The root of plant-plant interactions: Belowground special cocktails

Laura Mathieu, Elsa Ballini, Jean Benoît Morel, Louis-Valentin Méteignier

To cite this version:

Laura Mathieu, Elsa Ballini, Jean Benoît Morel, Louis-Valentin Méteignier. The root of plant-plant interactions: Belowground special cocktails. Current Opinion in Plant Biology, 2024, 80, pp.102547. 10.1016/j.pbi.2024.102547 . hal-04622627

HAL Id: hal-04622627
https://hal.inrae.fr/hal-04622627v1

Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Plant Biology

The root of plant-plant interactions: Belowground special cocktails

Laura Mathieu, Elsa Ballini, Jean-Benoit Morel and Louis-Valentin Méteignier

Abstract

Plants interact with each other via a multitude of processes among which belowground communication facilitated by specialized metabolites plays an important but overlooked role. Until now, the exact targets, modes of action, and resulting phenotypes that these metabolites induce in neighboring plants have remained largely unknown. Moreover, positive interactions driven by the release of root exudates are prevalent in both natural field conditions and controlled laboratory environments. In particular, intraspecific positive interactions suggest a genotypic recognition mechanism in addition to non-self perception in plant roots. This review concentrates on recent discoveries regarding how plants interact with one another through belowground signals in intra- and interspecific mixtures. Furthermore, we elaborate on how an enhanced understanding of these interactions can propel the field of agroecology forward.

Addresses

PHIM Plant Health Institute, Univ Montpellier, INRAE, CIRAD, Institut Agro, IRD, Montpellier, France

Corresponding author: Méteignier, Louis-Valentin (louis-valentin.meteignier@inrae.fr)

Current Opinion in Plant Biology 2024, **80**:102547

This review comes from a themed issue on **Physiology and metabolism 2024**

Edited by **Vincent Courdavault** and **Anne Osbourn**

For complete overview of the section, please refer the article collection - Physiology and metabolism 2024

Available online 14 May 2024

https://doi.org/10.1016/j.pbi.2024.102547

Keywords

Plant-plant communication, Allelobiosis, Exudates, Specialized metabolites, Mixtures, Agroecology.

Introduction

The phenotypic effects of belowground molecular communication events between plants were first observed 2300 years ago by Theophrastus, a student of Aristotle. Theophrastus noted that neighboring chickpea plants had growth inhibition effects on the promiscuous focal plant, conditioning the soil in a way that prevented subsequent cropping [1]. Allelopathy was therefore defined as a negative phenotypic response of the focal plant to the presence of specific neighbor plant species secreting allelochemicals. Since then, the range of possible phenotypes induced by neighboring plants on focal plants has expanded significantly, including positive effects defined as allelobiosis [2]. Positive plant-plant interaction effects encompass higher land use efficiency and protein content in seeds [3], decreased disease severity [4] and pesticide use [5], and higher tolerance to drought stress [6] highlighting plant-plant interactions as a tool toward a more sustainable agriculture.

These various effects and other plant-plant interaction-dependent phenotypes, such as changes in root placement in intra- and interspecific interactions, indicate that multiple mechanisms coexist to detect neighbor roots. The detection of non-self roots can be defined as the perception of another organism regardless of the genetic distance [7], while genotypic recognition, a subtype of non-self detection, was defined as the recognition of roots of the same species but not the same genotype, i.e., intraspecific interaction mediated by a putative allorecognition mechanism [8]. Another mechanism claimed as “kin recognition” was also reported [9]. However, kin strictly refers to direct family relationships (parent-offspring from a unique reproduction event) and the evidence supporting the existence of such a mechanism is limited [10—12], with most studies focusing on distinguishing genetically close from genetically distant individuals. Recent studies provide mechanistic insights into non-self detection in intra- and interspecific interactions, while the mechanisms underlying genotypic recognition remain unknown, as emphasized in this review.

Specific allelochemicals produced in above- and belowground organs by specialized metabolic pathways are involved in non-self-induced effects [13]. The role of above-ground specialized volatile metabolites in plant-plant interactions is well-documented, including their molecular mechanisms of action and their roles at the ecological scale [14,15]. In contrast, the mechanisms controlling plant-plant interactions through belowground signals in root exudates are much less understood, particularly in intraspecific interactions [13]. Recent studies indicate that the mechanisms are numerous and complex. Root exudates refer to dynamic and growth condition-specific [16] molecules produced by the roots and released in the rhizosphere, where their effects on the microbiome [17] and the turnover of soil organic matter are well-described [18]. Root exudates contain a plethora of potentially bioactive molecules such as soluble and volatile specialized metabolites (allelochemicals and hormones), peptides, DNA, RNA, carbohydrates, and even cells defined as border cells [19–21], and their roles in plant-plant interactions are emerging. Here, exploring recent findings in both intra- and interspecific plant-plant interactions, we propose strategies to discover the exuded molecules involved in genotypic recognition that could contribute to novel biosolutions and breeding programs to accelerate agroecological crop farming.

Allelobiosis, the neglected bright side of allelochemical communication suggests novel molecular mechanisms

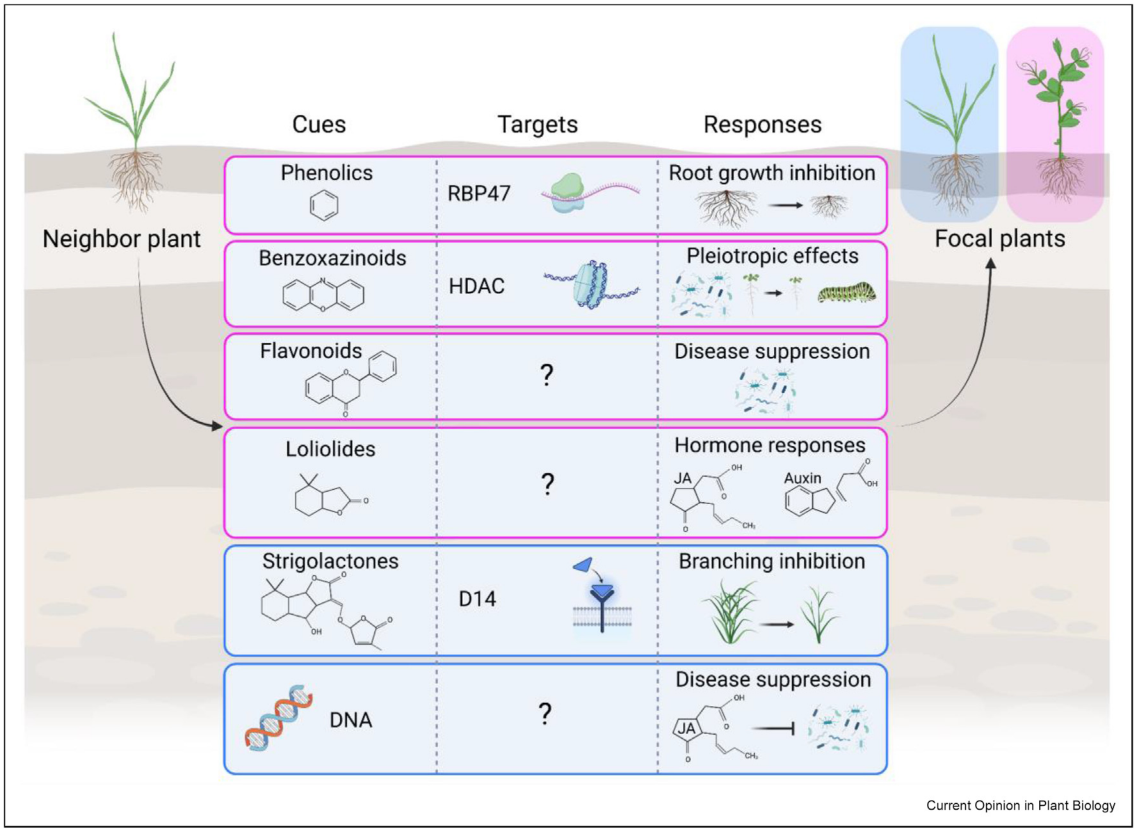
While plant-plant interactions were initially described as having negative effects, it is now clear that they can also have positive outcomes. A comprehensive 50-year interspecific plant community succession study revealed that positive plant-plant interactions are widespread in native plant communities and protect native communities against exotic species invasion, particularly in the early stages of plant-plant interactions before competition for resources intensifies [22]. Additionally, in mixtures of species with low phylogenetic distance, the negative effects were less prominent than in mixtures with high phylogenetic distance [23]. In crops, allelobiosis is also pervasive as reported in maize intercroppings that enable higher land use efficiency and seed protein content [3], and in intraspecific rice and wheat mixtures where specific neighbor genotypes induce decreased disease severity in specific focal genotypes [24]. Thus, the studies highlighted above demonstrate that plant-plant interactions can produce allelobiotic effects, a less understood phenomenon in comparison to allelopathy. Both allelopathy and allelobiosis coexist in nature and are achieved through the release of specialized metabolites by neighboring plants, inducing either negative or positive effects on focal phenotypes, respectively [25]. A major question in the field of research on plant-plant interactions is to identify and understand the molecular mechanisms underlying positive effects.

Several external factors can affect allelochemical effects. Soil chemistry strongly impacts the direction of allelochemical effects. Notably, benzoxazinoids-conditioned soil with maize can either promote [26] or suppress [27] the growth of specific wheat varieties relative to soil chemistry. Moreover, recent studies indicate other unknown mechanisms working together with allelochemical communication. Native plant mixtures exuding less flavonoids and strigolactones than invasive mixtures recruited fewer mutualistic soil microbes while developing positive effects, suggesting allelobiosis does not depend on the soil microbiome [28]. In rice, allelopathic cultivar mixtures with close genetic proximity produced fewer allelochemicals than more genetically distant allelopathic cultivar mixtures. Yet, they inhibited the growth of multiple neighboring weeds to a greater extent without significantly altering the soil microbiome [29], again minimizing the role of the microbiome and indicating that in addition to soil chemistry, mixture effects might hinge on a genotypic recognition mechanism.

In line with that, a genome-wide association study (GWAS) has uncovered a neighbor QTL (quantitative trait loci) associated with modulation of disease severity in a focal plant genotype. To achieve that, the authors quantified disease severity on a single focal plant genotype in binary mixture with ∼250 distinct rice genotypes. Importantly, changes in gene expression were observed in the focal rice genotype based on the neighbor haplotype at the identified QTL [30]. In addition, decreased disease severity in wheat intraspecific mixtures depended on the genotypic identity of the neighbor [24]. Decreased disease severity remained in sterilized soil or when artificially separating aboveground infected or healthy organs, but not when preventing physical/chemical contact between the root systems [31]. The evidence described above together with older studies shows that roots detect and respond to neighbors via allelochemicals, and can take into account the genetic distance through an allorecognition mechanism likely occurring at the root tip [8] where specialized metabolites [32] and border cells [33] are produced.

Since belowground metabolites involved in plant-plant interactions are so far generic as exposed below (Figure 1), and because specialized metabolites diversity is quantitative rather than qualitative at the intraspecific level [34], it seems unlikely that a single one can mediate intraspecific interaction. Moreover, a recent meta-analysis assessing the impact of allelopathic plants and exudates on the performances of focal plants showed that the predominant negative effects were variable and less pronounced in plant-plant co-culture conditions compared to single molecule treatments. This indicates that effects of single allelochemicals can not be extrapolated to co-culture-induced effects [23]. We thus propose that the cocktail of molecules contained in exudates could be causative of intra- and interspecific plant-plant interactions, including signals displaying the genetic distance such as peptides and

Figure 1



Identified cues, targets, and responses involved in plant-plant interactions. The left panel displays molecules identified as neighbor cues. Cognate host targets are shown when demonstrated. However, no targets have been identified yet for flavonoids, loliolides, and DNA. The right panel schematizes focal plant responses. Created with BioRender.com under agreement #BC26KGYHP0.

DNA. Collectively, these studies indicate that numerous mechanisms play a role in belowground plant-plant interactions, among which the impact of a genotypic recognition mechanism might have been masked by confounding factors.

Mechanisms of allelochemical-mediated plant-plant interactions

To date, allelochemicals mechanistically involved in belowground plant-plant interactions are composed by three distinct scaffolds: phenolics, indole-containing rings, and terpenes. Derived from the shikimic acid pathway, phenolic acids, flavonoids and benzoxazinoids mediate interspecific plant-plant interactions. Two recent studies highlighted the phenolic ring as a regulator of plant-plant interactions. In the first publication [35], novel phenolic acid receptors were searched based on the evidence that some of them such as salicylic acid induce phase-separated RNA bodies that regulate translation in animals and plants. Salicylic acid and other phenolic acids interacted with contrasting affinities to the RNA binding protein and translational regulator RBP47 *in vitro*, and induced global translational shutdown and root growth inhibition *in vivo* (Figure 1). By using allelopathic or non-allelopathic rice varieties in co-culture with wild-type or *rbp47* mutant Arabidopsis plants, seedling emergence was affected by allelopathic rice in comparison to non-allelopathics. In comparison, emergence rate inhibition was not observed in the *rbp47* mutant, although this could be due to germination defects of the mutant itself. However, decomposed straws of allelopathic or non-allelopathic rice induced RNA granule formation in Arabidopsis roots but the translational activity within root cells was not reported. Although some evidence supports the role of neighbor phenolic acids in the translational regulation of focal plants, the mechanism remains to be formally demonstrated in co-culture conditions [35] (Figure 1). A second independent study involved a phenolic acid-related metabolite in belowground plant-plant interactions. Using an elegant bioassay-guided exudate fractionation of *Vicia faba* infested with an aphid herbivore, the study shows that the non-protein amino acid L-DOPA triggered a systemic signal in uninfested *V. faba* neighbor plants leading to volatile organic compound emission that attracted a parasitoid of the aphid herbivore [36]. The potential binding of L-DOPA to RBP47 remains to be tested.

Benzoxazinoids are synthesized by specific grasses such as maize, wheat, and a few dicots [37], and were initially considered as herbicides and herbivore deterrents. They are structurally analogous to well-described inhibitors of histone deacetylases and indeed inhibit growth and genome-wide deacetylation of H3K27 when exogenously applied on Arabidopsis seedlings *in vitro* [38] (Figure 1). At the same time, benzoxazinoids shape the maize root microbiota that in turn modulate plant defense responses [39—41]. In addition, maize-peanut intercropping performances rely on the recruitment of siderophore-synthetizing *Pseudomonas* sp., which improved peanut iron nutrition while the contribution of maize-secreted benzoxazinoids in this process was not reported [42] although they act as phytosiderophores in the soil [27]. Positive effects of maize-conditioned soils were observed on wheat yield as compared to soil conditioned with a benzoxazinoid-depleted maize mutant line in field conditions [26]. In this specific context, the soil microbiota signature was equivalent in both soils, suggesting that increased wheat yield was independent of the root microbiota [26]. Yet, the relative contributions of chromatin regulation and the microbiome remain to be assessed in maize intercroppings.

In tomato-potatoonion intercropping, potatoonion-secreted taxifolin induced global quantitative changes in tomato root exudates. These changes were associated with the recruitment of *Bacillus* sp. in the soil that were required to reduce Verticillium wilt disease, either by direct antagonism or indirectly by priming tomato defenses [43]. Although some mechanisms remain to be elucidated in this tomato-potatoonion intercrop, the study by Zhou et al. has suggested that roots of healthy plants communicate to “cry for help” against a disease-causing fungus (Figure 1). Another study highlighted that higher amounts of flavonoids were observed in legumes when intercropped with durum wheat supporting a dynamic regulatory role of flavonoids in plant-plant interactions [44]. However, flavonoid transporters and receptors are yet to be identified.

Loliolides derive from the carotenoid biosynthesis pathway and are involved in interspecific interactions. Loliolide biosynthesis is induced by biotic and abiotic stress and induces jasmonic acid-related responses and the biosynthesis of defense metabolites, but loliolide targets remain unknown (Figure 1) [45]. In wheat-Arabidopsis co-culture experiments, loliolides from Arabidopsis induced benzoxazinoid accumulation in wheat that in turn mediated the redistribution of auxin receptors in Arabidopsis roots, expanding the role of loliolide in regulating auxin metabolism (Figure 1) [46].

Strigolactones are ubiquitous hormones that derive from carotenoids similar to loliolides and regulate parasitic plant-plant interactions in specific soil chemical contexts [47]. Recently, strigolactones were involved in neighbor root detection in pea and rice plants grown in hydroponics and pure conditions. The authors showed very elegantly that an intact strigolactone biosynthesis pathway in the neighbor was required for shoot branching regulation in focal plants. Likewise, intact perception by the cognate strigolactone receptor was required in focal plants for the regulation of shoot branching [48,49] (Figure 1). Taken together, the studies reviewed above show that chromatin and translational regulation are involved in plant-plant interactions and that further work is needed to understand how allelochemicals are exuded and perceived.

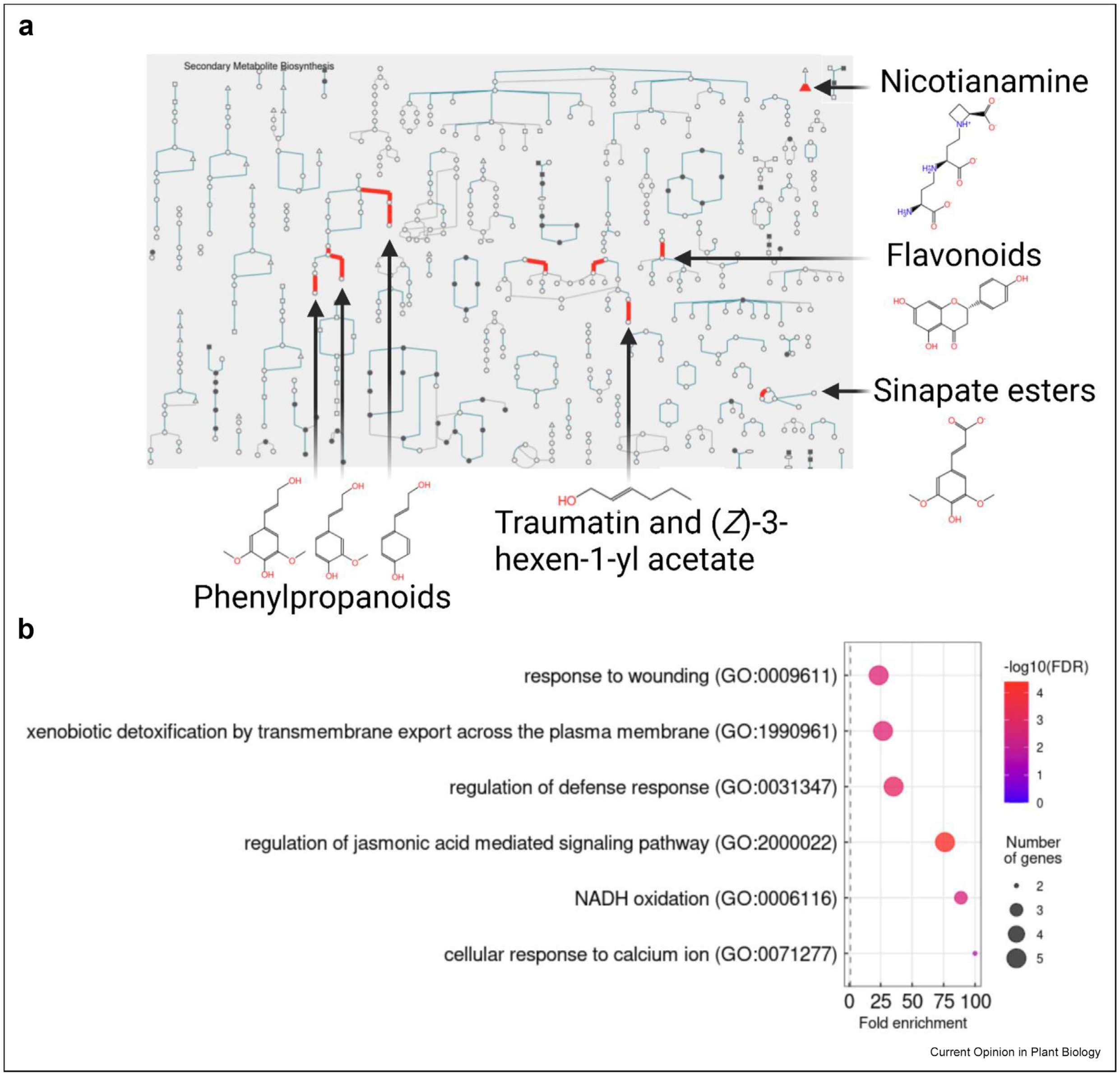
What else except specialized metabolites?

Exudates form an intricate matrix of biomolecules that includes soluble and volatile metabolites, and DNA, to which border cells add complexity [50]. Recent evidence suggests that self-DNA can adversely affect plant growth both in natural environments and controlled laboratory settings, an effect not observed with non-self DNA [51]. Although it remains unclear how self-DNA could be distinguished from non-self DNA, self-DNA induced jasmonic acid-dependent defense responses and growth inhibition [52] (Figure 1). Extracellular self-DNA also plays a crucial role in forming a matrix essential for border cell integrity at the root tip [50]. Single-cell RNA sequencing analysis of wheat roots revealed the unique transcriptomic signature of border cells [33]. A more detailed exploration of the border cell transcriptome via metabolic network enrichment analysis confirmed that enzymes critical for the biosynthesis of phenolic acids, flavonoids and volatiles [53,54]—which all play significant roles in plant-plant interactions—are expressed (illustrated in Figure 2a). Moreover, gene ontology analysis of biological processes revealed that the 100 most expressed genes in border cells belong to signaling-related and xenobiotics export ontologies (Figure 2b). This suggests that border cells could express missing transporters and receptors responsible for export and/or detection of the allelochemicals presented in Figure 1. Considering these insights, we posit that delving into the functional biology of border cells might uncover novel mechanisms of plant-plant interactions that have yet to be elucidated.

Perspectives

Allelochemicals are vital in how plants interact with one another and hold a key to fostering sustainable agriculture through the creation of natural products-based biosolutions and the improvement of crop diversification practices. We propose that there are still undiscovered cues/signals in root exudates that act in addition to allelochemical-dependent interplant communication,

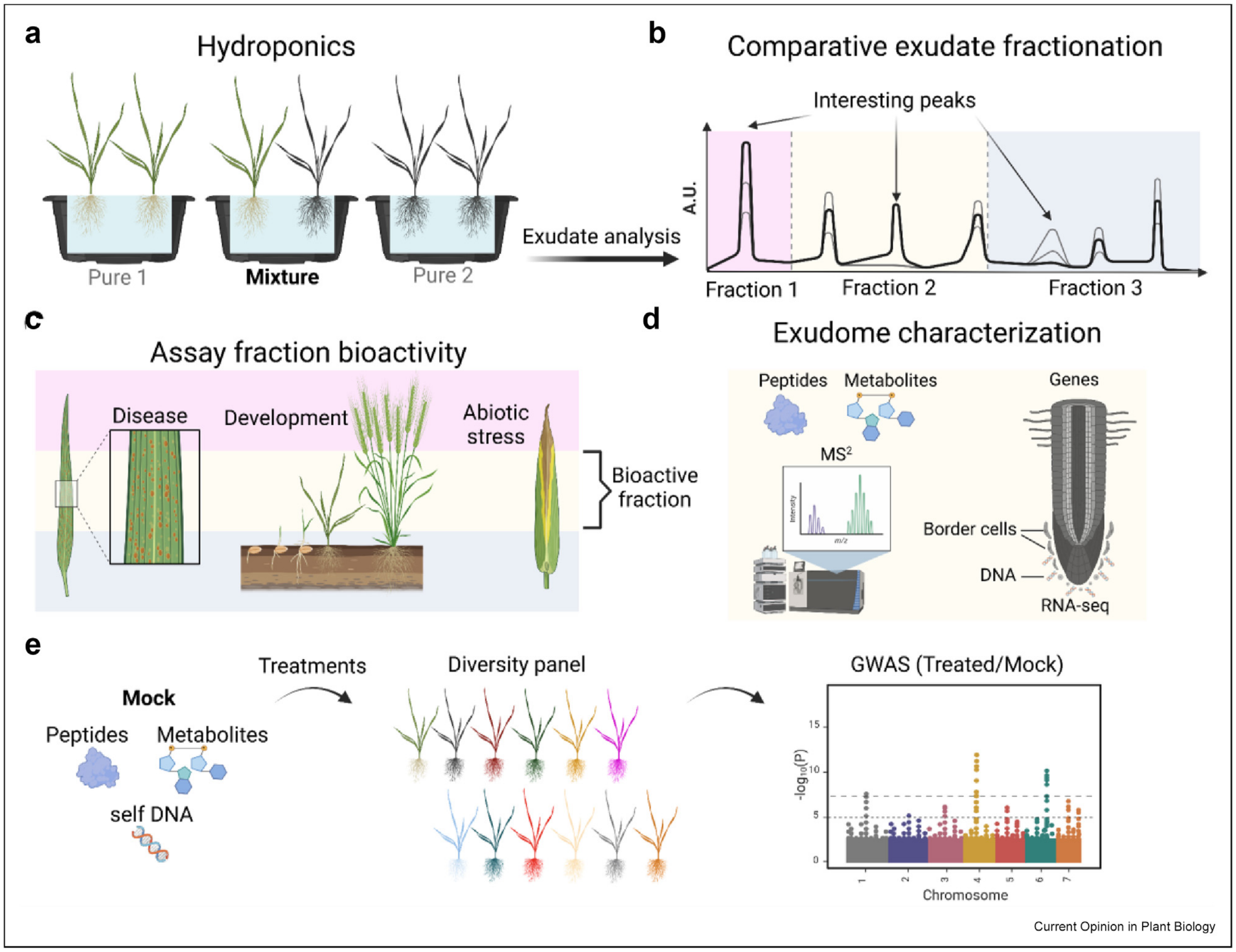
Figure 2



Potential significance of border cells in plant-plant interaction functional studies. a, Arabidopsis orthologs of the 100 most highly expressed genes in wheat border cells were analyzed using the AraCyc cellular overview tool. Biosynthesis genes were highlighted in red on the Arabidopsis specialized metabolic map. **b**, The 100 most highly expressed genes in bread wheat border cells, as identified by scRNA-seq [33], were subjected to gene ontology analysis using the Panther database with bread wheat genes as a background. Created with BioRender.com under agreement #ZX26KK8TMQ.

particularly in intraspecific interactions. To identify these elusive signals and their cognate receptors, we propose a holistic approach that expands a bioassay-guided identification approach of root allelochemicals [36], as illustrated in Figure 3. Here, exudates are collected from hydroponically grown plants (Figure 3a) and then fractionated using chromatography (Figure 3b). The effects of different exudate fractions that change in mixtures on focal plant phenotypes are studied to identify fractions potentially involved in plant-plant interactions (Figure 3c). Characterization of exudates present in this fraction using mass spectrometry and RNA sequencing could allow the identification the causative molecules (Figure 3d). With sufficient amounts of the validated fractions, a GWAS could be performed to identify the loci involved in focal plant responses to the tested exudate (Figure 3d). Although allelobiosis has proven effective in the field, the lack of a molecular framework has slowed the breeding of allelobiotic varieties. The method proposed in Figure 3

Figure 3



Current Opinion in Plant Biology

Untargeted approaches for the identification of genotypic recognition signaling pathways. a. Mixtures are cultivated hydroponically to facilitate easy access to root exudates and their dynamics [16]. **b**, The exudates from the mixtures of interest are fractionated using HPLC (High-Performance Liquid Chromatography). **c**, The focal plant is exposed to exudate fractions based on qualitative and quantitative changes in the mixture when compared to pure samples. The fraction showing effects on various phenotypes is selected for further characterization. **d**, The protein and metabolite content of bioactive fractions are identified through untargeted mass spectrometry, and root RNA-seq data are used for candidate gene identification. High-priority peptides, metabolites, or pathways can then be validated through reverse genetics. **e**, Validated molecules can be used to treat diversity panels and compare the responses of individuals relative to mock treatment on relevant traits as identified in C. Genome-Wide Association Study can identify genomic regions potentially containing receptor genes and other genes involved in signal perception. Created with BioRender.com under agreement #UF26KGYFBB.

could offer new genetic markers for breeding programs and could advance our understanding on the cues that enable plants to detect and respond to intraspecific neighbors. In addition to gene/molecule-based approaches, trait-based approaches can also be used to harness the positive effects in intra- and interspecific mixtures [55,56]. In Arabidopsis intraspecific mixtures, 85% of focal biomass variation was explained by 11 neighbor loci enriched for genes involved in salicylic acid-related processes [57], a prominent phenolic acid in plant defense and plant-plant communication as highlighted here (Figures 1 and 2a). The potential utility of allelochemicals goes beyond their utilization as biological control agents. They can be targeted directly through marker-assisted selection, incorporating both functional and quantitative genetics, or indirectly through trait-driven methods. However, to fully leverage these approaches, a deeper comprehension of the dynamics behind allelochemical synthesis and plant-plant interactions is needed. This understanding is crucial for creating effective programs for selecting plant mixtures that can sustain agroecosystems.

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 paper.

Data availability

Data used in Figure 2 are available in Table S2 of [33] (https://doi.org/10.1186/s13059-023-02908-x).

Acknowledgments

We acknowledge funding from the ANR MoBiDiV project (ANR-20-PCPA-0006) and the Plant Health and Environment department of INRAE.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pbi.2024.102547.

References

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest
** of outstanding interest

1. Rice EL: **Allelopathy — an overview**. In *Chemically mediated interactions between plants and other organisms*. Edited by Cooper-Driver GA, Swain T, Conn EE, Springer US; 1985:81–105.
2. Ninkovic V, Glinwood R, Pettersson J: **Communication between undamaged plants by volatiles: the role of allelobiosis**. In *Communication in plants*. Edited by Baluška F, Mancuso S, Volkmann D, Springer; 2006:421–434.
3. Li C, Stomph T-J, Makowski D, Li H, Zhang C, Zhang F, van der Werf W: **The productive performance of intercropping**. *Proc Natl Acad Sci* 2023, **120**, e2201886120.
4. Pélissier R, Violle C, Morel J-B: **Plant immunity: good fences make good neighbors?** *Curr Opin Plant Biol* 2021, **62**, 102045.
5. Guinet M, Adeux G, Cordeau S, Courson E, Nandillon R, Zhang Y, Munier-Jolain N: **Fostering temporal crop diversification to reduce pesticide use**. *Nat Commun* 2023, **14**:1–11.
6. Barkaoui K, Volaire F: **Drought survival and recovery in grasses: stress intensity and plant-plant interactions impact plant dehydration tolerance**. *Plant Cell Environ* 2023, **46**:1489–1503.
7. Gruntman M, Novoplansky A: **Physiologically mediated self/non-self discrimination in roots**. *Proc Natl Acad Sci* 2004, **101**:3863–3867.
8. Fang S, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN: **Genotypic recognition and spatial responses by rice roots**. *Proc Natl Acad Sci* 2013, **110**:2670–2675.
9. Anten NPR, Chen BJW: **Detect thy family: mechanisms, ecology and agricultural aspects of kin recognition in plants**. *Plant Cell Environ* 2021, **44**:1059–1071.
10. Dudley SA, File AL: **Kin recognition in an annual plant**. *Biol Lett* 2007, **3**:435–438.
11. File AL, Klironomos J, Maherali H, Dudley SA: **Plant kin recognition enhances abundance of symbiotic microbial partner**. *PLoS One* 2012, **7**, e45648.
12. Pickles BJ, Wilhelm R, Asay AK, Hahn AS, Simard SW, Mohn WW: **Transfer of 13C between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas**. *New Phytol* 2017, **214**:400–411.
13. Yoneyama K, Bennett T: **Whispers in the dark: signals regulating underground plant–plant interactions**. *Curr Opin Plant Biol* 2023, https://doi.org/10.1016/j.pbi.2023.102456.
14. Kessler A, Mueller MB, Kalske A, Chautá A: **Volatile-mediated plant–plant communication and higher-level ecological dynamics**. *Curr Biol* 2023, **33**:R519–R529.
15. Barbour MA, Kliebenstein DJ, Bascompte J: **A keystone gene underlies the persistence of an experimental food web**. *Science* 2022, **376**:70–73.
16. McLaughlin S, Zhalnina K, Kosina S, Northen TR, Sasse J: **The core metabolome and root exudation dynamics of three phylogenetically distinct plant species**. *Nat Commun* 2023, **14**:1649.
17. Ghatak A, Chaturvedi P, Waldherr S, Subbarao GV, Weckwerth W: **PANOMICS at the interface of root–soil microbiome and BNI**. *Trends Plant Sci* 2022, https://doi.org/10.1016/j.tplants.2022.08.016.
18. Chari NR, Taylor BN: **Soil organic matter formation and loss are mediated by root exudates in a temperate forest**. *Nat Geosci* 2022, **15**:1011–1016.
19. Wang N-Q, Kong C-H, Wang P, Meiners SJ: **Root exudate signals in plant–plant interactions**. *Plant Cell Environ* 2021, **44**:1044–1058.
20. Borniego ML, Innes RW: **Extracellular RNA: mechanisms of secretion and potential functions**. *J Exp Bot* 2023, **74**:2389–2404.
21. Driouich A, Gaudry A, Pawlak B, Moore JP: **Root cap–derived cells and mucilage: a protective network at the root tip**. *Protoplasma* 2021, **258**:1179–1185.
22. Yin D, Meiners SJ, Ni M, Ye Q, He F, Cadotte MW: **Positive interactions of native species melt invasional meltdown over long-term plant succession**. *Ecol Lett* 2022, **25**:2584–2596.
23. Zhang Z, Liu Y, Yuan L, Weber E, van Kleunen M: **Effect of allelopathy on plant performance: a meta-analysis**. *Ecol Lett* 2021, **24**:348–362.
24. * Pélissier R, Ballini E, Temple C, Ducasse A, Colombo M, Frouin J, Qin X, Huang H, Jacques D, Florian F, *et al.*: **The genetic identity of neighboring plants in intraspecific mixtures modulates disease susceptibility of both wheat and rice**. *PLoS Biol* 2023, **21**, e3002287.

This study demonstrates that plant disease severity in specific focal wheat and rice genotypes depends on indirect genetic effects from specific neighbor genotypes.

25. Kong C-H, Li Z, Li F-L, Xia X-X, Wang P: **Chemically mediated plant–plant interactions: allelopathy and allelobiosis**. *Plants* 2024, **13**:626.
26. Gfeller V, Waelchli J, Pfister S, Deslandes-Hérold G, Mascher F, Glauser G, Aeby Y, Mestrot A, Robert CA, Schlaeppi K, *et al.*: **Plant secondary metabolite-dependent plant-soil feedbacks can improve crop yield in the field**. *Elife* 2023, **12**, e84988.
27. Hu L, Wu Z, Robert CAM, Ouyang X, Züst T, Mestrot A, Xu J, Erb M: **Soil chemistry determines whether defensive plant secondary metabolites promote or suppress herbivore growth**. *Proc Natl Acad Sci* 2021, **118**, e2109602118.
28. Yu H, He Y, Zhang W, Chen L, Zhang J, Zhang X, Dawson W, Ding J: **Greater chemical signaling in root exudates enhances soil mutualistic associations in invasive plants compared to natives**. *New Phytol* 2022, **236**:1140–1153.
29. Xu Y, Cheng H-F, Kong C-H, Meiners SJ: **Intra-specific kin recognition contributes to inter-specific allelopathy: a case study of allelopathic rice interference with paddy weeds**. *Plant Cell Environ* 2021, **44**:3709–3721.
30. Pélissier R, Ducasse A, Ballini E, Frouin J, Violle C, Morel J-B: **A major genetic locus in neighbours controls changes of gene expression and susceptibility in intraspecific rice mixtures**. *New Phytol* 2023, **238**:835–844.
31. Pélissier R, Buendia L, Brousse A, Temple C, Ballini E, Fort F, Violle C, Morel J-B: **Plant neighbour-modulated susceptibility**

to pathogens in intraspecific mixtures. *J Exp Bot* 2021, **72**: 6570–6580.

32. Méteignier L-V, Nützmann H-W, Papon N, Osbourn A, Courdavault V: **Emerging mechanistic insights into the regulation of specialized metabolism in plants**. *Nat Plants* 2023, **9**:22–30.

33. Zhang L, He C, Lai Y, Wang Y, Kang L, Liu A, Lan C, Su H, Gao Y, Li Z, *et al.*: **Asymmetric gene expression and cell-type-specific regulatory networks in the root of bread wheat revealed by single-cell multiomics analysis**. *Genome Biol* 2023, **24**:65.
**
By applying single-cell multi-omics in wheat roots, the authors provide the transcriptomic signature of border cells and validate the expression of border cell-specific marker genes.

34. Li D, Halitschke R, Baldwin IT, Gaquerel E: **Information theory tests critical predictions of plant defense theory for specialized metabolism**. *Sci Adv* 2020, **6**, eaaz0381.

35. Xie Z, Zhao S, Li Y, Deng Y, Shi Y, Chen X, Li Y, Li H, Chen C, Wang X, *et al.*: **Phenolic acid-induced phase separation and translation inhibition mediate plant interspecific competition**. *Nat Plants* 2023, https://doi.org/10.1038/s41477-023-01499-6.
*
This study shows that phenolic acids bind to an RNA-binding protein regulating translation and that rice-mediated allelopathic effects on Arabidopsis could rely on this mechanism.

36. Cascone P, Vuts J, Birkett MA, Dewhirst S, Rasmann S, Pickett JA, Guerrieri E: **L-DOPA functions as a plant pheromone for belowground anti-herbivory communication**. *Ecol Lett* 2023, **26**:460–469.
**
The authors fractionated *Vicia faba* root exudates, tested the bioactivity of fractions on healthy plants, and identified L-DOPA as a cue in triggering aphid tolerance in uninfested neighbor *Vivia faba* plants.

37. Wu D, Jiang B, Ye C-Y, Timko MP, Fan L: **Horizontal transfer and evolution of the biosynthetic gene cluster for benzoxazinoids in plants**. *Plant Commun* 2022, **3**, 100320.

38. Venturelli S, Belz RG, Kämper A, Berger A, von Horn K, Wegner A, Böcker A, Zabulon G, Langenecker T, Kohlbacher O, *et al.*: **Plants release precursors of histone deacetylase inhibitors to suppress growth of competitors**. *Plant Cell* 2015, **27**:3175–3189.

39. Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, Van Der Heijden MGA, *et al.*: **Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota**. *Nat Commun* 2018, **9**:1–13.

40. Cotton TEA, Pétriacq P, Cameron DD, Meselmani MA, Schwarzenbacher R, Rolfe SA, Ton J: **Metabolic regulation of the maize rhizobiome by benzoxazinoids**. *ISME J* 2019, **13**: 1647–1658.

41. Gfeller V, Thönen L, Erb M: *Root-exuded secondary metabolites can alleviate negative plant-soil feedbacks*. 2023, https://doi.org/10.1101/2023.04.09.536155.

42. Wang N, Wang T, Chen Y, Wang M, Lu Q, Wang K, Dou Z, Chi Z, Qiu W, Dai J, *et al.*: **Microbiome convergence enables siderophore-secreting-rhizobacteria to improve iron nutrition and yield of peanut intercropped with maize**. *Nat Commun* 2024, **15**:839.

43. Zhou X, Zhang J, Rahman MK u, Gao D, Wei Z, Wu F, Dini-Andreote F: **Interspecific plant interaction via root exudates structures the disease suppressiveness of rhizosphere microbiomes**. *Mol Plant* 2023, **16**:849–864.

44. Leoni F, Hazrati H, Fomsgaard IS, Moonen A-C, Kudsk P: **Determination of the effect of Co-cultivation on the production and root exudation of flavonoids in four legume species using LC–MS/MS analysis**. *J Agric Food Chem* 2021, **69**: 9208–9219.

45. Li L-L, Li Z, Lou Y, Meiners SJ, Kong C-H: **(-)-Loliolide is a general signal of plant stress that activates jasmonate-related responses**. *New Phytol* 2023, **238**:2099–2112.

46. Wang C-Y, Li L-L, Meiners SJ, Kong C-H: **Root placement patterns in allelopathic plant–plant interactions**. *New Phytol* 2023, **237**:563–575.

47. Ogawa S, Cui S, White ARF, Nelson DC, Yoshida S, Shirasu K: **Strigolactones are chemoattractants for host tropism in Orobanchaceae parasitic plants**. *Nat Commun* 2022, **13**:4653.

48. Wheeldon CD, Hamon-Josse M, Lund H, Yoneyama K, Bennett T: **Environmental strigolactone drives early growth responses to neighboring plants and soil volume in pea**. *Curr Biol* 2022, **32**:3593–3600.e3.

49. Yoneyama K, Xie X, Nomura T, Yoneyama K, Bennett T: **Supra-organismal regulation of strigolactone exudation and plant development in response to rhizospheric cues in rice**. *Curr Biol* 2022, **32**:3601–3608.e3.

50. Wen F, Curlango-Rivera G, Huskey DA, Xiong Z, Hawes MC: **Visualization of extracellular DNA released during border cell separation from the root cap**. *Am J Bot* 2017, **104**:970–978.

51. Bonanomi G, Zotti M, Idbella M, Termolino P, De Micco V, Mazzoleni S: **Field evidence for litter and self-DNA inhibitory effects on Alnus glutinosa roots**. *New Phytol* 2022, **236**: 399–412.

52. Zhou X, Gao H, Zhang X, Khashi u Rahman M, Mazzoleni S, Du M, Wu F: **Plant extracellular self-DNA inhibits growth and induces immunity via the jasmonate signaling pathway**. *Plant Physiol* 2023, https://doi.org/10.1093/plphys/kiad195.

53. Gfeller V, Huber M, Förster C, Huang W, Köllner TG, Erb M: **Root volatiles in plant–plant interactions I: high root sesquiterpene release is associated with increased germination and growth of plant neighbours**. *Plant Cell Environ* 2019, **42**: 1950–1963.

54. Huang W, Gfeller V, Erb M: **Root volatiles in plant–plant interactions II: root volatiles alter root chemistry and plant–herbivore interactions of neighbouring plants**. *Plant Cell Environ* 2019, **42**:1964–1973.

55. Wuest SE, Peter R, Niklaus PA: **Ecological and evolutionary approaches to improving crop variety mixtures**. *Nat Ecol Evol* 2021, **5**:1068–1077.

56. Moore VM, Peters T, Schlautman B, Brummer EC: **Toward plant breeding for multicrop systems**. *Proc Natl Acad Sci* 2023, **120**, e2205792119.

57. Montazeaud G, Helleu Q, Wuest SE, Keller L: **Indirect genetic effects are shaped by demographic history and ecology in Arabidopsis thaliana**. *Nat Ecol Evol* 2023, https://doi.org/10.1038/s41559-023-02189-4.
**
The authors identified 11 neighbor QTLs responsible for increased biomass in focal Arabidopsis plants and tracked the worldwide demographic history of these loci by studying their frequency in worldwide accessions of Arabidopsis.