation of histone H3 at lysine 4 (H3K4me3), which marks loci for potentiated transcriptional activation (Luna et al., 2012).

Luna et al. (2012) made the striking observation that SAR in *Arabidopsis* can be transmitted to offspring through an epigenetic memory. F1 progeny of infected plants showed enhanced resistance and altered DNA methylation patterns at key defence gene loci — specifically, hypomethylation of SA-responsive gene promoters — demonstrating that the primed state established by SA accumulation can be encoded in chromatin in a heritable form. Whether natural farming management — through the provision of continuous low-level biological stimuli over multiple growing seasons — can establish analogous heritable epigenetic defence states in commercially grown crops is a genuinely open and experimentally tractable question with potentially significant implications for the design of natural farming systems.

7.2 Post-Translational Regulation and Redox Control

Beyond transcription, SA-mediated defence is regulated at the post-translational level through reversible modifications of key signalling proteins. The redox-regulated nucleo-cytoplasmic shuttling of NPR1, described in Section 3.2, is one example. Additional regulatory mechanisms include phosphorylation-dependent targeting of NPR1 for proteasomal degradation following gene activation, enabling signal reset after immune induction (Fu & Dong, 2013; Klessig et al., 2018). S-nitrosylation of NPR1 at Cys156 by nitric oxide promotes NPR1 oligomerisation and thereby modulates its nuclear activity, directly linking nitric oxide signalling to SA receptor function (Herrera-Vásquez et al., 2015).

Nitric oxide production in soils is substantially influenced by nitrogen cycling dynamics, which differ between naturally managed and conventionally managed agroecosystems. Organically managed soils tend to show altered nitrogen turnover rates and nitrification dynamics that could influence rhizosphere nitric oxide availability and thereby indirectly modulate NPR1 activity. This remains a speculative but biochemically plausible connection between soil management practice and SA signalling at the cellular level, and it merits direct experimental investigation.

Table 3 summarises the key priming mechanisms through which natural farming-associated microorganisms and amendments are thought to modulate SA-centred defence.

Table 3. Mechanisms by Which Natural Farming Inputs Prime SA-Centred Plant Defence

Input/Agent	**Molecular Mechanism**	**SA Pathway Component Affected**	**Evidence Base**
Pseudomonas spp. PGPR	Epigenetic priming of PR gene loci; ISR pathway activation	SA-responsive gene expression amplified upon challenge	Pieterse et al. (2014); Van der Ent et al. (2009)
Bacillus spp. (volatile 2,3-butanediol)	Volatile-mediated SA accumulation; PR gene activation	ICS1/PAL pathway; PR-1, PR-2, PR-5	Ryu et al. (2004); Chowdhury et al. (2015)
Arbuscular mycorrhizal fungi	Primed systemic resistance; potentiated SA/JA response upon challenge	SA receptor priming without constitutive activation	Cameron et al. (2013); Pozo & Azcón-Aguilar (2007)
Trichoderma spp.	Dual SA and JA pathway priming; mycoparasitism	SA-responsive PR genes + JA-responsive defence	Hermosa et al. (2012); Shoresh et al. (2010)
Vermicompost/compost extracts	PAL-dependent SA biosynthesis enhancement; PR gene activation	PAL pathway SA; PR-1, PR-2	Zhou et al. (2022); Pane et al. (2013)
Biochar amendment	Rhizosphere PGPR enrichment; altered microbial community	Indirect via ISR pathways	Harel et al. (2012); Huang et al. (2023)
Cover crop residues	Phenolic precursor supply; PGPR stimulation	PAL-derived SA substrates	Peng et al. (2021); Omirou et al. (2011)

Sources: Pieterse et al. (2014); Van der Ent et al. (2009); Ryu et al. (2004); Chowdhury et al. (2015); Cameron et al. (2013); Pozo & Azcón-Aguilar (2007); Hermosa et al. (2012); Shoresh et al. (2010); Zhou et al. (2022); Pane et al. (2013); Harel et al. (2012); Huang et al. (2023); Peng et al. (2021); Omirou et al. (2011).

8. Mechanisms of Disease Suppression in Natural Farming Systems

8.1 Suppressive Soils and SA-Mediated Mechanisms

The phenomenon of pathogen-suppressive soils — in which the natural microbial community prevents disease establishment even in the presence of both the pathogen and a susceptible host — is one of the most compelling ecological demonstrations of the agronomic importance of soil microbiome ecology (Raaijmakers & Mazzola, 2016). Natural farming systems that enrich soil microbial biomass and diversity through organic amendment and the exclusion of synthetic biocides are more likely to develop and maintain suppressive soil properties, though the link between soil suppression and systemic plant immunity — as distinct from direct pathogen antagonism in the rhizosphere — is often difficult to disentangle experimentally.

Durán et al. (2018) provided important evidence for the role of microbial community ecology in plant health, demonstrating in *Arabidopsis* that bacterial–fungal interkingdom interactions in the rhizosphere critically influence plant survival. Their study showed that the inter-kingdom structure of the root-associated microbial network — rather than the abundance of any single taxon — is a key determinant of plant health outcomes, with specific bacterial–fungal interactions either promoting or undermining the capacity of the microbiome to support its host. This community-level perspective on rhizosphere–plant immunity represents a methodological and conceptual advance that highlights the importance of whole-community ecology, rather than single-taxon biocontrol, in understanding microbiome contributions to disease suppression. These findings complement the theoretical framework advanced by Berendsen et al. (2012), who argued that integrating microbiome ecology with plant immunity research is essential for understanding how natural soil communities shape disease outcomes in agroecosystems.

Raaijmakers & Mazzola (2016) critically reviewed the literature on suppressive soils, noting that the most robustly characterised cases involve direct pathogen antagonism by rhizosphere bacteria — for example, antibiotic-producing *Pseudomonas* strains suppressing *Fusarium* wilt — but arguing that a second, undercharacterised tier involving host plant immunity activation is likely to be important in many field situations. They identified conceptual integration between suppressive soil ecology and the ISR/SAR paradigm as a priority for future research — an agenda directly served by natural farming system studies of the kind reviewed here.

8.2 Pathogen-Specific Evidence for SA-Mediated Suppression

SA-dependent systemic resistance has been demonstrated against a taxonomically diverse range of pathogens in experimental systems, including hemibiotrophic bacterial pathogens such as *Pseudomonas syringae* and *Xanthomonas* species, biotrophic oomycetes such as *Hyaloperonospora arabidopsidis*, and certain hemibiotrophic fungi (Fu & Dong, 2013). Field-level evidence that SA-mediated mechanisms specifically contribute to reduced pathogen incidence in naturally managed agroecosystems is less mechanistically resolved but increasingly available.

Szczech & Smolinska (2001) demonstrated that compost amendments reduced disease severity caused by *Phytophthora nicotianae* in tomato, in association with elevated SA concentrations in leaf tissue — one of the earlier field-system indications that organic amendment-mediated SA accumulation may contribute mechanistically to pathogen suppression. More recently, Latz et al. (2012) showed that bacterial community diversity in organically managed soils was negatively correlated with *Rhizoctonia solani* disease incidence in sugarbeet, with functional pathway analysis pointing to the enrichment of taxa with ISR-triggering potential in suppressive organic soils. Vallad & Goodman (2004) conducted a systematic comparison of ISR and SAR in tomato against bacterial speck and bacterial spot caused by *Pseudomonas syringae* and *Xanthomonas campestris*, demonstrating that PGPR-triggered ISR under field-like conditions provided disease suppression quantitatively comparable to that achieved by SAR-inducing chemical agents — supporting the agronomic equivalence of biologically induced and chemically induced SA-associated resistance.

8.3 Fungal Pathogens and Systemic Resistance in Organic Crops

Fungal pathogens represent the most economically consequential class of crop diseases in most agricultural systems worldwide. Several major fungal and oomycete diseases are substantially influenced by SA-mediated systemic immunity, though their vulnerability to SA-based defences varies with nutritional strategy. Biotrophic fungi, including powdery mildews (*Blumeria*, *Erysiphe*, and related genera) and rust fungi, are particularly sensitive to SA-induced PR protein accumulation — notably PR-2 (β-1,3-glucanases) and PR-3 (chitinases) that directly degrade fungal cell wall components (van Loon et al., 2006). Multiple studies have documented reduced powdery mildew incidence in organically managed vineyards and cereal systems in association with enhanced PR gene expression, consistent with biologically induced SA-mediated resistance contributing to pathogen suppression (Reganold & Wachter, 2016).

Particularly relevant here is the work of Bigirimana & Höfte (2002), who demonstrated in bean that ISR against *Colletotrichum lindemuthianum* could be induced by both a benzothiadiazole derivative — a well-established chemical SA-pathway activator — and the rhizobacterium *Rhizobium etli* CNPAF512, illustrating a meaningful convergence between chemically and biologically induced systemic resistance. This observation, and subsequent work across multiple crop–pathogen systems, illustrates that the mechanistic boundaries between SA-mediated SAR and JA/ET-mediated ISR are not as cleanly defined in crop species as the original *Arabidopsis*-based model implied — creating practical opportunities for biological control strategies in natural farming that harness multiple pathways simultaneously.

9. Mechanisms of Insect Suppression and the SA–JA Trade-Off in Natural Farming

9.1 Arthropod Pest Management in Low-Input Systems

Arthropod pest management in natural farming systems operates at multiple ecological levels — through predation and parasitism by arthropod natural enemies, through physical and behavioural barriers, and through plant-intrinsic resistance mechanisms — with the relative importance of each varying by pest, crop, and management context (Gurr et al., 2016). At the level of plant-intrinsic mechanisms, JA-responsive defences constitute the primary biochemical arsenal deployed against chewing herbivores, including direct defences such as protease inhibitors, polyphenol oxidases, and glucosinolates, and indirect defences comprising herbivory-induced plant volatiles that attract natural enemies of herbivores (Howe & Jander, 2008). SA-mediated defences are less directly effective against chewing insects but may contribute to resistance against piercing-sucking insects such as aphids and whiteflies, which are subject to SA-dependent callose deposition blocking phloem access and to deterrent effects of SA-induced PR proteins (Moran & Thompson, 2001).

The SA–JA antagonism thus creates a real management challenge in natural farming: conditions that elevate SA-mediated disease resistance may simultaneously diminish JA-dependent resistance to chewing herbivores. Several empirical observations support this concern. Thaler et al. (2012) compiled evidence showing that both natural pathogen infection and exogenous SA treatment reduce caterpillar performance and JA-responsive gene expression in tomato, demonstrating that the SA–JA trade-off operates under relatively realistic conditions. Koornneef et al. (2008) showed that SA pre-treatment of *Arabidopsis* suppressed JA-responsive *Pdf1.2* expression and reduced resistance to the necrotrophic pathogen *Alternaria brassicicola*, demonstrating pathologically significant consequences of SA-mediated JA antagonism.

9.2 Herbivory-Induced Volatiles and Natural Enemy Attraction

Herbivory-induced plant volatiles represent one of the most ecologically consequential indirect defence mechanisms available to plants in natural and low-input farming systems, functioning to attract parasitoid wasps and predatory arthropods to plants under insect attack (Turlings & Erb, 2018). The emission of these volatiles is predominantly regulated through the JA pathway, with most volatile blend constituents — including monoterpenes, sesquiterpenes, homoterpenes, and green leaf volatiles produced through the lipoxygenase pathway — induced by JA signalling in a manner suppressible by SA (Turlings & Erb, 2018; Caarls et al., 2015). Farm management conditions that lead to chronically elevated SA status in plants therefore carry the potential to reduce volatile emissions attractive to natural enemies, potentially undermining a key component of the ecological pest management that natural farming systems rely upon.

This concern must, however, be placed in context. Natural farming systems — precisely because they support diverse and active rhizosphere microbial communities — may tend to prime both SA and JA pathways simultaneously rather than chronically activating one at the expense of the other (Pieterse et al., 2014). The priming model predicts that endogenous SA and JA remain near baseline in biologically primed but unchallenged plants, with both pathways responding more rapidly and strongly when their specific elicitors are encountered. Whether field-grown crops under natural farming management show measurably reduced volatile emission under herbivore attack relative to conventionally grown crops has not been directly tested with the necessary combination of phytohormone quantification, volatile profiling, and arthropod community monitoring — an important gap in the current evidence base.

9.3 Piercing-Sucking Insect Resistance and SA

The relationship between SA signalling and resistance to piercing-sucking insects such as aphids and whiteflies is more directly positive than for chewing herbivores, primarily because SA-mediated responses include callose deposition at sieve plates that physically impedes phloem feeding (Moran & Thompson, 2001). Aphids and related hemipteran pests represent major challenges in organic agroecosystems partly because synthetic insecticides effective against them are excluded, and partly because their natural enemies — though favoured by natural farming conditions — are also subject to bottom-up effects mediated by plant nutritional and defence chemistry.

Li et al. (2008) showed that *Arabidopsis* NPR1 mutants compromised in SA-mediated PR gene expression displayed enhanced susceptibility to the green peach aphid *Myzus persicae*, indicating that SA signalling contributes to basal resistance against this piercing-sucking pest. Goggin (2007) reviewed the phytohormone biology of plant–aphid interactions and concluded that the integration of SA and JA signals — where SA-mediated callose deposition reduces aphid probing success whilst JA-responsive proteins reduce aphid fecundity on phloem tissue — together constitute a multi-layered defence system. In naturally managed soils, where biological priming by PGPR tends to enhance SA responsiveness without chronically suppressing JA at the resting state, the primed plant may deploy both components of this multilayered resistance more effectively upon aphid challenge.

Table 4 provides a comparative summary of SA and JA contributions to resistance against major pest and pathogen categories in natural farming contexts.

Table 4. Contributions of SA and JA Defence Pathways to Resistance Against Key Pest and Pathogen Categories in Natural Farming Systems

Attacking Organism	Predominant Pathway	Role of SA	Role of JA	SA–JA Trade-off Significance	Representative Reference
Biotrophic fungi (e.g. powdery mildew, rusts)	SA	Primary defence (PR-2, PR-3, PR-5)	Limited	Low	van Loon et al. (2006)
Hemibiotrophic bacteria (e.g. *P. syringae*)	SA	Primary (PR-1, SAR)	Suppressed by SA	Moderate	Fu & Dong (2013)
Necrotrophic fungi (e.g. *Botrytis cinerea*)	JA/ET	May suppress JA-based defence	Primary defence	High (SA antagonises JA)	Glazebrook (2005); Caarls et al. (2015)
Chewing herbivores (caterpillars, beetles)	JA	Suppresses JA; indirect antagonism	Primary (PI, PPO, glucosinolates)	High (SA reduces JA defences)	Thaler et al. (2012); Howe & Jander (2008)
Piercing-sucking insects (aphids, whiteflies)	SA + JA	Callose deposition; PR proteins	Reduces fecundity	Moderate (both pathways needed)	Moran & Thompson (2001); Goggin (2007)
Soil-borne oomycetes (e.g. *Phytophthora* spp.)	SA	Contributes via SAR	Moderate	Low	Durrant & Dong (2004)

Sources: van Loon et al. (2006); Fu & Dong (2013); Glazebrook (2005); Caarls et al. (2015); Thaler et al. (2012); Howe & Jander (2008); Moran & Thompson (2001); Goggin (2007); Durrant & Dong (2004)

10. Field-Scale Evidence and Translational Challenges

10.1 Field Observations in Organically Managed Agroecosystems

Translating mechanistic insights from controlled laboratory and greenhouse settings to field-scale agroecological contexts is never straightforward, and SA-centred defence research is no exception. The conditions prevailing in naturally managed agroecosystems — temporal and spatial heterogeneity in soil microbiome composition, climatic variability, crop genotype effects, and the frequent co-occurrence of multiple biotic and abiotic stresses — create an exceptionally complex environment in which isolating the contribution of SA-mediated mechanisms to observed disease and pest outcomes is genuinely difficult (Lori et al., 2017; Reganold & Wachter, 2016).

Several meta-analyses and long-term comparative studies have provided useful field-scale context. Lori et al. (2017) conducted a meta-analysis of 105 peer-reviewed studies comparing soil microbial biomass and diversity in organic versus conventional farming systems, finding significant and consistent enrichments in microbial indicators across organic systems. Whilst this study did not directly assess plant immunity outcomes, the microbial parameters enriched — particularly bacterial functional diversity and AMF colonisation rates — are precisely those associated with enhanced ISR and defence priming in controlled systems. Mbuthia et al. (2015) provided complementary evidence from a 12-year long-term organic farming trial, documenting that organic management significantly enriched soil bacterial and fungal taxa with known biocontrol and plant-priming functions.

More directly, Finney et al. (2017) demonstrated in a five-year field experiment that cover crop diversity in organic systems enhanced rhizosphere microbial diversity and was correlated with reduced pathogen incidence in subsequent cash crops, with molecular analysis pointing to enhanced expression of SA-responsive defence markers in cover crop-diversified plots. This study stands out for integrating agronomic management, microbiome ecology, and plant molecular biology across multiple growing seasons under real field conditions — a design that most earlier work on SA-mediated immunity in controlled systems lacked.

10.2 Methodological Challenges and the Need for Multi-Omic Approaches

The central methodological challenge in bridging laboratory SA biology and field agroecological observations is the integration of information across levels of biological organisation that have historically been the territory of different scientific communities using incompatible methodologies. Molecular plant immunologists working on SA signalling have typically used genetic model systems under highly controlled conditions; rhizosphere ecologists working on organic farming microbiomes have applied metagenomic and metabarcoding approaches under field conditions but without plant transcriptomic measurements; agronomists studying disease and pest outcomes in organic systems have typically measured end-point outcomes without mechanistic attribution. Each community has produced important knowledge, but the interfaces between them remain underdeveloped.

Recent advances in plant phenotyping, portable transcriptomics, field-deployable metabolomics, and spatial soil metagenomics offer real prospects for bridging these silos in ways that were simply not feasible a decade ago (Durán et al., 2018; Schlaeppi & Bulgarelli, 2015). Combined studies measuring rhizosphere bacterial and fungal community composition, plant leaf transcriptome responses including SA-responsive gene expression, SA and JA concentrations in leaf tissue, and agronomic pest and disease outcomes in the same experimental plots across multiple organic farming treatments would substantially advance the field. Berendsen et al. (2012) articulated the theoretical framework for such an integrative "rhizosphere microbiome to plant immunity" research agenda, and Durán et al. (2018) demonstrated its practical feasibility at moderate scale. Expanding this approach to long-term, replicated field trials that capture seasonal variation and crop rotation effects remains an important unmet need.

10.3 Crop Species Variation in SA-Mediated Defence

A notable complexity in translating *Arabidopsis*-derived mechanistic insights to agroecological contexts is the substantial variation in SA signalling architecture across crop species. NPR1 homologues with conserved function have been identified in major crops including tomato, rice, wheat, maize, soybean, and *Brassica* species, but the quantitative role of SA in immunity, its metabolic flux through IC versus PAL pathways, and its crosstalk with JA all show species-specific differences that must be considered when extrapolating from model organism findings (Peng et al., 2021). Rice, for example, accumulates substantially lower basal SA concentrations than *Arabidopsis* and shows a different pattern of SA-responsive gene activation, with the WRKY factors involved in SA-dependent immunity partially distinct from their *Arabidopsis* orthologues (Shimono et al., 2007).

The SA economy of monocot crops — which include cereals that together provide the majority of global caloric intake and which are grown under diverse farming systems including natural and organic management — is therefore an important area for continued mechanistic work. Given that much of the rhizosphere priming literature reviewed here draws primarily on dicot model systems, extending field-based SA signalling studies to major cereals managed under natural farming is both scientifically important and practically consequential.

11. Emerging Concepts and Future Research Directions

11.1 Transgenerational Epigenetic Priming and Natural Farming

The demonstration by Luna et al. (2012) that SAR-associated epigenetic states in *Arabidopsis* can be transmitted to offspring opens a genuinely novel possibility: that the cumulative epigenetic history of plant generations grown under natural farming management could influence the SA-mediated defence capacity of current crop plants. If natural farming systems, through the provision of recurring biological stimuli from enriched rhizosphere communities, epigenetically prime plant defence across growing seasons, the implications for disease resistance in organically grown crops would be substantial — and the mechanism would only become visible in long-term field experiments (Conrath et al., 2015).

This hypothesis is scientifically plausible and experimentally tractable, though it has not been directly tested in the context of multi-generational organic farming management. An appropriate experimental design would require controlled propagation of crop seeds harvested from long-term organic and conventional management plots, combined with SA-responsive transcriptomic profiling and DNA methylation analysis under standardised challenge conditions. Such an experiment would significantly advance understanding of how farming history shapes the molecular defence physiology of the current crop generation.

11.2 Microbiome Engineering for SA-Pathway Optimisation

A growing research frontier concerns the deliberate engineering of rhizosphere microbial communities in natural farming systems to optimise SA-pathway priming whilst minimising SA–JA antagonism at the whole-plant level. This might be achieved through consortium-based bioinoculant formulations combining SA-priming PGPR with JA-priming PGPR and AMF, relying on the additivity or synergy of their priming effects to work around the constraints of single-agent inoculation (Berendsen et al., 2012; Pieterse et al., 2014). Targeted application of specific microbial consortia — informed by knowledge of the rhizosphere microbiome structure associated with natural disease suppression in field-scale organic systems — represents a rational strategy for replicating the defence-priming benefits of mature naturally managed soils in newly converted organic systems where the suppressive microbiome has not yet fully developed.

Schlaeppi & Bulgarelli (2015) argued that understanding the assembly rules governing plant-associated microbiomes under different management regimes is a prerequisite for their rational manipulation towards desired functional outcomes, including enhanced plant defence. The growing availability of culturomics-based approaches enabling high-throughput isolation and characterisation of rhizosphere bacteria, combined with targeted bacterial trait engineering, increasingly makes deliberate microbial community design a practical prospect for agroecological applications.

11.3 SA Signalling in the Context of Climate Change Interactions

Under natural farming management, plants face not only biotic stresses but also altered abiotic stress profiles that intersect with SA signalling. Climate change-driven increases in temperature variability, drought intensity, and atmospheric CO_2 concentration all influence plant immune hormonal balance in ways that interact with SA-centred defence (Atkinson & Urwin, 2012). Elevated CO_2 has been shown to suppress SA-mediated defence gene expression in *Arabidopsis* and several crop species, potentially through enhanced carbon supply and altered source–sink relationships (Guo et al., 2013). Drought-induced ABA accumulation suppresses SA signalling, as reviewed in Section 4.2, and the severity of drought experienced in natural farming systems — which often have greater soil water-holding capacity through higher organic matter but frequently lack irrigation in low-input contexts — will modulate the SA–ABA interaction in complex, context-specific ways.

Understanding how climate change alters the SA-mediated defence landscape in natural farming systems is not merely an academic question. Disease pressure profiles will shift as pathogen ranges expand with rising temperatures, and the SA priming status of naturally managed plants will partly determine how effectively they respond to pathogens arriving in regions where evolutionary co-adaptation has not yet occurred (Bebber et al., 2013). Integrating climate projections with rhizosphere microbiome ecology and plant SA signalling represents a genuinely novel research frontier for agroecological plant pathology.

Table 5 summarises the emerging research priorities at the interface of SA signalling, natural farming, and future challenges discussed in this section.

Table 5. Emerging Research Priorities in SA-Centred Defence Signalling Under Natural Farming Systems

Research Priority	Key Question	Methods Needed	Representative Reference
Transgenerational epigenetic priming	Do multi-generational organic management histories alter DNA methylation at SA-responsive loci?	Multi-generational controlled trials; bisulphite sequencing; transcriptomics	Luna et al. (2012); Conrath et al. (2015)
Microbiome engineering	Can designed PGPR consortia prime SA and JA pathways simultaneously without antagonism?	Consortium inoculation; dual-pathway transcriptomics; field trials	Pieterse et al. (2014); Schlaeppi & Bulgarelli (2015)

Research Priority	Key Question	Methods Needed	Representative Reference
Crop species diversity in SA responses	How do SA signalling differences between major crop species affect priming outcomes under organic management?	Comparative transcriptomics; hormone profiling across multiple crop species	Peng et al. (2021); Shimono et al. (2007)
Climate × SA priming interactions	How do elevated CO_2 and drought alter PGPR-mediated SA priming in natural farming contexts?	Growth chamber climate modelling; rhizosphere metagenomics; hormone profiling	Guo et al. (2013); Atkinson & Urwin (2012)
NHP signalling in organic soils	Do rhizosphere-enriched microorganisms in organic soils modulate NHP biosynthesis or accumulation?	SA/NHP metabolite profiling; organic versus conventional soil comparisons	Hartmann et al. (2018); Chen et al. (2018)
Field-scale multi-omics integration	Can integrated rhizosphere–plant immunity studies be replicated at field scale across seasons?	Spatial metagenomics; in-field transcriptomics; long-term disease monitoring	Durán et al. (2018); Berendsen et al. (2012)

Sources: Luna et al. (2012); Conrath et al. (2015); Pieterse et al. (2014); Schlaeppi & Bulgarelli (2015); Peng et al. (2021); Shimono et al. (2007); Guo et al. (2013); Atkinson & Urwin (2012); Hartmann et al. (2018); Chen et al. (2018); Durán et al. (2018); Berendsen et al. (2012)

12. Conclusions

This review has synthesised a broad body of evidence establishing that natural farming systems create rhizosphere conditions broadly conducive to the activation and priming of SA-centred plant immunity, with consequential effects on the suppression of biotrophic and hemibiotrophic pathogens. The molecular pathways through which this occurs — including PGPR-triggered ISR with SA-priming components, AMF-induced mycorrhiza-associated resistance, *Trichoderma*- and *Bacillus*-mediated dual-pathway priming, and organic amendment-enhanced SA biosynthesis — have sufficient mechanistic grounding in the primary literature to constitute a coherent framework, even as important gaps remain in direct field-scale evidence.

The SA–JA antagonism remains the most important mechanistic tension in applying this knowledge to natural farming crop protection. The evidence reviewed here suggests that the priming mode of defence activation favoured by the enriched rhizosphere conditions of natural farming is inherently less vulnerable to antagonistic SA–JA trade-offs than constitutive pathway activation — but this inference requires field-level validation, particularly with respect to herbivore resistance and indirect defence volatile emission, before it can confidently inform management guidance. The asymmetric dependence of different herbivore types on JA-responsive defences — chewing herbivores most heavily, piercing-sucking pests rather less so — means that the practical consequences of hormonal balance shifts in natural farming systems are pest-specific and require targeted assessment rather than generalised conclusions.

The emerging concepts discussed in Section 11, particularly transgenerational epigenetic priming and microbiome engineering, represent potentially transformative directions for natural farming plant defence research. If confirmed, the possibility that multi-generational organic farming history epigenetically primes the SA-responsive defence landscape of crop plants would provide a novel mechanistic rationale for the disease resistance advantages empirically observed in well-established organic systems — advantages that have been documented at the agronomic level for some time but have lacked adequate molecular explanation. Advancing this understanding requires long-term, multidisciplinary field experiments that integrate rhizosphere microbial ecology, plant molecular physiology, and agronomic outcome measurement within the same experimental frameworks — a demanding but increasingly feasible undertaking given recent advances in field-deployable omics technologies.

Overall, the convergence of molecular plant biology and agroecological research reviewed here presents a credible case that managing the rhizosphere microbiome through natural farming practices constitutes a mechanistically grounded approach to enhancing plant-intrinsic disease and pest resistance. The molecular foundations for this enterprise are increasingly secure; what is now needed is the sustained interdisciplinary effort required to translate them into durable, field-validated crop protection strategies.

13. Limitations

This review draws on a literature that is markedly uneven in its taxonomic and geographic representation. The molecular mechanisms of SA biosynthesis, signalling, and systemic resistance have been most thoroughly characterised in *Arabidopsis thaliana*, and many of the field and greenhouse studies on rhizosphere priming of SA-mediated immunity also rely on temperate vegetable and model crops, particularly tomato, bean, and wheat. The degree to which mechanistic findings in these systems generalise to major tropical crops — including rice, maize, cassava, sorghum, and legumes widely grown under natural and organic farming practices in the Global South — is incompletely established. The molecular SA signalling machinery in these crops is not fully characterised, and the rhizosphere microbiome ecology of organic and natural farming systems in tropical agricultural contexts remains understudied relative to temperate systems.

A second limitation concerns the predominance of greenhouse and growth chamber studies in the mechanistic literature on PGPR- and AMF-mediated defence priming. Whilst controlled condition studies are necessary for establishing causal mechanism, their extrapolation to field conditions is complicated by environmental variability that is difficult to capture experimentally. Temperature fluctuations, spatially heterogeneous soil moisture, crop variety differences, and the complex timing interactions between pest and pathogen pressure that characterise real agricultural seasons all influence the expression and consequence of SA-mediated priming in ways that greenhouse studies cannot fully represent. The field-scale studies cited in this review are valuable precisely because of their realism, but they are fewer in number and in several cases limited in mechanistic depth.

A third limitation is inherent in the narrative review methodology adopted here. Whilst this approach was selected as appropriate for the multidisciplinary scope of the question, narrative synthesis is susceptible to selective citation and confirmatory framing in ways that systematic approaches can partially mitigate. The authors have sought to represent conflicting evidence and mechanistic uncertainties throughout, but the absence of a formal protocol-driven inclusion and weighting scheme means that the synthesis presented here should be regarded as an expert assessment rather than a definitive quantitative conclusion. Future systematic reviews or meta-analyses focused on specific sub-questions — for example, the effect of organic amendment on PR gene expression in field-grown crops, or the quantitative impact of PGPR inoculation on aphid resistance in organic vegetables — would provide complementary evidence to the broader narrative framework presented here.

Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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