



HAL
open science

The ecologically relevant genetics of plant-plant interactions

Claude Becker, Richard Berthomé, P Delavault, Timothée Flutre, Hélène Fréville, Stéphanie Gibot-Leclerc, Valérie Le Corre, Jean Benoît Morel, Nathalie Moutier, Stephane Munos, et al.

► **To cite this version:**

Claude Becker, Richard Berthomé, P Delavault, Timothée Flutre, Hélène Fréville, et al.. The ecologically relevant genetics of plant-plant interactions. *Trends in Plant Science*, 2023, 28 (1), pp.31-42. 10.1016/j.tplants.2022.08.014 . hal-03800896

HAL Id: hal-03800896

<https://hal.science/hal-03800896>

Submitted on 6 Oct 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Opinion

The ecologically relevant genetics of
plant–plant interactions

The international PLANTCOM network, Claude Becker,¹ Richard Berthomé,² Philippe Delavault,³ Timothée Flutre,⁴ H  l  ne Fr  ville,⁵ St  phanie Gibot-Leclerc,⁶ Val  rie Le Corre,⁶ Jean-Benoit Morel,⁷ Nathalie Moutier,⁸ St  phane Mu  nos,² C  line Richard-Molard,⁹ James Westwood,¹⁰ Pierre-Emmanuel Courty,^{6,13} Alexandre de Saint Germain,^{11,13} Ga  tan Louarn,^{12,13} and Fabrice Roux ^{2,13,*}

Interactions among plants have been long recognized as a major force driving plant community dynamics and crop yield. Surprisingly, our knowledge of the ecological genetics associated with variation of plant–plant interactions remains limited. In this opinion article by scientists from complementary disciplines, the international PLANTCOM network identified four timely questions to foster a better understanding of the mechanisms mediating plant assemblages. We propose that by identifying the key relationships among phenotypic traits involved in plant–plant interactions and the underlying adaptive genetic and molecular pathways, while considering environmental fluctuations at diverse spatial and time scales, we can improve predictions of genotype-by-genotype-by-environment interactions and modeling of productive and stable plant assemblages in wild habitats and crop fields.

Why study the genetics of plant–plant interactions?

During the course of its life cycle, a plant can interact directly and/or indirectly, sequentially and/or simultaneously, with multiple neighboring plants. Plant networks include interactions among individuals of different species (i.e., interspecific interactions) and among individuals from the same species (i.e., intraspecific interactions). Concepts, ideas, and experiments developed for decades (Box 1) led plant–plant interactions to be recognized as a major factor shaping plant community structure and evolution [1]. However, in comparison to ecology, genetics has been rarely considered for understanding the functioning of plant communities. Yet, deciphering the genetic and molecular bases of plant–plant interactions would be key for (i) understanding plant community diversity, productivity, and stability [2,3], and (ii) predicting the dynamics of plant communities over several years [4]. This would be especially relevant in the context of plant community shifts driven by global changes [5], and the paradigm change whereby diversity is prioritized to develop more sustainable agro-ecosystems under low input farming systems [6].

However, in comparison with other types of biotic interactions such as plant response to microbial pathogens and symbionts and, to a lesser extent, herbivores, there is still very limited knowledge about the genetics associated with variation of ecologically realistic plant–plant interactions, a discrepancy that may originate from the complexity of establishing experiments involving interactions with neighboring plants (see [7]). There is therefore a need for a thorough understanding of the genetic and molecular bases underlying diverse categories of plant–plant interactions both at the intraspecific and interspecific levels, ranging from competitive to positive interactions [e.g., **facilitation** (see Glossary) and **reciprocal helping**], through asymmetric interactions (i.e., benefits for one of the interacting plants at the expense of the other) such as plant–**parasitic plant** interactions. In

Highlights

A better understanding of plant community diversity, productivity, and stability relies on deciphering the ecological genetics and molecular bases of plant–plant interactions in wild and crop species, which range from competitive to positive interactions.

Compared with other categories of biotic interactions, we have limited knowledge of the genetics associated with natural variation of plant–plant interactions.

Interdisciplinary projects are needed to explore the genetic and molecular underpinnings of key interacting phenotypic traits involved in plant–plant interactions, at complementary observation scales in a complex biotic and abiotic environment.

Our future knowledge on the genetics of plant–plant interactions can fuel models aimed at predicting the best performing and/or stable plant assemblages, leading to alternative and eco-friendly agricultural systems.

¹Genetics, Faculty of Biology, Ludwig Maximilians-University, 82152 Martinsried, Germany

²LIPME, INRAE, CNRS, Universit   de Toulouse, Castanet-Tolosan, France

³US2B, CNRS, Nantes Universit  , Nantes, France

⁴Universit   Paris-Saclay, INRAE, CNRS, AgroParisTech, UMR GQE-Le Moulon, 91190 Gif-sur-Yvette, France

⁵AGAP, Universit   Montpellier, CIRAD, INRAE, Institut Agro, Montpellier, France

⁶Agro  cologie, INRAE, Institut Agro, Universit   du Bourgogne, Universit   Bourgogne-Franche-Comt  , F-21000 Dijon, France

Box 1. Application of modern genetics to historical concepts and ideas on plant–plant interactions

For decades, immeasurable efforts were made to describe the diversity, structure and dynamics of plant communities. The resulting descriptive and correlative studies highlighted key patterns of the functioning of plant communities and were accompanied by theoretical and experimental studies aimed at understanding the processes that generate those patterns [92–94]. Interspecific competition for resources and niche differences are classically proposed as processes to explain stable species coexistence at a local scale [93,95], albeit a limited number of experimental studies support the segregation of plant species along diverse environmental niche axes [96]. Alternatives for explaining species co-existence and hence species diversity, rely, for instance, on the role of competitive ability [97], which corresponds to 'components of fitness defined by differences among neighbors in their abilities to leave descendants when these neighbors make demands on the same resource units and when the combined demands of these neighbors on resources exceed the supply' [98]. The main causes of variation in competitive ability, that is, genetic variation and environmental variation and their interactions, led to several hypotheses on the absence of competitive exclusion over the spatial and time scales under investigation [98]. Of particular importance for this opinion article are:

- (i) the 'environmental heterogeneity hypothesis' assuming that competitive ability is a genetic variable and transitive among plant species and that this genetically based transitivity depends on environmental conditions under which a given species has a superior competitive ability over neighboring species [98].
- (ii) the 'circular networks hypothesis' assuming an environment-independent genetically based intransitivity among plant species [98].
- (iii) the 'competitive combining ability hypothesis' assuming a genetically based intransitivity among genotypes within plant species, which crosses taxonomic boundaries [98]. This genetically based intransitivity at the intraspecific level may be further affected by environmental variation.

Since the 1980s, numerous experimental studies supported the role of genetic variation in competitive ability on community diversity, structure, and dynamics. Either directly by reporting within-species diversity for competitive ability, G×G interactions at various spatial scales and biotic specialization [99–105], or indirectly by reporting the identification of QTLs associated with the response of a focal species to complex plurispecific neighborhoods that cannot be predicted from the identification of QTLs associated with response of the same focal species to bispecific neighborhoods [4,76]. The constant development of ever-more powerful next-generation sequencing technologies paired with extensive traditional ecological studies would certainly help to estimate the relative importance of competitive ability related hypotheses.

line with this, the international PLANTCOM network was set up to gather scientists from complementary disciplines (molecular and cellular biology, chemistry, ecophysiology, functional genetics, ecology, evolutionary biology, quantitative genetics, agronomy, modeling, etc.), for dialogue and exchanges of ideas on the genetics of plant–plant interactions involving wild and crop species. The purpose of PLANTCOM is to promote the emergence of approaches, models, and tools for better managing plant communities within agro-ecosystems and optimizing breeding programs. Based on several brainstorming sessions in 2021, we identified four questions that, in our opinion, deserve particular attention in the coming years and that require the establishment of interdisciplinary projects.

Which phenotypic traits and which connections between them are relevant for the study of plant–plant interactions?

Like other categories of biotic interactions, plant–plant interactions are investigated at complementary observation scales, ranging from single cells to plant communities (Figure 1A), and for a diverse set of phenotypic traits, including molecular, biochemical, functional, and community traits (Figure 1B). During the last decades, phenotypic traits used to for studying plant–plant interactions were dominated by **functional traits** (Figure 1B), in particular in the aboveground parts of plants such as height [8], owing to the difficulty to access belowground traits [9–11]. However, manually phenotyping a large number of such traits on a substantial number of individuals is still a bottleneck. Therefore, it is important to combine accurate trait estimation with nondestructive methods and automated analysis with high-throughput phenotyping, such as for leaf area [12] and internode length [13], although this remains challenging in outdoor conditions [14]. In addition, despite the development of image analysis tools enabling quantitative analysis of root system architecture [15], high-throughput phenotyping on roots is still rare and usually limited to single plants early in their life cycle in controlled conditions.

⁷PHIM Plant Health Institute, Université Montpellier, INRAE, CIRAD, Institut Agro, IRD, Montpellier, France

⁸Institute for Genetics, Environment and Plant Protection (IGEPP), INRAE, Institut Agro, Université Rennes 1, 35650 Le Rheu, France

⁹Université Paris-Saclay, INRAE, AgroParisTech, UMR EcoSys, 78850 Thiverval-Grignon, France

¹⁰School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, VA, USA

¹¹Université Paris-Saclay, INRAE, AgroParisTech, Institut Jean-Pierre Bourgin (JPB), 78000 Versailles, France

¹²INRAE, UR P3F, F-86600, Lusignan, France

¹³These authors contributed equally

*Corresponding author:
fabrice.roux@inrae.fr (F. Roux).

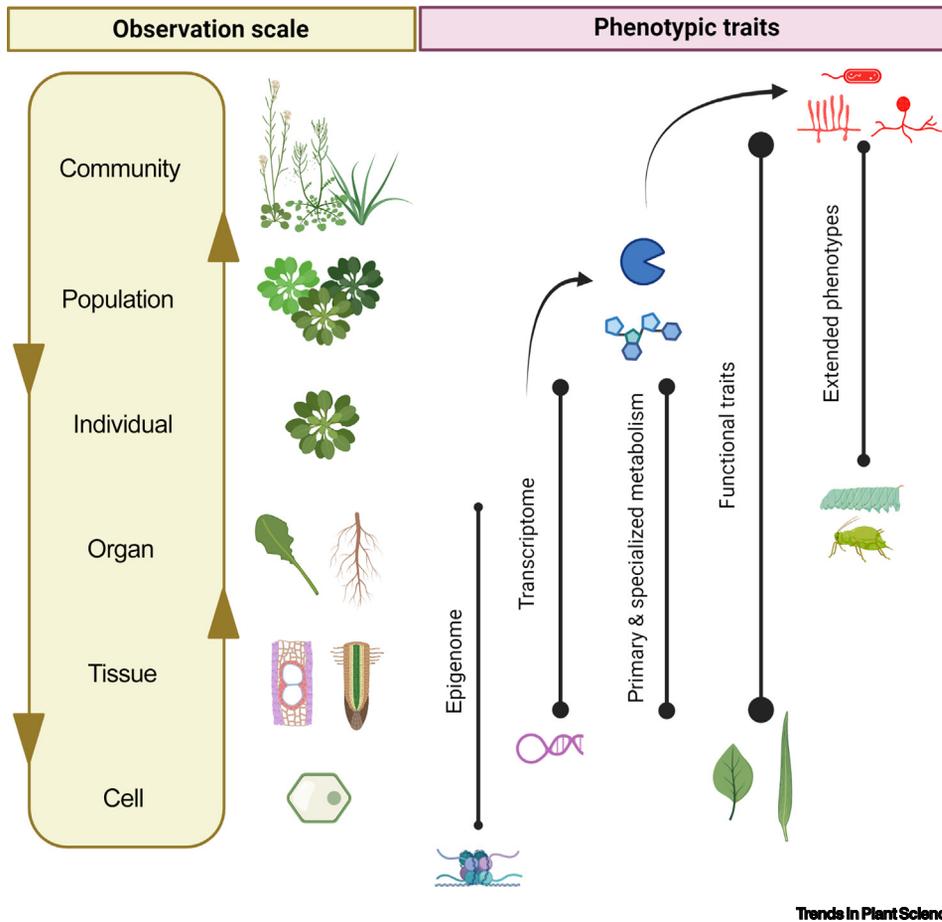


Figure 1. Identification of key traits involved in plant–plant interactions and the relationships between them. Left panel. Observation scales from single cell to plant communities, with *Arabidopsis thaliana* as a focal plant species. At the population scale, different genotypes are represented by different shades of green. At the community scale, *A. thaliana* interacts with other plant species such as *Cardamine hirsuta* and a grass species. Right panel. Illustration of five categories of phenotypic traits measured to study plant–plant interactions, ranging from molecular traits (epigenome, transcriptome and metabolome) to functional and community traits. Solid straight lines depict the range of observation scales for each category of phenotypic traits. The size of the black circles on the extremities of the straight lines illustrates the relative importance in the number of studies on plant–plant interactions reporting results associated with each category of phenotypic traits. Curved lines illustrate an example of the domino effect of changes in transcriptomic profiles on microbial communities, through changes in metabolomic profiles. Created with [BioRender.com](https://www.biorender.com).

Although less studied, other categories of phenotypic traits can shed light on additional and complementary mechanisms involved in plant–plant interactions (Figure 1). In particular, the rise of omics technologies made it possible to phenotype plant–plant interactions at the molecular and biochemical levels. The limited number of transcriptomic studies conducted at the leaf and root levels revealed several classes of candidate genes involved in the response of a plant to the presence of a neighboring plant, including photosynthesis and hormones, nutrient transporters and defense pathways against pathogens [7,16]. Recent progress in single-cell transcriptomics, such as during lateral root initiation [17], would certainly help to capture the first molecular events of neighbor perception occurring in a small number of cells. Epigenetics was recently added to transcriptomics in the quest of individual biomarkers involved in plant–plant interactions [18,19]. For instance, a bidirectional transfer of mRNA was reported between the parasitic plant *Cuscuta pentagona* and the host plants *Arabidopsis thaliana* and tomato

Glossary

Allelochemicals: specialized metabolites produced and released by plants and having allelopathic effects.

Allelopathic interactions: direct or indirect, positive (growth-promoting) or negative (growth-inhibiting) effects, of one plant on another through the release of chemical compounds into the environment.

Co-GWAS: joint association analysis method allowing the description of the genomic landscape of interactions between two organisms, by identifying QTLs associated with genomic regions in both organisms.

Common mycorrhizal network: a continuous network formed by mycorrhizal fungi, which connects interacting plants via their mycelium and allows exchanges of nutrients and other chemical substances between connected plants.

Competition: simultaneous demand by two or more individuals/species for a limiting or non-limiting resource leading to negative interactions among intra- or interspecific individuals.

Eco-transcriptomics and eco-metabolomics: application of transcriptomics and metabolomics to biotic interactions in (agro-)ecologically relevant conditions.

Facilitation: process by which a plant benefits from the presence of another plant. Facilitation is achieved when a genotype alters features of the local environment to the benefit of neighboring genotypes at the intra- or interspecific level.

Functional redundancy: similar ecosystem functionality among plant species within communities. For instance, one plant species with a specific functional trait may substitute for another.

Functional traits: morphological, physiological, and phenological traits that affect individual performance (i.e., growth, reproduction, survival). Functional traits are usually measured at the individual level, and are widely used for comparisons across species.

Holobiont: an ecological or a functional unit, typically a host organism and its network of microbes living on, near or within it.

Over-yielding: a phenomenon of increased community productivity when species/genotypes are grown in a mixture, as opposed to a monospecific/monogenotypic stand.

[20]. More recently, the transfer of microRNAs has been implicated in both parasitic [21] and non-parasitic plant interactions [22]. Still within the framework of identifying individual biomarkers of plant–plant communications, the continuing progress in high-throughput metabolomics revealed key mediators of plant–plant interactions [23], such as specialized metabolites – called **allelochemicals** – including volatile organic compounds [24,25] and root exudates [26]. As an example of **allelopathic interactions**, a reciprocal transfer of secondary metabolites at the root level followed by a root-to-shoot translocation was detected between rye and other crop and weed species [27].

Beyond the individual level, plant–plant interactions can have consequences on the taxonomic diversity, taxonomic composition and functionality (at the genetic and transcriptomic level) of biotic communities such as microbial and arthropod communities, thereby representing extended taxonomic and/or functional phenotypes (Figure 1). For instance, in line with the concept of **holobiont**, the diversity and composition of leaf and rhizospheric microbial communities depend on the identity of interacting plants and whether plants are grown in pure stands or mixtures [28,29]. Another example of a community trait is related to the effect of plant–plant interactions on **common mycorrhizal networks**, which in turn affect nutrient availability for plants growing in subsequent generations [30].

In our opinion, while phenotyping functional traits remains essential to describe plant–plant interactions, molecular and community traits deserve more attention in the foreseeable future, in order to improve our understanding of the domino effect of phenotypic variation involved in plant–plant interactions at complementary integrative levels (Figure 1). This multi-trait analysis requests establishing connections among the different categories of traits listed above, by phenotyping them in the same experimental study. For instance, in *A. thaliana*, combining complementary omics approaches highlighted that the shade avoidance syndrome upon **competition** for light [31] alters the trade-off between plant immunity (by downregulating the expression of defense-associated genes in leaves [32,33]) and starch/carbon metabolism, which in turn triggers a growth rescue by root bacterial communities mediated by the host transcriptional regulator MYC2 [34].

What are the molecular pathways and molecular networks governing plant interactions with neighboring plants?

Beyond using diverse molecules as phenotypic traits to describe plant–plant interactions, a challenge remains to identify and validate the series of genes and/or molecules that act in concert to establish the genetic and molecular dialogue between two neighboring plants. So far, our knowledge of the genetic and molecular pathways underlying plant–microbe and plant–macro-organism interactions mainly relies on a substantial number of large-scale transcriptomics and metabolomics studies [35–37]. By contrast, as previously mentioned, the number of studies addressing changes in global gene expression and metabolic profiles in plants directly challenged by other plants remains limited (Figure 1) [7, 16,38,39]. In addition, despite the rising interest in considering positive interactions to explain plant community composition, productivity and **overyielding** [40], most transcriptomics and metabolomics studies on plant–plant interactions focused on competitive or parasitic interactions [40]. Therefore, conducting **eco-transcriptomics** and **eco-metabolomics** studies on diverse and complementary categories of plant–plant interactions would undoubtedly help to identify the main genetic and molecular mechanisms of plant–plant interactions (Figure 2).

Because extensive genotype-by-genotype (G×G) interactions have been detected both at the inter- and intra-specific levels [41], we stress the need to conduct transcriptomics and metabolomics studies on several pairs of genotypes (Figure 2A). Furthermore, in line with the domino

Parasitic plant: a plant that obtains some or all of its nutrients from another living plant (the host) without contributing to the benefit of the host.

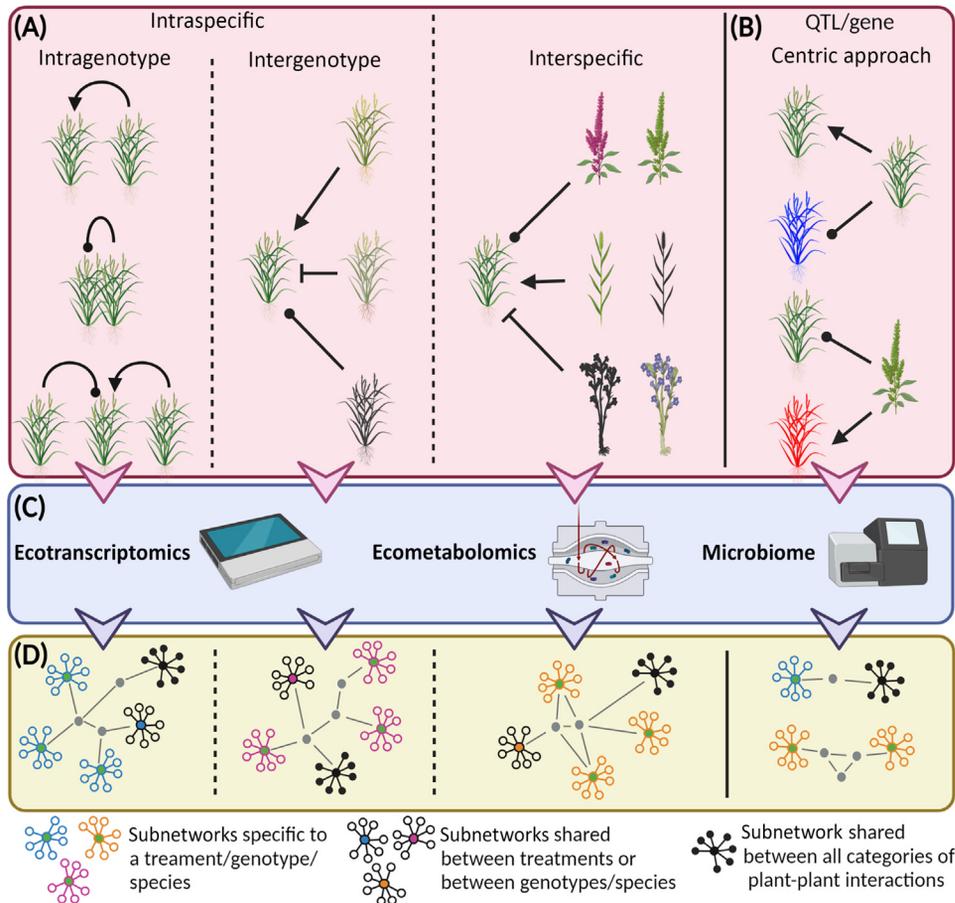
Phenomenological and mechanistic models: two possible ways of describing the relationships among phenomena, either by empirical relationships in agreement with a theory, or by the description of the interactions among the sub-parts in the studied system.

Plant assemblages: a group of interacting plant species populations that occur together in space and time.

Reciprocal helping: interactions between two plant partners where each benefits from the presence of the other.

Strigolactones: plant hormones and allelochemicals produced by plants and involved in (i) stimulating germination of parasitic plants, (ii) mediating interactions between plants and arbuscular mycorrhizal fungi, and (iii) contributing to the regulation of plant architecture.

Systems biology: an approach for understanding inter-relationships among networks of biological processes.



Trends in Plant Science

Figure 2. Combining complementary high-throughput technologies to dissect the genetic and molecular pathways associated with natural variation of plant–plant interactions in (agro-)ecologically realistic conditions. (A) Diverse categories of plant–plant interactions, with rice as an example of a focal species, ranging from intraspecific to interspecific interactions (with *Amaranthus* sp., *Setaria* sp. and *Phelipanche* sp., from top to bottom). Intraspecific interactions range from intra-genotypic (including various number of neighboring plants as well as density levels) to intergenotypic interactions. Different genotypes in any neighboring species are represented by different colors. Arrowheads with a circle, a triangle or a T shape, respectively, represent competitive, positive, and asymmetric interactions by the neighboring plants on the focal plant. (B) A QTL/gene centric approach to strongly reduce the number of gene, metabolite and microbial candidates selected for functional validation. This approach consists in comparing genome-wide RNA sequencing expression, metabolic profiles and microbiomes between isogenic lines differing by a single QTL, a single gene, or a single polymorphism (artificial or natural) associated with plant–plant interactions. (C) Illustration of ecotranscriptomics, ecometabolomics and microbiome studies performed with an RNA MinION sequencer (Oxford Nanopore Technologies, Oxford, UK), an Orbitrap (Thermo Scientific, Waltham, MA, USA), and an Illumina MiSeq Sequencer (Illumina Inc., San Diego, CA, USA), respectively. (D) Systems biology based on comparative network analysis to disentangle genetic, molecular, and microbial subnetworks from being specific to a treatment/species/genotype up to being shared between all categories of plant–plant interactions. Each dot corresponds to a specific gene, metabolite or microbial entity (either at the taxonomic or functional level). Abbreviation: QTL, quantitative trait locus. Created with [BioRender.com](https://www.biorender.com).

effect of changes in transcriptomic and metabolomic profiles on microbiota [42], conducting microbiome studies may ultimately reveal some causal functional links (Figure 2C).

Changes in transcriptomic, metabolomic, and microbiome profiles can be assessed simultaneously in multiple vegetative and reproductive organs, down to the tissue or single cell level (Figure 1) [43], in particular where physical interactions occur between plants [44,45]. Although the analysis of genome-wide RNA sequencing expression, metabolic profiles and microbiomes

provides hundreds to thousands of genes, metabolite and microbial candidates, the validation of causal candidates involved in plant–plant interactions remains scarce [46,47]. An approach to decrease the number of candidates is to apply omics approaches on plant lines differing at the functionally validated gene underlying a major quantitative trait locus (QTL) [48] or mutant plants [49] (Figure 2B), as this has been valuable in dissecting other types of biotic interactions [50]. Such an approach may be readily applied in plant–plant interactions, albeit a small number of QTLs have been cloned [7,51]. So far, only five studies led to the identification and functional validation of six genes, all in response to parasitic plants owing to the underlying oligogenic architecture. Interestingly, these genes encode diverse molecular functions, such as a coiled-coil nucleotide-binding site leucine-rich repeat [52], a leucine-rich repeat receptor-like kinase [51], a receptor-like protein [53], two cytochrome P450 genes [54], and a sulfotransferase [55].

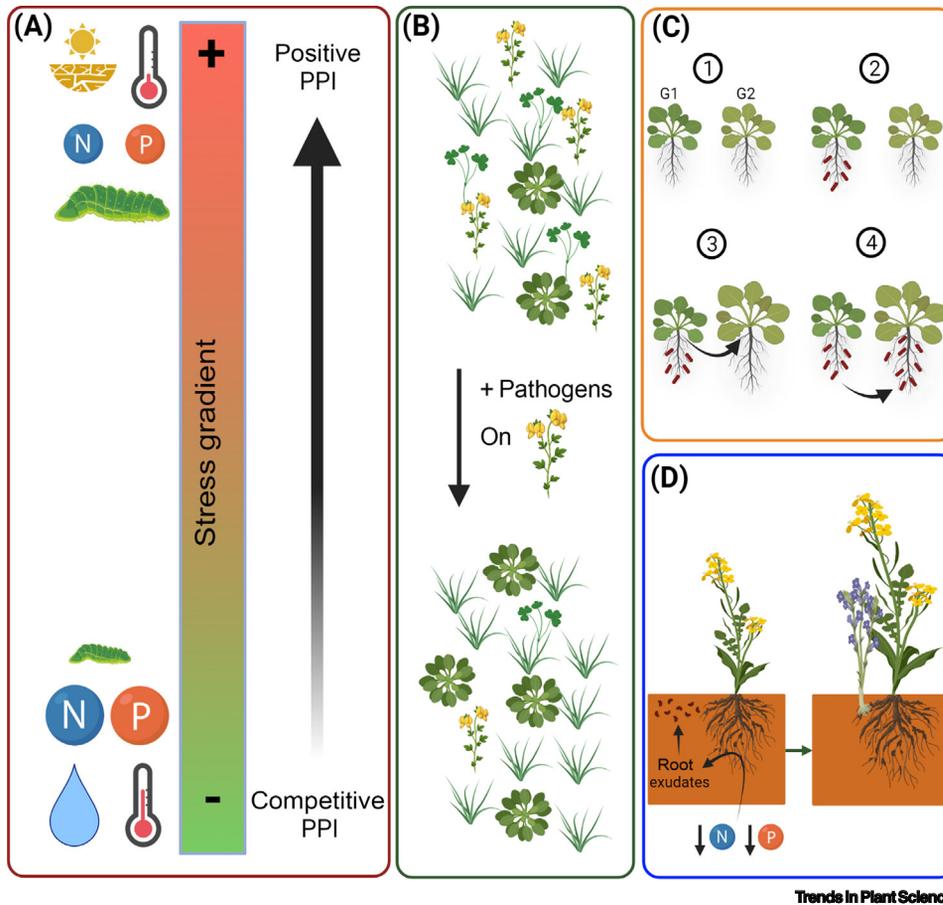
Transcriptomics, metabolomics, and microbiome studies generate large data matrices with thousands of features, which are the basis to build gene regulatory, metabolic, and ecological networks [56]. A comparative network analysis based on **systems biology** may help to identify common signaling and regulatory pathways involved in the response of a plant to a neighbor, ranging from competitive to positive interactions and across a large set of crop plant species and their wild relatives (Figure 2D).

How do plant–environment interactions influence plant–plant interactions?

The effects of a particular environmental factor on the net outcome of plant–plant interactions are well documented [41,57]. However, most observational data involved rough descriptions of the habitats from which genotypes were sampled, and were made at a single time point during community dynamics. Hence, the relevance of the imposed abiotic or biotic treatments considered in experimental studies may be questioned. This in turn leads to a broader question: what are the abiotic and biotic factors shaping plant–plant interactions and driving their evolution? Addressing this question in wild species, crop ancestral species, or crop relatives might help identify key environmental factors that would mediate plant–plant interactions in crop fields.

In the 1990s, the ‘stress gradient hypothesis’ (SGH) emerged as a concept predicting a shift of plant–plant interactions at the interspecific level from competitive to positive with increasing environmental stress, combining resource-related, physical, and biotic stresses by herbivores (Figure 3A) [58–60]. While a synthesis of 727 experimental tests supports the validity of the SGH in plant communities [57], the underlying functional and genetic mechanisms remain poorly understood and deserve deeper investigation in the near future. For instance, an increase of root interactions between plants through changes in root system architecture was observed at elevated temperature [61]. In addition, it will be important to test the SGH at the intraspecific level [41]. This may be especially relevant in the design of varietal mixtures within crop species in the context of global warming.

Beyond the SGH, which has been extensively studied at the interspecific level, we identified from our brainstorming sessions, two categories of environmental stress emerging as key factors that can affect the net outcome of plant–plant interactions and the underlying genetic architecture. Firstly, microbes, as a key part of the biotic environment, can affect the net outcome of plant–plant interactions [38]. For instance, because microbial pathogens preferentially spillover onto closely related species, both phylogenetic distances among plant species and host abundance drive disease pressure in plant communities, thereby modifying the network of plant–plant interactions (Figure 3B) [62]. Also, a computational model recently supported the intriguing hypothesis that the evolution of host altruistic behavior can be better explained by microbe-induced altruism than host-centered theories, with microbes manipulating the donating host to favor horizontal transfer of microbes to the recipient host [63]. In the context of plant–plant interactions, microbes



Trends in Plant Science

Figure 3. Environmental effects on plant–plant interactions. (A) Stress gradient hypothesis (SGH). According to the SGH, competition in plant communities decreases and positive interactions increases with increasing abiotic/biotic stress. Stress can be related to resources-related factors (e.g., content of soil in nitrogen and inorganic phosphorus, water), physical factors (e.g., temperature) and biotic factors (e.g., herbivory). (B) Disease pressure on interactions within plant communities. Hypothetical scenario: pathogen attack on *Lotus japonicus* (Fabaceae) also reduces abundance of *Clover* sp. (Fabaceae) owing to a preferential pathogen spillover onto closely related species, thereby leading to an increase of abundance of *Arabidopsis thaliana* (Brassicaceae) and the grass species (e.g., Poaceae). (C) Evolution of plant altruism driven by microbes. Hypothetical scenario: (1) two genotypes of *A. thaliana*, G1 (focal plant) and G2 (neighboring plant), grow in proximity; (2) genotype 1 is colonized by a microbial species at the rhizospheric and/or root level; (3) microbes induce an altruistic behavior of genotype 1 towards genotype 2; resulting in (4) a horizontal transfer of microbes from the donating genotype to the recipient genotype during plant–plant interactions, even if the two genotypes are unrelated. (D) Deficiencies in nitrogen and inorganic phosphorus increase the release of root exudates in the rhizosphere, which in turn can, for instance, stimulate the germination of seeds from parasitic plants. Here is represented a rapeseed plant interacting with a *Phelipanche* sp. Created with [BioRender.com](https://www.biorender.com). Abbreviations: N, nitrogen; P, inorganic phosphorus; PPI, plant–plant interactions.

from the rhizosphere or root compartments may induce an altruistic behavior of a focal plant towards a neighboring plant, resulting in a horizontal transfer of microbes from the focal plant to the neighboring plant, even if the two plants are genetically unrelated (Figure 3C). These strong experimentally and theoretically documented effects of microbes on plant–plant interactions could bring a breath of fresh air to the SGH and deserve particular attention.

Secondly, nutrient stress can promote the establishment of certain plant–plant interactions through triggering the production of signaling chemicals. For instance, in soils depleted in inorganic phosphorus or nitrogen, many plant species release higher amounts of **strigolactones** into the rhizosphere [64], ostensibly to recruit mycorrhizal fungi, but which are also used by parasitic plants

as cues to germinate and then initiate host infection (Figure 3D). Yet, the intraspecific genetic variation of inorganic phosphorus and nitrogen regulation of strigolactone biosynthesis and exudation and the underlying mechanisms remain to be investigated. In addition, nutrient stress can strongly affect the genetic architecture underlying the competitive response of a plant to the presence of a neighboring plant. When challenging 195 genotypes of *A. thaliana* with the presence of the grass *Poa annua* in three soils differing in pH and nitrogen concentration, a Genome-Wide Association Study (GWAS) revealed that the number and identity of QTLs largely differed between the three soil conditions, for each of the 29 phenotypic traits (including seed production) scored on *A. thaliana* plants [65]. Similar experimental studies in other plant species are required to support the generality of this environment-dependent genetic architecture of plant–plant interactions.

Can a better understanding of the genetics of plant–plant interactions improve the prediction of plant assemblages?

Considerable progress in modeling has been achieved in our understanding and ability to predict the most productive and/or stable **plant assemblages** in controlled experiments. Examples include the prediction of short-term dynamics of mixtures of two species in contrasting environments [66] or the assemblage of more diverse communities from subsets of experimental assemblages [67] (Figure 4A). However, predicting more complex plant assemblages both at the inter- and intraspecific levels (i.e., species and genotypic diversity and composition) in more ecologically relevant conditions (Figure 4B) requires integrating data from three additional major drivers of plant community dynamics that remain studied separately. Firstly, considering multi-level interactions between plants (Figure 1) would help move from a competition-centric view of plant interactions to embrace other ecological processes including positive interactions, direct trophic effects, and diverse chemical and physical signaling.

Secondly, improving the prediction of high productive and/or stable assemblages will require considering within-species genetic diversity [68] and its effects on intra- and interspecific interactions (Box 1, Figure 4C), as exemplified in wheat fields and temporary grasslands [69,70]. We identified two complementary approaches to integrate G×G interactions in the modeling of plant–plant interactions. The trait-centric (at the level of genotypes) approach offers quantitative prediction methods ranging from statistical inference (e.g., multi-trait analyses) [71,72] and **phenomenological** models to **mechanistic models** (Figure 4C). In particular, the development of trait-based models for crop and weed population dynamics (e.g., FLORSYS, [73] VGL, [74]) appears (i) promising to integrate phenotypic traits and their connections, (ii) suitable to predict the outcome of plant–plant interactions both in intra- and interspecific plant mixtures, and (iii) helpful to prioritize the underlying traits and driving processes. On the other hand, the QTL-centric approach (at the level of genetic polymorphisms) may help resolve the issue of **functional redundancy** of the trait-centric approach (Figure 4C). **Co-GWAS** methodologies have been developed to identify intergenomic QTL–QTL interactions in host–pathogen pairwise interactions [75], but remain to be applied to plant–plant interactions. Because plants interact with a large number of plant species throughout their life cycle, an alternative method developed in *A. thaliana* allowed detecting QTLs associated with *in situ* plant community descriptors, thereby suggesting that plant community diversity and composition select for specific genetic variants in the genome of a plant species [4,76].

Thirdly, considering the effects of environmental gradients on the relative extent of intra- and interspecific phenotypic variability [77] as well as on G×G interactions [41] represents an additional level of information that may improve plant assemblage predictions (Box 1, Figure 4D). This means estimating the relative fraction of variance of community functioning explained by genotype-by-genotype-by-environment (G×G×E) interactions for diverse abiotic and biotic factors as well as agricultural management practices.

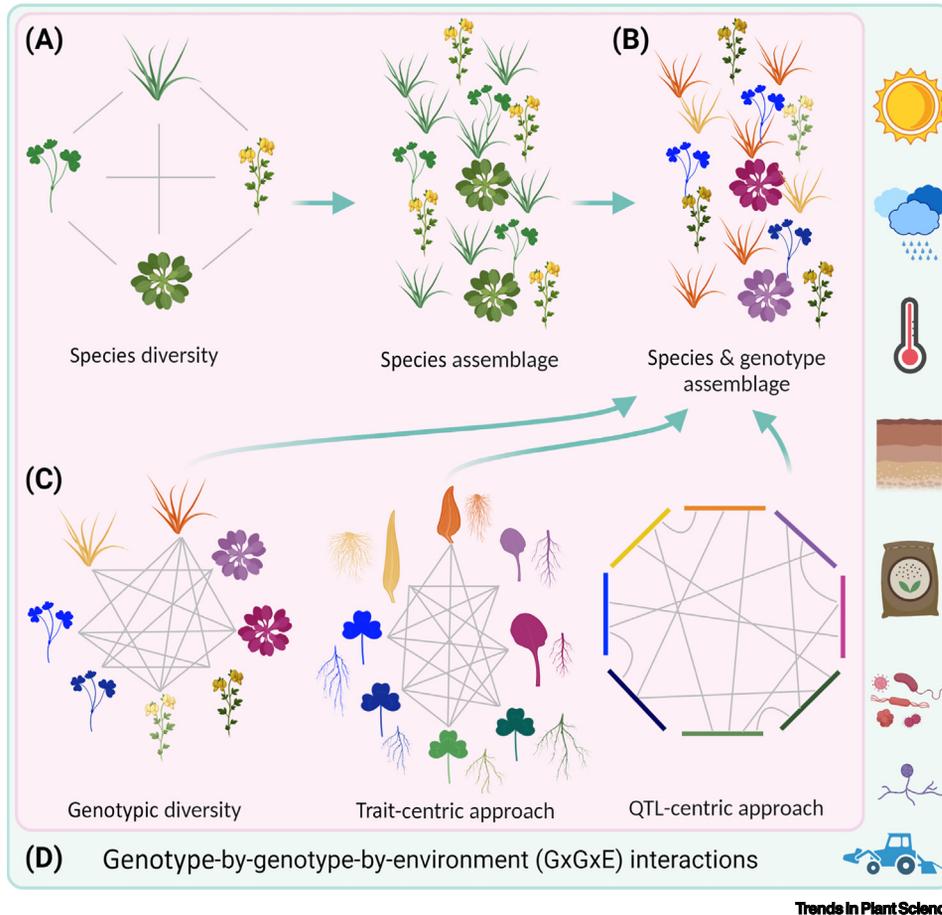


Figure 4. Predicting the most productive and/or stable plant assemblages. (A) Prediction of one plant assemblage (absolute and relative abundance of each species) based on pairwise interactions between four species (*Arabidopsis thaliana*, *Clover* sp., *Lotus japonicus* and a grass species). (B) A complex plant assemblage both at the inter- and intraspecific levels by considering both species and genotypic diversity as well as composition. (C) Improving predictions of complex plant assemblages based on a matrix of pairwise interactions between genotypes of four species, a trait-centric approach (at the aboveground and/or belowground levels) or a QTL-centric approach (i.e., network of intergenomic QTL-QTL interactions). (D) Testing the effects of abiotic and biotic factors as well as agricultural management practices on the relative extent of intra- and interspecific phenotypic variability as well as on genotype-by-genotype interactions. In (B) and (C), each species is represented by a different color and each genotype is represented by different shades of the color of the corresponding species. Abbreviation: QTL, quantitative trait locus. Created with [BioRender.com](https://www.biorender.com).

We foresee considerable interest at mixing both trait and QTL-centric approaches to predict the most productive and/or stable plant assemblages in a target environment. Their current strengths (combinatorial power, trait-blind approach) and limitations (data availability, polygenic traits) tend to complement each other.

Concluding remarks and future perspectives

The growing global demand for sustainable food supplies combined with the need to reduce reliance on synthesized fertilizers and pesticides in an ever more human-driven multi-stress environment requires finding the most efficient eco-friendly solutions. Similar to plant-microbiota interactions, there is therefore growing interest in the potential of harnessing the genetic variation of plant-plant interactions (in wild and crop species) to achieve conservation and agricultural goals, especially with an eye towards developing restoration programs to maintain endangered

Outstanding questions

Are the major traits identified at a specific observation scale still important at other scales? Are the key phenotypic traits, revealed under controlled conditions, still valid under field or natural conditions? Do the identity and range of variation of phenotypic traits relevant to plant-plant interactions differ between crops and wild plants? How have plant domestication and breeding shaped plant-plant interactions and the phenotypic traits driving intra- and interspecific interactions? Were phenotypes involved in beneficial interactions lost during domestication and breeding?

What are the main environmental factors (resource related, physical and abiotic) driving plant-plant interactions in natural settings? Does the stress gradient hypothesis apply to plant-plant interactions at the intraspecific level? Can the response of plant-plant interactions to combined stresses be predicted from the response of plant-plant interactions to multiple single stresses? To which extent does the environment affect extent genotype-by-genotype interactions?

Do genetic and molecular pathways involved in natural variation of plant-plant interactions differ from competitive to positive interactions and between intraspecific and interspecific interactions? Are genetic and molecular pathways involved in plant-plant interactions specific to a given plant species, genus, family etc.? Do genetic and molecular pathways involved in plant-plant interactions differ from the pathways involved in plant-microbe or plant-herbivore interactions? Do the gene networks involved include both specific and common components?

What is the genetic architecture underlying plant-plant interactions? Does the genetic architecture depend on the type of interactions (e.g., competitive vs. positive interactions, intraspecific vs. interspecific interactions...)? Does a matrix of intergenomic QTL-QTL interactions better predict the performance and/or stability of plant assemblage than a phenotypic matrix of species/genotypes interactions?

species and personalized agricultural practices (e.g., increasing weed suppression and pest regulation) [78,79]. In addition, a better understanding of beneficial plant–plant interactions can help predicting the resilience of natural plant communities to anthropogenic-related global changes [80] and developing more sustainable agriculture by designing optimized species and/or genotype mixtures (i.e., ‘ideomixes’) [81]. The mechanisms underlying beneficial plant–plant interactions has been the subject of several recent critical reviews [41,82–85], in particular on the relative importance of two main nonexclusive hypotheses underlying intraspecific positive interactions, each with opposite relationships between the extent of genetic relatedness among neighbors and the level of positive interactions [86,87]. The first hypothesis is based on one special part of the kin selection theory assuming the existence of kin recognition mechanisms, which trigger phenotypic plasticity in competitive traits and reduce competition toward neighboring relatives [88,89]. On the other hand, the elbow-room hypothesis predicts that resource partitioning allows avoidance of sibling competition and increases as the intraspecific genetic distance between neighbors increases [90].

In line with the recent creation of the new field of Function of Evolving Systems, which focuses on the function of organisms in their communities over periods of time as interactions evolve [91], a better understanding of the (agro)ecologically relevant genetics of plant–plant interactions would require more than ever the establishment of interdisciplinary projects. This in turn would require reinforcing bridges between reductionism and holism (see [Outstanding questions](#)).

Acknowledgments

This International PLANTCOM network is financially supported by the Plant Health and Environment division of INRAE. We thank Dominique Roby, Paul Neve as well as three anonymous reviewers for the valuable comments on the manuscript.

Declaration of interests

No interests are declared.

References

- Martorell, C. and Freckleton, R.P. (2014) Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage. *J. Ecol.* 102, 74–85
- Turner, K.G. *et al.* (2020) Effects of genomic and functional diversity on stand-level productivity and performance of non-native *Arabidopsis*. *Proc. Biol. Sci.* 287, 20202041
- Wuest, S.E. and Niklaus, P.A. (2018) A plant biodiversity effect resolved to a single chromosomal region. *Nat. Ecol. Evol.* 2, 1933–1939
- Frachon, L. *et al.* (2019) Adaptation to plant communities across the genome of *Arabidopsis thaliana*. *Mol. Biol. Evol.* 36, 1442–1456
- Baldwin, A.H. *et al.* (2014) Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. *Glob. Chang. Biol.* 20, 835–850
- Chen, J. *et al.* (2021) Diversity increases yield but reduces harvest index in crop mixtures. *Nat. Plants* 7, 893–898
- Subrahmaniam, H.J. *et al.* (2018) The genetics underlying natural variation of plant–plant interactions, a beloved but forgotten member of the family of biotic interactions. *Plant J.* 93, 747–770
- Westoby, M. *et al.* (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159
- Zhang, D. *et al.* (2020) Neighbouring plants modify maize root foraging for phosphorus: coupling nutrients and neighbours for improved nutrient-use efficiency. *New Phytol.* 226, 244–253
- Huber, M. *et al.* (2021) Light signalling shapes plant–plant interactions in dense canopies. *Plant Cell Environ.* 44, 1014–1029
- Brachi, B. *et al.* (2013) Investigation of the geographical scale of adaptive phenological variation and its underlying genetics in *Arabidopsis thaliana*. *Mol. Ecol.* 22, 4222–4240
- Paulus, S. (2019) Measuring crops in 3D: using geometry for plant phenotyping. *Plant Methods* 15, 103
- Boogaard, F.P. *et al.* (2020) Robust node detection and tracking in fruit-vegetable crops using deep learning and multi-view imaging. *Biosyst. Eng.* 192, 117–132
- Araus, J.L. and Cairns, J.E. (2014) Field high-throughput phenotyping: the new crop breeding frontier. *Trends Plant Sci.* 19, 52–61
- Narisetti, N. *et al.* (2021) Fully-automated root image analysis (faRIA). *Sci. Rep.* 11, 16047
- Calabrese, S. *et al.* (2019) Imbalanced regulation of fungal nutrient transports according to phosphate availability in a symbiosome formed by poplar, *Sorghum*, and *Rhizophagus irregularis*. *Front. Plant Sci.* 10, 1617
- Gala, H.P. *et al.* (2021) A single-cell view of the transcriptome during lateral root initiation in *Arabidopsis thaliana*. *Plant Cell* 33, 2197–2220
- Ramos-Cruz, D. *et al.* (2021) Epigenetics in plant organismic interactions. *Curr. Opin. Plant Biol.* 61, 102060
- Alonso, C. *et al.* (2019) The role of plant epigenetics in biotic interactions. *New Phytol.* 221, 731–737
- Kim, G. *et al.* (2014) Plant science. Genomic-scale exchange of mRNA between a parasitic plant and its hosts. *Science* 345, 808–811
- Shahid, S. *et al.* (2018) MicroRNAs from the parasitic plant *Cuscuta campestris* target host messenger RNAs. *Nature* 553, 82–85
- Betti, F. *et al.* (2021) Exogenous miRNAs induce post-transcriptional gene silencing in plants. *Nat. Plants* 7, 1379–1388
- Kong, C.-H. *et al.* (2018) Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. *Nat. Commun.* 9, 3867

24. Chen, Y. *et al.* (2020) Root ethylene mediates rhizosphere microbial community reconstruction when chemically detecting cyanide produced by neighbouring plants. *Microbiome* 8, 4
25. Picazo-Aragón, J. *et al.* (2020) Plant volatile organic compounds evolution: transcriptional regulation, epigenetics and polyploidy. *Int. J. Mol. Sci.* 21, 8956
26. Wang, N.-Q. *et al.* (2021) Root exudate signals in plant-plant interactions. *Plant Cell Environ.* 44, 1044–1058
27. Hazrati, H. *et al.* (2021) Mass spectrometry-based metabolomics unravel the transfer of bioactive compounds between rye and neighbouring plants. *Plant Cell Environ.* 44, 3492–3501
28. Pivato, B. *et al.* (2017) Positive effects of plant association on rhizosphere microbial communities depend on plant species involved and soil nitrogen level. *Soil Biol. Biochem.* 114, 1–4
29. Meyer, K.M. *et al.* (2022) Plant neighborhood shapes diversity and reduces interspecific variation of the phyllosphere microbiome. *ISME J.* 16, 1376–1387
30. Wipf, D. *et al.* (2019) Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks. *New Phytol.* 223, 1127–1142
31. Ballaré, C.L. and Pierik, R. (2017) The shade-avoidance syndrome: multiple signals and ecological consequences. *Plant Cell Environ.* 40, 2530–2543
32. de Wit, M. *et al.* (2013) Perception of low red:far-red ratio compromises both salicylic acid- and jasmonic acid-dependent pathogen defences in *Arabidopsis*. *Plant J.* 75, 90–103
33. Péliissier, R. *et al.* (2021) Plant neighbour-modulated susceptibility to pathogens in intraspecific mixtures. *J. Exp. Bot.* 72, 6570–6580
34. Hou, S. *et al.* (2021) A microbiota-root-shoot circuit favours *Arabidopsis* growth over defence under suboptimal light. *Nat. Plants* 7, 1078–1092
35. Delplace, F. *et al.* (2021) Network organization of the plant immune system: from pathogen perception to robust defense induction. *Plant J.* 109, 447–470
36. Singh, S. *et al.* (2021) Transcriptomics studies revealing enigma of insect-plant interaction. In *Plant-Pest Interactions: From Molecular Mechanisms to Chemical Ecology* (Singh, I.K. and Singh, A., eds), pp. 31–55. Springer, Singapore
37. Calabrese, S. *et al.* (2017) Transcriptome analysis of the *Populus trichocarpa*-*Rhizophagus irregularis* mycorrhizal symbiosis: regulation of plant and fungal transportomes under nitrogen starvation. *Plant Cell Physiol.* 58, 1003–1017
38. Péliissier, R. *et al.* (2021) Plant immunity: good fences make good neighbors? *Curr. Opin. Plant Biol.* 62, 102045
39. Peters, K. *et al.* (2018) Current challenges in plant Eco-metabolomics. *Int. J. Mol. Sci.* 19, 1385
40. Wending, M. *et al.* (2017) Specific interactions leading to transgressive overyielding in cover crop mixtures. *Agric. Ecosyst. Environ.* 241, 88–99
41. Subrahmaniam, H.J. *et al.* (2021) Toward unifying evolutionary ecology and genomics to understand positive plant-plant interactions within wild species. *Front. Plant Sci.* 12, 683373
42. Hu, L. *et al.* (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nat. Commun.* 9, 2738
43. Hatzepichler, R. *et al.* (2020) Next-generation physiology approaches to study microbiome function at single cell level. *Nat. Rev. Microbiol.* 18, 241–256
44. Delavault, P. Are root parasitic plants like any other plant pathogens? *New Phytol.* 226, 641–643
45. Bouwmeester, H. *et al.* (2021) Parasitic plants: physiology, development, signaling, and ecosystem interactions. *Plant Physiol.* 185, 1267–1269
46. Su, C. *et al.* (2020) SHR4z, a novel decoy effector from the haustorium of the parasitic weed *Striga gesnerioides*, suppresses host plant immunity. *New Phytol.* 226, 891–908
47. Musembi Mutuku, J. *et al.* (2015) The WRKY45-dependent signaling pathway is required for resistance against *Striga hermonthica* parasitism. *Plant Physiol.* 168, 1152–1163
48. Yang, P. *et al.* (2019) Fungal resistance mediated by maize wall-associated kinase ZmWAK-RLK1 correlates with reduced benzoxazinoid content. *New Phytol.* 221, 976–987
49. Bergelson, J. *et al.* (2021) Assessing the potential to harness the microbiome through plant genetics. *Curr. Opin. Biotechnol.* 70, 167–173
50. Delplace, F. *et al.* (2020) Robustness of plant quantitative disease resistance is provided by a decentralized immune network. *Proc. Natl. Acad. Sci. U. S. A.* 117, 18099–18109
51. Duriez, P. *et al.* (2019) A receptor-like kinase enhances sunflower resistance to *Orobanche cumana*. *Nat. Plants* 5, 1211–1215
52. Li, J. and Timko, M.P. (2009) Gene-for-gene resistance in *Striga*-cowpea associations. *Science* 325, 1094
53. Hegenauer, V. *et al.* (2016) Detection of the plant parasite *Cuscuta reflexa* by a tomato cell surface receptor. *Science* 353, 478–481
54. Cardoso, C. *et al.* (2014) Natural variation of rice strigolactone biosynthesis is associated with the deletion of two MAX1 orthologs. *Proc. Natl. Acad. Sci. U. S. A.* 111, 2379–2384
55. Gobena, D. *et al.* (2017) Mutation in sorghum LOW GERMINATION STIMULANT 1 alters strigolactones and causes *Striga* resistance. *Proc. Natl. Acad. Sci. U. S. A.* 114, 4471–4476
56. Ruan, X. *et al.* (2021) Dissection of the complex transcription and metabolism regulation networks associated with maize resistance to *Ustilago maydis*. *Genes (Basel)* 12, 1789
57. He, Q. *et al.* (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecol. Lett.* 16, 695–706
58. Smit, C. *et al.* (2009) Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. *J. Ecol.* 97, 1215–1219
59. Callaway, R.M. and Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958
60. Bertness, M.D. and Callaway, R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193
61. Luo, H. *et al.* (2020) High temperature can change root system architecture and intensify root interactions of plant seedlings. *Front. Plant Sci.* 11, 160
62. Parker, I.M. *et al.* (2015) Phylogenetic structure and host abundance drive disease pressure in communities. *Nature* 520, 542–544
63. Lewin-Epstein, O. *et al.* (2017) Microbes can help explain the evolution of host altruism. *Nat. Commun.* 8, 14040
64. Bouwmeester, H. *et al.* (2021) Adaptation of the parasitic plant lifecycle: germination is controlled by essential host signaling molecules. *Plant Physiol.* 185, 1292–1308
65. Frachon, L. *et al.* (2017) Intermediate degrees of synergistic pleiotropy drive adaptive evolution in ecological time. *Nat. Ecol. Evol.* 1, 1551–1561
66. Faverjon, L. *et al.* (2019) A generic individual-based model can predict yield, nitrogen content, and species abundance in experimental grassland communities. *J. Exp. Bot.* 70, 2491–2504
67. Maynard, D.S. *et al.* (2020) Predicting coexistence in experimental ecological communities. *Nat. Ecol. Evol.* 4, 91–100
68. Kraft, N.J.B. *et al.* (2014) Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos* 123, 1391–1399
69. Meilhac, J. *et al.* (2019) Increasing the benefits of species diversity in multispecies temporary grasslands by increasing within-species diversity. *Ann. Bot.* 123, 891–900
70. Borg, J. *et al.* (2018) Unfolding the potential of wheat cultivar mixtures: a meta-analysis perspective and identification of knowledge gaps. *Field Crops Res.* 221, 298–313
71. Albert, C.H. *et al.* (2010) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Funct. Ecol.* 24, 1192–1201
72. Marjakangas, E.-L. *et al.* (2022) Trait-based inference of ecological network assembly: a conceptual framework and methodological toolbox. *Ecol. Monogr.* 92
73. Colbach, N. *et al.* (2021) The FLORSYS crop-weed canopy model, a tool to investigate and promote agroecological weed management. *Field Crops Res.* 261, 108006
74. Louarn, G. *et al.* (2020) Towards intercrop ideotypes: non-random trait assembly can promote overyielding and stability of species proportion in simulated legume-based mixtures. *Ann. Bot.* 126, 671–685

75. Wang, M. *et al.* (2018) Two-way mixed-effects methods for joint association analysis using both host and pathogen genomes. *Proc. Natl. Acad. Sci. U. S. A.* 115, E5440–E5449
76. Libourel, C. *et al.* (2021) The genomic architecture of competitive response of *Arabidopsis thaliana* is highly flexible among plurispecific neighborhoods. *Front. Plant Sci.* 12, 741122
77. Jacob, S. and Legrand, D. (2021) Phenotypic plasticity can reverse the relative extent of intra- and interspecific variability across a thermal gradient. *Proc. Biol. Sci.* 288, 20210428
78. Khanh, T.D. *et al.* (2007) Rice allelopathy and the possibility for weed management. *Ann. Appl. Biol.* 151, 325–339
79. Worthington, M. and Reberg-Horton, C. (2013) Breeding cereal crops for enhanced weed suppression: optimizing allelopathy and competitive ability. *J. Chem. Ecol.* 39, 213–231
80. Roux, F. and Bergelson, J. (2016) The genetics underlying natural variation in the biotic interactions of *Arabidopsis thaliana*: the challenges of linking evolutionary genetics and community ecology. *Curr. Top. Dev. Biol.* 119, 111–156
81. Litrico, I. and Violle, C. (2015) Diversity in plant breeding: a new conceptual framework. *Trends Plant Sci.* 20, 604–613
82. Fréville, H. *et al.* (2022) Shift in beneficial interactions during crop evolution. *Evol. Appl.* 15, 905–918
83. Bilas, R.D. *et al.* (2021) Friends, neighbours and enemies: an overview of the communal and social biology of plants. *Plant Cell Environ.* 44, 997–1013
84. Pennisi, E. (2019) Do plants favor their kin? *Science* 363, 15–16
85. Fréville, H. *et al.* (2019) Preferential helping to relatives: a potential mechanism responsible for lower yield of crop variety mixtures? *Evol. Appl.* 12, 1837–1849
86. Dudley, S.A. *et al.* (2013) Kin recognition and competition in plants. *Funct. Ecol.* 27, 898–906
87. Dudley, S.A. (2015) Plant cooperation. *AcB Plants* 7, p1113
88. Hamilton, W.D. (1963) The evolution of altruistic behavior. *Am. Nat.* 97, 354–356
89. Depuydt, S. (2014) Arguments for and against self and non-self root recognition in plants. *Front. Plant Sci.* 5, 614
90. Young, J.P. (1981) Sib competition can favour sex in two ways. *J. Theor. Biol.* 88, 755–756
91. Bergelson, J. *et al.* (2021) Functional biology in its natural context: a search for emergent simplicity. *Elife* 10
92. Grime, J.P. (2002) *Plant Strategies, Vegetation Processes, and Ecosystem Properties* (2nd edn), John Wiley & Sons
93. Tilman, D. (1982) Resource competition and community structure. *Monogr. Popul. Biol.* 17, 1–296
94. Harper, J.L. (1981) *Population Biology of Plants*, Academic Press
95. Aarssen, L.W. *et al.* (1979) Neighbour relationships in grass-legume communities. II. Temporal stability and community evolution. *Can. J. Bot.* 57, 2695–2703
96. Silvertown, J. (2004) Plant coexistence and the niche. *Trends Ecol. Evol.* 19, 605–611
97. Aarssen, L.W. (1989) Competitive ability and species coexistence: a “plant’s-eye” view. *Oikos* 56, 386
98. Aarssen, L.W. (1992) Causes and consequences of variation in competitive ability in plant communities. *J. Veg. Sci.* 3, 165–174
99. Turkington, R. and Harper, J.L. (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture: IV. Fine-scale biotic differentiation. *J. Ecol.* 67, 245
100. Aarssen, L.W. and Turkington, R. (1985) Within-species diversity in natural populations of *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* from four different-aged pastures. *J. Ecol.* 73, 869
101. Aarssen, L.W. and Turkington, R. (1985) Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *J. Ecol.* 73, 605
102. Baron, E. *et al.* (2015) The genetics of intra- and interspecific competitive response and effect in a local population of an annual plant species. *Funct. Ecol.* 29, 1361–1370
103. Turkington, R. (1989) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. V. the coevolution of competitors. *J. Ecol.* 77, 717
104. Taylor, D.R. and Aarssen, L.W. (1990) Complex competitive relationships among genotypes of three perennial grasses: implications for species coexistence. *Am. Nat.* 136, 305–327
105. Lüscher, A. *et al.* (1992) Neighbour specificity between *Lolium perenne* and *Trifolium repens* from a natural pasture. *Oecologia* 91, 404–409