Plant immunity: Good fences make good neighbors?

Rémi Pélissier, Cyrille Violle, Jean-Benoit Morel

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Rémi Pélissier[1], Cyrille Violle[2] and Jean-Benoit Morel[3]

Abstract

Plant immunity is modulated by several abiotic factors, and microbiome has emerged as a major biotic driver of plant resistance. Recently, a few studies showed that plants also modify resistance to pests and pathogens in their neighborhood. Several types of neighborhood could be identified depending on the biological processes at play: intraspecific and interspecific competition, kin and stranger recognition, plant-soil feedbacks, and danger signaling. This review highlights that molecules exchanged aboveground and belowground between plants can modulate plant immunity, either constitutively or after damage or attack. An intriguing relationship between allelopathy and immunity has been evidenced and should merit further investigation. Interestingly, most reported cases of modulation of immunity by the neighbors are positive, opening new perspectives for the understanding of natural plant communities as well as for the design of more diverse cultivated systems.

Addresses
[1] PHIM Plant Health Institute, CEFE, Univ Montpellier, Institut Agro, INRAE, CIRAD, TA A-54/K Campus International de Baillarguet, 34398, Montpellier Cedex 5, France
[2] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry, Campus du CNRS, 1919, Route de Mende, 34293 Montpellier Cedex 5, France
[3] PHIM Plant Health Institute, Univ Montpellier, INRAE, CIRAD, Institut Agro, IRD, TA A-54 / K Campus International de Baillarguet, 34398, Montpellier Cedex 5, France

Corresponding author: Jean-Benoit, Morel (jean-benoit.morel@inrae.fr)

Introduction

Plants possess a basal immune system that is constitutively expressed at low levels and can be induced by pathogens [1]. The expression of this immune system confers basal levels of immunity and leads to full or partial resistance to pathogens and insects. Plants, which integrate complex external cues and signals throughout their life span, can be considered as 'multi-layer perceptrons' [2]. Environmental factors, whether abiotic [3] or microbiotic [4], can modulate their basal immunity. In particular, in their natural habitat, plants grow and compete with other plants. Plant—plant interactions can modify plant physiology [5*], as manifested for instance by massive transcriptional changes; plant—plant interactions also affect their interactions with other organisms, for example, the plant microbiome [6,7]. However, little attention has been paid to plants themselves as neighbors and their possible ability to modulate basal immunity and pathogen resistance [8].

Plant—plant interactions are mediated by cues (constitutively produced) and signals (induced by different triggers) from emitter/neighbor plants and perceived by receiver/focal plants [7,9]. Numerous studies have shown that plant—plant interactions, notably mediated by volatile organic compounds (VOCs), influence the resistance to herbivorous insects of a focal plant [10]. This is ecologically consistent with the elevated mobility of insects and the requirement of biological systems that protect the population and not just individual plants. Besides, very few studies report on the impact of plant—plant interactions on resistance to pathogens [11]. This sounds logical for threats such as pathogens that have limited mobility in the environment. However, recent but still sparse evidences now indicate that plant—plant interactions can strongly modify plant immunity and resistance not only to insects but also to many pathogens. This understudied capacity of plants to interact with each other and to fine tune immunity raises many questions, including on the underlying biological processes and on the ecological significance of such a behavior.

As a step to the development of a comprehensive framework for plant—plant interactions influencing their response to biotic stresses, we review recent findings on the modification of immunity and susceptibility due to plant—plant interactions (Table 1), the mechanisms by which these modifications occur, and the signals or cues exchanged between plants that are responsible for these modifications (Figure 1). We first asked whether such phenomenon could be influenced by the genetic distance between plants, by distinguishing genetically close neighbors (conspecifics) vs. plants of different species (heterospecific). We also

Table 1

Recent and key studies showing modulation of plant defense by plant–plant interactions or signals involved in plant–plant interactions.

Process	Nature of the signal (localization)	Focal plant	Neighbor plant or signal	Immune and resistance response in focal plant	Reference
Competition	*Change of light quality* (Aboveground)	*A. thaliana*	Synthetic change of light	Defense gene downregulated (*ERF1*, *PDF1.2*) Susceptibility to *B. cinerea* increased	[14,15]
	Root density (Belowground)	*Nicotiana rustica*	*Nicotiana rustica*	Increase of chemical defense, SA, JA, ABA	[16]
	Plant density (Below- Above-ground)	*Asclepias syriaca* *Triticum aestivum*	*Asclepias syriaca* *Triticum aestivum*	Increase of lignin production and deposition on secondary cell wall.	[17,18]
Kin recognition	Root exudates (Belowground)	*A. thaliana*	*A. thaliana*	Defense gene upregulated (*PR1*, *PDF1.3*, *PDF1.2b*, *CA1*)	[21*]
Stranger recognition	DIMBOA and derivatives (Belowground)	*A. thaliana*	Synthetic molecule	Inhibition of histone acetylation and enhanced expression of stress-related genes	[28**]
	Allantoin (Belowground)	*A. thaliana*	Synthetic molecule	Activation of the *MYC2*-regulated JA signaling pathway through ABA production	[30]
	(–)-Loliolide (Belowground)	*Oryza sativa*	Echinocloa Crus-gali	Increased synthesis of tricin, momilactone and expression of genes involved in defense	[31]
	(–)-Loliolide (Belowground)	*A.thaliana* *Solanum lycopersicum*	Synthetic molecule	Defenses genes and herbivory resistance increased	[32]
	(–)-Loliolide, JA and other (Belowground)	*Triticum aestivum*	100 other species	Increase of DIMBOA production	[25*]
	1,8-cineole, menthone and menthol (Aboveground)	*Glycine max* and *Brassica rapa*	*Mentha piperita*	Defenses genes and herbivory resistance increased	[22*]
	sesquiterpene (E)-β-caryophyllene (Belowground)	*Centaurea stoebe*	*Taraxacum officinale*	Increased herbivory	[59]
	Diallyl disulfide (Belowground)	*Solanum lycopersicum*	Synthetic molecule	Defense gene and pathogenesis-related proteins upregulated	[27]
Plant-soil Feedbacks and legacies	Modification of soil microbiota (Belowground)	*A. thaliana*	*A. thaliana*	Defenses genes and *H. arabidopsidis* resistance increased	[35**]
	Modification of soil microbiota (Belowground)	*Zea mays*	*Zea mays*	Defenses genes (*PR10*,*OX10*,*PR1* etc..), SA, JA and herbivory resistance increased	[35**]
	Modification of soil microbiota (Belowground)	*Jacobaea vulgaris*	*Jacobaea vulgaris* (damaged or undamaged)	Increase of pyrrolidine alkaloid concentration	[36*]
	Modification of soil microbiota (Belowground)	*A. thaliana*	*A. thaliana* infected by *P. syringae*	Defense metabolism and *P. syringae* resistance increased	[38]
	Modification of soil microbiota (Belowground)	*D. grandiflora*	37 other species	Resistance to *P. ultimum* and concentration of chlorogenic acid increased	[34]

Danger signalization	Systemin (excreted soil peptide) (Belowground)	*S. lycopersicum*	Damaged *S. lycopersicum*	Defenses genes (*WRKY40, Ap2ERF* etc..) and herbivory resistance increased	[75]
	Unknown root exudate compound (Belowground)	*A. thaliana*	*A. thaliana* infected by *P. brassicae* eggs	Transmission of SAR reaction, SA induction and resistance against *P. brassicae* increased	[49**]
	Inducible VOCs emission (Aboveground)	*Zea mays*	Touched *Zea mays*	Defenses genes (*APX, BX1, SOD* etc..), and herbivory resistance increased	[76*]
	Inducible monoterpene emission (Aboveground)	*A. thaliana*	*A. thaliana* infected by *P. syringae*	Transmission of SAR reaction, defense gene (*PR1*) and resistance against *P. brassicae* increased	[48**]
	Inducible α-pinene, β-myrcene, and limonene (Aboveground)	*Glycine max*	Cut Goldenrods (*Solidago* spp.)	Herbivory resistance against *S.litura* and seed isoflavone increased	[53**]
	Inducible *cis*-3-hexenyl acetate (Aboveground)	*P. lunatus*	Synthetic z3HAC	Herbivory resistance increased	[51]

ABA, abscisic acid; **z3HAC**, cis-3-hexenyl acetate.

reviewed studies showing that plant–plant interactions occur across time, with one plant influencing immunity and resistance of another plant that succeeds to the former. Finally, besides the intuitive notion that an attacked/damaged plant can signal danger to its neighbor, there is now evidence that healthy neighbors can also modify immunity and resistance in their neighborhood. We further discuss the ecological and agronomical implications of these findings and highlight the major lines of research which, to our opinion, should be followed (Box 1).
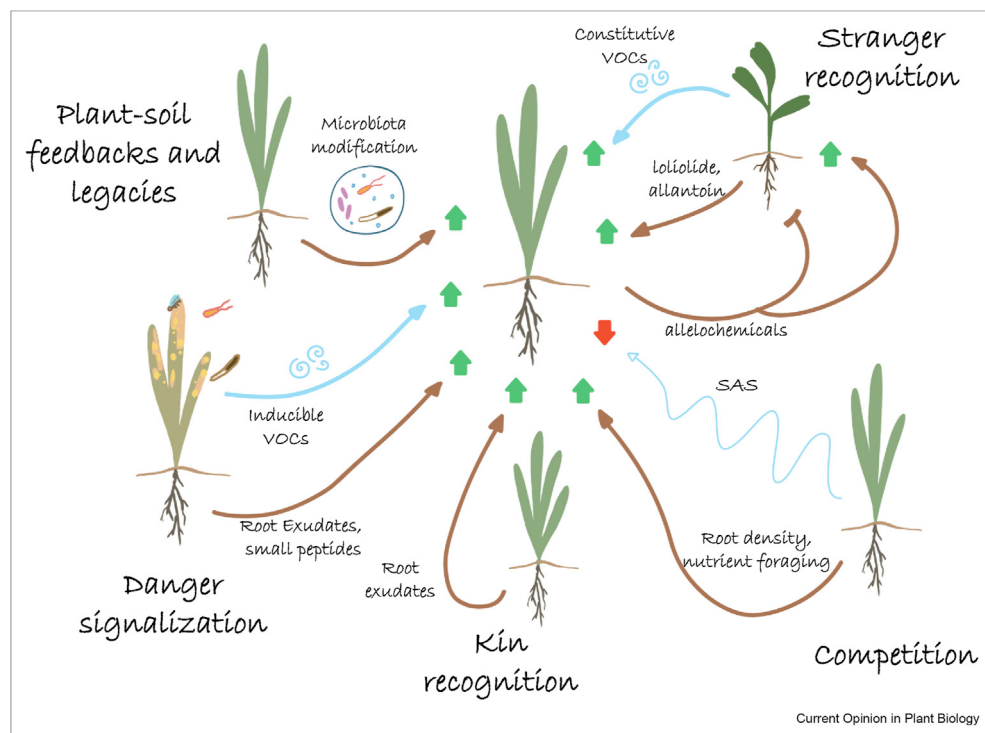
Main text of review
Conspecific neighborhoods can modulate plant susceptibility

The intensity of plant–plant interactions increases with density and is associated with competition for resources (e.g., soil nutrients and light) [12]. Importantly, competition can induce multiple physiological and transcriptomic changes within the plant [5]. A well-known example is the cascade of reactions triggered by the shade-avoidance syndrome on competition for light [13], including a reduction of the expression of defense-associated genes and resistance to pathogens [14,15]. Aboveground defenses on the contrary can be induced by increased root–root interactions. For instance, the presence of intraspecific tobacco roots was associated with the accumulation of defense chemicals like phenolic compounds and lignin derivatives that participate to mechanical defenses [16]. These changes were accompanied by the enhanced accumulation in leaves of phytohormones implicated in defense, such as jasmonic acid (JA), salicylic acid (SA), and abscisic acid. Other studies indicated that plant density affects components of plant immunity but did not test its impact on plant susceptibility to biotic stresses [17,18]. Except for these few examples, belowground competition and its impact on plant immunity has been overlooked and deserves further investigation.

Besides responding to neighborhood density, there is evidence that plants can identify their kins, in particular by perceiving root exudates in the soil [7,19]. On the one hand, genetic relatedness has been shown to modify the defense response of one focal plant to signals from neighboring, attacked plants [10,20]. On the other hand, in the absence of danger, only one example shows a possible effect of genetic relatedness in the expression of immunity [21]. In this case, the induction of defense genes in *Arabidopsis thaliana* by root exudates was higher with exudates produced by a genetically distant ecotype. However, it remains to be demonstrated whether kin recognition per se can modify plant susceptibility (Box 1).

Figure 1

Conceptual framework for plant–plant interactions modulating immunity and susceptibility. Plant neighbors interact with a focal plant (at the center) by producing above and below ground signals (blue and brown arrows, respectively; arrowheads indicate activation and broken arrow inhibition). On interaction, the immune system or resistance of the focal plant is increased (green arrows) or reduced (red arrow). Five types of processes resulting from plants neighborhoods are defined: Plant-soil feedbacks and legacies, danger signalization, kin or stranger recognition and competition. Plant-soil feedbacks and legacies are situations where plants precondition soil, often through microbiome modifications, in such a way that the next growing plants have their immunity/susceptibility modified. Danger signalization represents situations where attacked or damaged plants send signals in their neighborhood. Kin and stranger recognition (allelopathy) represents cases where the genetic distance between plants trigger signals. Competition represents situations where the response to neighbors does not require signaling but rather is an indirect consequence of competition for resource. Except for the shade-avoidance syndrome, most interactions are positive. During the allelopathic response (stranger recognition), both neighbor and focal plants have their immunity modified. The list of studies behind this framework can be found in Table 1.

Constitutive cues and induced signals from heterospecific, healthy neighbors: *strangers' things*

Several studies have now demonstrated that the presence of neighbors from different species (heterospecifics) affects plant immunity (Table 1). Constitutive cues produced by heterospecific neighbors are a first category of signals that can affect immunity in their neighborhood. When co-cultivated with mint, soybean showed reduced herbivory both in the field and in controlled conditions [22*]. Volatile menthol constitutively released from mint was responsible for this increase of resistance by enhancing the expression of defense genes like *PR1* in soybean. This enhancement of immunity occurred through the targeting and regulation of histone acetylation on promoters of defense-associated genes.

Plants also produce a cocktail of allelopathic molecules in response to their plant neighborhood [23,24]. In some instances, it is likely that these allelopathic molecules

lead to broad effects besides their known herbicidal activities on plant neighbors. For instance, the secondary metabolite DIMBOA produced by many Poaceae species in response to neighbors (e.g., [25*]) is well known for its direct antimicrobial and insecticidal activities [26]. Thus some neighbors and the allelopathic response they trigger could indirectly increase resistance to pathogens and pests [11,27].

Some molecules known to participate to the allelopathic response were also shown to directly modulate the expression of genes involved in defense and resistance to biotic stress (Table 1). One of the earliest report of such indirect effects of allelopathic compounds was that DIMBOA, by modifying some specific histone deacetylases, increased the expression immunity-related genes [28**]. More recently, the ureide allantoin (involved in kin recognition in rice [29]) has been shown to induce the expression of JA-responsive genes as well as *MYC2*, a key gene known to mediate defense against

pathogens in *A. thaliana* [30]. Similarly loliolide, a secondary soil-secreted metabolite shown to activate an allelopathic response in rice [31] and wheat [25], induced plant defense and increased herbivore resistance in *A. thaliana* and tomato [32]. There is a thus a potentially complex interplay between the recognition of a stranger, the mechanisms that plants activate in response to such neighborhood and immunity (Fig. 1). However, it remains to be shown whether and how the actual plant–plant interactions involving loliolide or allantoin can modulate immunity and resistance to biotic stress. More generally, the intriguing relationship between allelopathic and immune responses remains to be further explored (Box 1).

Plants leave a message: plant-soil feedbacks and legacy effects

By modifying soil properties, in particular through the production of allelopathic compounds, plants have also an effect on soil microbial communities [33]. Recently, several studies showed that the modification of soil microbes by plants can alter the defense responses or resistance properties of plants grown in pre-conditioned soils [34—36*] (Table 1). In particular, DIMBOA and its

derivatives produced by roots of healthy maize plants were capable of altering communities of bacteria of the rhizosphere. Maize plants growing in soil where microbial communities were previously conditioned by maize plants producing DIMBOA, showed significant induction of defense marker genes, defense hormones (SA and JA) and a reduction of caterpillar weight after feeding [35**]. These changes were not observed when using maize mutants that do not produce DIMBOA, providing a clear demonstration that DIMBOA biosynthesis was required for such plant-soil feedbacks.

Similarly, attacked plants can modify the leaf or soil microbiome in such a way that the next coming plants will display greater immunity [37*]. Plants of *A. thaliana* infected by pathogenic bacteria produced root exudates altering microbiome composition that in turn induced an increase of JA in the leaves that prevented further pathogen infections [38]. Another recent study demonstrated that downy mildew-infected *A. thaliana* plants conditioned the soil for resistance-inducing activity, providing protection against this pathogen in consecutive sowings [39]. Such legacies may have strong implications in the processes selecting genotypes across generations, and should be taken into account when studying to process of niche construction [40—42] (Box 1).

Signaling danger between plants: a neighborhood watch

In situations of biotic stress, plants release a cocktail of compounds above and belowground, such as VOCs, root exudates, or small peptides. Neighboring plants can detect these signals and activate their own defense system to be protected in case of future attacks [43]. This phenomenon is called eavesdropping [44] and is well known in response to insects, where VOCs are involved [9,20,45].

Recent findings demonstrate that eavesdropping is not limited to defense against insects but also occurs on pathogen attack (Table 1). Indeed, systemic acquired resistance (SAR), a defense priming mechanism initially discovered between infected and uninfected tissues within the same plant [46], was observed between neighboring plants [47,48]. Volatile monoterpenes emitted from bacterial-infected leaves moved to distant leaves of the same plant (within-plant SAR) but also to leaves of neighboring plants, and activated an SA-associated immunity (between-plant SAR) through classical SAR signaling *LLP1* and *AZI1* genes. The activation of theses specific genes also drove a positive feedback loop stimulating monoterpene biosynthesis and emission, potentially promoting the generation of a wave of plant-derived volatile defense signals moving

between leaves of neighboring plants [48**]. In another sophisticated experimental setup, signaling was evaluated between plants on which eggs (or egg extracts) were deposited and distant bacteria-infected plants [49**]. An uncharacterized soil-born signal from plants stimulated by eggs diffused up to 6 cm away to neighbor plants where it triggered an increase of bacterial resistance in leaf tissues. While this phenomenon enhanced SA production in the receiver plant, it did not require a functional production of SA in the sender plant.

Quite surprisingly, plants can also detect signals of danger from heterospecific neighbors that boost their defense [50*]. For example, cis-3-hexenyl acetate, an herbivore-induced plant volatile released from most plants, has been shown to prime defense in numerous plants, to reduce herbivory in lima bean [51], and to increase wheat resistance against the head blight fungal pathogen *Fusarium graminearum* [52]. Similarly, soybean plants exposed to volatiles from wounded-cut golden-rods showed less damage upon herbivory attack by *Spodoptera litura* larvae, in the field and in laboratory conditions [53**]. Such interspecific eavesdropping may protect different plant species within a community from generalist herbivores.

Ecological and agronomical relevance
In the field of community ecology, the competition for resources is a *usual suspect* for explaining the outcome of plant—plant interactions [54]. Inversely, exchange of signals between plants could lead to the emergence of cooperation [55—57] and altruistic behavior [58]. From such ecological perspective, it is noteworthy that with a few exceptions [14,15,59], most plant—plant interactions reviewed here have positive effects on plant immunity or biotic stress resistance (Figure 1; Table 1). Including pathogens back to the (ecological) game could help solving a long-term paradox coming from opposing predictions between ecological and evolutionary theories (niche and kin selection theories, respectively [60—62]). Indeed, while close relatives should compete more for the same resources (niche theory), leading to competitive exclusion, recognizing and collaborating with relatives is crucial for organisms living together to reduce competition among them (kin selection theory). In that respect, the fitness loss due to competition could be counter-balanced by the benefits due to enhanced resistance provided by increased immunity.

Resistance to pests and pathogens is also crucial in an agricultural context. Using species or genotypic mixtures at the field level is a well-known way to reduce pathogen propagation [63—67] through inoculum dilution in particular [70,71]. Because inoculum dilution is only efficient when inoculum comes from within the field, the reviewed evidences that one plant may induce immunity in neighboring plants are very promising because it may provide resistance to inoculum from outside the field. Again, the biological processes mediating this phenomenon are urgent to understand because they could be further mobilized in the design of intercropping systems [72,73] and varietal mixtures [74] (Box 1).

Conclusions
The recent studies reporting the effect of plant—plant interactions on immunity and resistance indicate that this phenomenon is widespread. It involves several biological processes and many questions remain to be answered (Box 1). Besides the genes and molecules underlying these processes to be discovered, the proposed framework (Figure 1) has broad ecological and agronomical consequences and may help our efforts to understand of how community are built in natural ecosystems and how we can built plant assemblages in crop fields that better resist to pests and pathogens.

Declaration of competing interest
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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