PCP
PLANT & CELL PHYSIOLOGY

Special Issue - Review

The Genetics of Plant–Plant Interactions and Their Cascading Effects on Agroecosystems—from Model Plants to Applications

Yasuhiro Sato[1,2,†,*] and Samuel E. Wuest[3,†,*]

[1]Faculty of Environmental Earth Science, Hokkaido University, Kita-ku N10W5, Sapporo, Hokkaido 060-0810, Japan
[2]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zurich CH-8057, Switzerland
[3]Group Breeding Research, Agroscope, Müller-Thurgau-Strasse 29, Wädenswil CH-8820, Switzerland
[†]These authors equally contributed to this work.

*Corresponding authors: Yasuhiro Sato, E-mail, yassato@ees.hokudai.ac.jp; Samuel E. Wuest, E-mail, samuel.wuest@agroscope.admin.ch

(Received 25 April 2024; Accepted 24 September 2024)

Plants are typically surrounded by neighboring individuals in agricultural fields or natural environments. In such circumstances, plant–plant interactions (PPI) are ubiquitous and represent not only important evolutionary forces but also have consequences on (agro-)ecosystem functioning, such as increased productivity and resistance. However, many mechanisms underlying these PPIs remain poorly understood. Recently, new genomic technologies and tools, such as genome-wide association studies, have facilitated genetic approaches to study PPIs, particularly among conspecific individuals. Here, we highlight emerging issues and advances in the field by focusing on three different aspects. First, we overview the current status of genetic mapping studies on PPIs and pinpoint that these studies open a new opportunity that is relevant to agriculture and breeding. Second, we introduce two proof-of-concept studies in *Arabidopsis thaliana*, in which genetic differences among plants improved the functioning of genotype mixtures. Both studies were able to predict effective mixtures with different experimental designs applied to different outcomes (productivity increase versus herbivory mitigation). Third, we discuss implications from these case studies about how PPIs have cascading effects that propagate to higher levels of biological organization, such as populations or communities. At the population level, plant yield or resistance can be optimized through breeding that achieves reduced competition or push–pull protection systems, respectively. At the community level, these population-level changes may have further beneficial effects on plant-associated organisms. Overall, we suggest that the increasing availability of genomic resources will improve our understanding of PPIs and thereby contribute to the management of crops or seminatural ecosystems.

Keywords: Agro-ecology • Plant–plant interaction • Population physiology • Quantitative genetics

Introduction

Plants are usually surrounded by neighboring individuals in natural and managed environments, and interactions among neighboring individuals influence both the evolution of plant populations and the functioning of ecosystems (Harper 1977, Brooker 2006, Grime and Pierce 2012). Understanding the mechanisms underlying plant–plant interactions (PPIs) can help us understand natural ecosystems or optimize crop yields and resistance in agroecosystems. Typically, direct negative interactions, such as shoot or root competition for light, water and soil nutrients, predominate among individual plants (Harper 1977, Keddy 2001). Indeed, competition is a pervasive force in the ecology and evolution of plants, and resource allocation to competitive structures and functions is a major determinant of crop yield potential (Donald 1968, Jennings and De Jesus 1968, Reynolds et al. 1994, Zhang et al. 1999, Weiner et al. 2017, Cossani and Sadras 2021). However, PPIs involve a broad range of processes. Some PPIs are more direct, while others are relatively diffuse or indirect (Brooker 2006, Pélissier et al. 2023), or they may affect population and ecosystem functions in complex ways. For example, herbivore or pathogen damage can induce defense responses in neighbors (Dahlin et al. 2018, Erb 2018), leading to increased community-wide defense. Interactions between individuals can therefore propagate to higher levels of biological organization, such as populations and communities (**Fig. 1A**). One such phenomenon, which has been of great interest among community ecologists, is that species or genotype diversity results in cascading effects on terrestrial ecosystems (Whitham et al. 2008, Naeem et al. 2009), e.g. resulting in increased functioning and stability of a plant community (Tilman and Downing 1994, Tilman et al. 1996, Hector et al. 1999).

While it is well recognized that PPIs are the main underlying driver of ecosystem functioning, the specific processes are

Plant Cell Physiol. 00(00): 1–13 (2024) doi:https://doi.org/10.1093/pcp/pcae092, Advance Access publication on 10 September 2024, available online at https://academic.oup.com/pcp

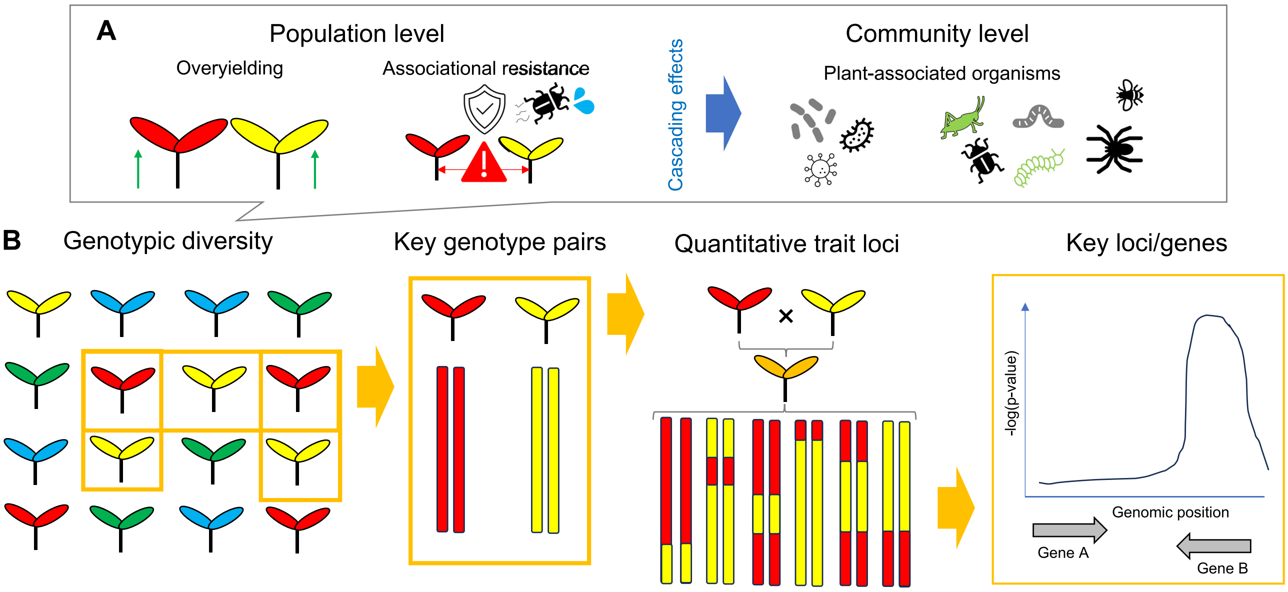


Fig. 1 Relevance of plant–plant interactions to the levels of biological systems from genes to the community. (A) Cascading effects of plant–plant interactions on the population- and community-level properties. Overyielding and associational resistance may occur as a result of interactions between key genotype pairs (A, left), which further affect the community structure of plant associated organisms (A, right). (B) Typical workflow of the genetic method; genetics provides reductionist approaches to resolve PPI and their effects on populations to specific causal drivers, e.g. from benefits of a genetically diverse population to those at a single locus.

also complex and likely include resource use complementarity or facilitation among plants (Naeem et al. 2009, Li et al. 2014, Brooker et al. 2021). It is also possible that the productivity or functioning of more diverse communities or populations are driven by dominant species with specific traits, though it has been shown that this is not the typical case (Loreau and Hector 2001, Barry et al. 2019). Beyond this, a multitude of mechanisms may contribute, e.g. greater taxonomic and microclimatic complexity can increase vegetation resistance to natural enemies, through so-called associational resistance (Tahvanainen and Root 1972, Barbosa et al. 2009, Jactel et al. 2021). Increases in plant yield and resistance can further exert wider effects on arthropods, microbes and other plant-associated organisms, which in turn would maintain species diversity at the community level (Crutsinger et al. 2006, Ebeling et al. 2008, Whitham et al. 2008, Bustos-Segura et al. 2017). These cases not only exemplify the rich and interesting nature of PPIs and their cascading effects on populations and communities but also provide a taste of the challenges to study them by means of a scientific method.

Despite their importance in evolution, ecology and agriculture, studying PPIs is complicated by a number of factors (see also Becker et al. 2023). First, these interactions cover a wide array of mutually non-exclusive processes, such as resource competition, facilitation or indirect defense signaling (Brooker 2006). Second, we often observe only the net outcome of several types of simultaneously operating interactions on the performance of plant individuals, populations or communities, but without reference to the underlying specific mechanisms (Subrahmaniam et al. 2018). Third, the strength and relative importance of these processes typically depend on environmental context (e.g. Callaway et al. 2002, Bronstein 2009). Finally, empirical studies of PPIs require relatively complex experimental designs (see 'Case studies' section further). For all these reasons, PPIs remain a major research focus in ecology and evolutionary biology, but have so far received relatively little attention from geneticists (Subrahmaniam et al. 2018). The genetics of PPIs could help us understand the biochemical, cellular and physiological processes involved, and would be of considerable interest in agriculture as they help design better crops. This applies particularly to intraspecific PPIs because modern agronomic practices focus on single-crop stands. For instance, earlier breeders attempted to achieve ideotypes that were weak competitors and reallocated resources from competitive structures to yield components (Jennings 1964, Donald 1968). Beyond the traditional monocultural practices, new breeding perspectives have proposed quantitative genetic studies on intercrops (Bourke et al. 2021). Within this outlook, intraspecific mixtures of multiple varieties, also known as variety mixtures, may enhance plant resistance or yield with minimal impacts on agronomically important trait variation such as flowering time (Zeller et al. 2012, Sato et al. 2024, Huang et al. 2024). Studying intraspecific PPIs also has the advantage that once variation in interactions or their effects on populations or communities have been identified, crosses between genotypes can be used as an effective way to further investigate the underlying genetic bases (**Fig. 1B** and case studies). Genetic studies of intraspecific PPIs may facilitate agroecosystem management and innovative breeding (Wuest et al. 2021). They may also provide good starting points and serve as models for studies that expand the focus from intraspecific interactions to interactions between species (Subrahmaniam et al. 2018, Becker et al. 2023).

Over the last decade, high-throughput sequencing technology has increased the availability of high-resolution and population-wide polymorphism data. This technological advancement has enabled genome-wide association studies (GWAS) in the model plant species *Arabidopsis thaliana* (Atwell et al. 2010, Alonso-Blanco et al. 2016) and crops (Kikuchi et al. 2017, Pang et al. 2020, Montazeaud et al. 2022) [see also Clauw et al. 2024 for a review]. In *A. thaliana*, GWAS has been enabled by the RegMap (Horton et al. 2012) and 1001 Genomes (Alonso-Blanco et al. 2016) projects. Importantly, such genomic resources also provide functional annotations of genes, which mean that, in many cases, the biochemical, cellular or physiological functions affected by specific genes can be predicted or inferred. Resources provided by the 1001 Genomes Project allow scientists to study evolutionary processes by assessing the abundance or phylogenetic and geographic distributions of sequence polymorphisms (Exposito-Alonso et al. 2019, Montazeaud et al. 2023). Many researchers have also utilized these rich genomic resources to conduct GWAS of biotic interactions with microbes (Horton et al. 2014, Wang et al. 2018) and herbivores (Brachi et al. 2015, Nallu et al. 2018, Groux et al. 2021) in *A. thaliana*. However, the genetic basis of PPIs has been less studied than other types of biotic interactions (reviewed by Subrahmaniam et al. 2018, Becker et al. 2023). In this paper, we review recent progress and current challenges in studying the genetics of PPIs. This review comprises of three parts. First, we outline the current status of, and provide examples for, the genetics of PPIs. We note that PPIs have so far been understudied, despite the notion that they have become amenable to forward and reverse genetics, and despite their utility for breeding. Second, we introduce two recent studies on *A. thaliana* that showcase ways to dissect the genetic architecture of intraspecific PPIs. Third, we discuss how PPIs exert cascading effects on higher levels of biological systems, such as populations and communities, and how this knowledge could be transferred to agronomy or breeding. Throughout the present review, we suggest that modern tools of quantitative genetics enhance our understanding of PPIs and their potential applications in agriculture and nature.

Current Status and Issues

Plant–plant interactions involve various mechanisms, and are affected by variation in morphology and growth, phenological shifts, chemical signaling and so on (Becker et al. 2023). Quantitative genetics has often adopted a phenomenological approach to dissect complex mechanisms and diverse outcomes of PPIs. In other words, published studies have often measured the outcomes of PPIs on plant performance. In this paragraph, we provide specific examples of genetic studies that examine PPIs, while also highlighting some complications that arise in such studies. **Table 1** presents a list of original research examples of the quantitative genetics of PPIs, highlighting the focus on various interaction types and the use of different methods. Earlier to the emergence of GWAS, PPIs were studied using conventional quantitative trait locus (QTL) mapping. For instance, Wolf and colleagues reported 13 QTLs underlying indirect genetic effects in intraspecific competition in *A. thaliana* and attributed some of these effects to a well-known flowering locus, *FRIGIDA* (Mutic and Wolf 2007, Wolf et al. 2011). Although this QTL overlapped with that of flowering time, its mapping resolution remained insufficient to gain further functional insights. Later studies used GWAS to examine PPIs, a method that typically has better genetic resolution than QTL mapping. For example, Frachon et al. (2017) studied interspecific PPIs between *A. thaliana* and the grass *Poa annua*, and detected the well-studied flowering regulator *FLOWERING LOCUS C* as a pleiotropic candidate gene at which natural variation affects plant interaction strength. These examples highlight the challenge of linkage disequilibrium or pleiotropy. Both may complicate the interpretation of genetic studies on PPIs (see also Case Study 1 and Wuest et al. 2022), either because the specific genes are not known, or because the multiple functions that genes exert in an organism make it difficult to specify the physiological or morphological characteristics relevant to PPIs.

In addition to quantitative genetics, single-gene studies have identified functional genes involved in PPIs in growth and defense. Shindo et al. (2008) reported that the outcome of intraspecific competition was modulated by the *BREVIS RADIX* (*BRX*) gene in *A. thaliana*. Loss of function of *BRX* results in a compact root system through disruption of several hormonal pathways, such as auxin, cytokinin and abscisic acid (Li et al. 2009, Rodrigues et al. 2009, Marhava et al. 2018), which resulted in plants that exhibited lower competitive abilities when grown with those that carried a functional *BRX*-allele (Shindo et al. 2008). At the same time, the loss-of-function allele of *BRX* has been proposed to represent an adaptation to acidic soils (Gujas et al. 2012), making it likely that the effects described earlier depend on environmental context, in particular soil pH. In studies that examine defense responses, *LIPOXYGENASEs* (*LOXs*) often play a key role in wound-induced jasmonic acid accumulation, which affects the production of plant volatiles that can attract insects and induce defense responses in neighboring plants (Takabayashi 2022). Schuman et al. (2015) have shown that *LOX2* and *LOX3* together with *TERPENE SYNTHASE 10* (*TPS10*) alter the volatile-mediated effects of neighboring plant genotypes on herbivores and other organisms in the wild tobacco *Nicotiana attenuata*. Such work on single genes and their effect on PPIs demonstrate that both reverse genetic studies can complement forward genetic studies, though in such cases, the roles of these genes in natural or managed populations or under different environmental contexts need further examination.

Table 1 Original research on the quantitative genetics of plant–plant interactions in growth and defense

Publication	Study species	Inter/intraspecific	Phenotype	Methods
Mutic and Wolf (2007)	*A. thaliana*	Intra	Growth	QTL mapping
Wolf et al. (2011)	*A. thaliana*	Intra	Growth	QTL mapping
Costa E Silva et al. (2017)	*Eucalyptus globulus*	Intra	Growth & defense	BLUP w/o mapping
Wuest and Niklaus (2018)	*A. thaliana*	Intra	Growth	QTL mapping
Frachon et al. (2017)	*A. thaliana*	Inter	Growth	GWAS
Frachon et al. (2019)	*A. thaliana*	Inter	Growth	GWAS
Libourel et al. (2021)	*A. thaliana*	Inter	Growth	GWAS
Turner et al. (2020)	*A. thaliana*	Intra	Growth	GWAS
Sato et al. (2021b)	*A. thaliana*	Intra	Defense	GWAS
Montazeaud et al. (2022)	*Triticum turgidum* ssp. *Durum*	Intra	Growth & defense	GWAS
Wuest et al. (2022)	*A. thaliana*	Intra	Growth	GWAS & QTL mapping
Montazeaud et al. (2023)	*A. thaliana*	Intra	Growth	GWAS
Wuest et al. (2023)	*A. thaliana*	Intra	Growth	GWAS & QTL mapping
Sato et al. (2024)	*A. thaliana*	Intra	Defense	GWAS

Related to this review on the genetics of (intraspecific) plant–plant interactions, see also Subrahmaniam et al. (2018) for more examples of conventional QTL mapping; Becker et al. (2023) for a broader opinion including interspecific examples; Wuest et al. (2021) for evolutionary and ecological viewpoints of variety mixtures.
Abbreviation: BLUP, best-linear unbiased predictor.

While several studies have examined variation in interspecific PPIs in wild and crop species (reviewed by Becker et al. 2023), major limitations are context-dependence (Frachon et al. 2019) and a lack of general insights that can be gained in them. Context dependence may not only refer to modulation of PPIs by environmental factors but also to epistasis between genetic variation at different loci (the ‘genomic context’ or background of an allele; Tsuchimatsu et al. 2020). In addition to scientific issues, outdoor cultivation of transgenic plants is legally prohibited in many countries, often restricting functional tests in a variety of environments. Therefore, despite the above-mentioned examples showing that PPIs are amenable to genetic study and manipulation, they have only received limited attention or application so far. We argue in this review, that PPIs are important for understanding natural processes and improving cropping methods. Contributing to this perspective, the model plant species *A. thaliana* provides an excellent test case for the ecological and functional genomics of PPIs. We also argue that one of the main challenges in studying PPIs is the relatively complicated design and difficulty in interpreting the outcomes of genetic studies. Below, we present two recent case studies on *A. thaliana*, which focus on intraspecific PPIs and their effects on population-level properties. These studies have employed different approaches to address the identified challenges. One case study adopted systematic pairing designs of genotypes in binary mixtures and investigated the complementary growth between genotypes under controlled conditions. Another case study planted genotypes randomly arranged in a regular grid in the field to study increased resistance to herbivore damage. These two cases revealed different genetic architectures, i.e. oligogenic versus polygenic bases, but both were able to predict effective genotype mixtures and detect plausible candidate genes with important roles in the interactions studied. We also highlight the potential consequences that the two case studies may have, either for furthering our understanding of ecological or evolutionary processes, or for devising new predictive tools for crop improvement.

Case Study 1—Increased Biomass Production in Systematically Paired Genotype Mixtures in a Greenhouse

Effective designs to study PPIs can be based on systematic pairing of genotypes, for example in diallel designs (all-with-all combinations among a sample of genotypes, **Fig. 2A**) or in factorial designs (a sample of genotypes combined with another sample of genotypes). These designs are traditionally also used in hybrid breeding schemes to evaluate the performance of F1 offspring from crosses (Griffing 1956), so a wide range of analytical methods have been developed for them. Wuest and Niklaus (2018) and Wuest et al. (2023) used natural accessions of *A. thaliana* and their recombinant inbred lines (RILs), and diallel or factorial systematic pairing designs to study diverse aspects of PPIs. The primary focus was on variation in biomass production in greenhouse pot experiments, and asking how specific genetic differences between plants in *A. thaliana* model populations increased overall productivities of mixtures—an effect that is likely mediated by reduced competition among plants. The first step in these studies was the identification of two genotype combinations that overyield when mixed. Combining the natural accession Bay-0 and Sha into such mixtures resulted in overyielding only on a specific, sand-rich substrate, while combining the accessions Sav-0 and Uk-1 resulted in overyielding across various pot sizes and substrate types. In both studies, these genotype pairs and 18 of the respective RILs (i.e. Bay-0 × Sha RILs in the first study, and Sav-0 × Uk-1 RILs in the second study) were used to establish new mixture combinations according to diallel designs. The advantage of these designs is that variation in the quality of mixtures (i.e. ‘better’ or ‘worse’ genotype mixtures) can be determined by partitioning the mixture biomass yields into general combining abilities of genotypes and specific combining abilities of genotype pairs (Griffing 1956, Norrington-Davies 1967, Forst et al. 2019). Subsequently, variation in specific combining ability among mixtures was genetically mapped, employing either molecular markers or whole-genome resequencing followed by genotype reconstruction of the RILs. Both Wuest and Niklaus (2018) and Wuest et al. (2023) found that substantial portions of the positive mixture effects could be attributed to between-plant genetic differences at specific regions in the genome (quantitative trait loci, QTLs), albeit the regions differed among studies and genotype pair examined. This was not necessarily expected, since variation in biomass production among individuals is considered a complex trait, with a complicated genetic basis (Lynch and Walsh et al. 1998). These and other recent studies showed, however, that PPIs and their complex effects on higher organizational levels can be strongly influenced by variation at a few genes (Barbour et al. 2022, McGale and Sanders 2022, Montazeaud et al. 2022). Wuest and Niklaus (2018) also showed that positive mixture effects between the Bay-0 and Sha accessions can be largely reproduced in mixtures of near-isogenic lines, i.e. in genotypes with identical genetic backgrounds that only differed at the chromosomal region identified by QTL mapping. At the same time, without resolution to specific genes, such a genetic approach falls short of providing more detailed insights into the mechanisms underlying positive mixture effects.

GWAS and QTL mapping can provide complementary approaches to study mixtures, whereby association studies have the potential to strongly narrow down genomic regions of interest, e.g. one identified in a QTL study. In order to do that for positive mixture effects, Wuest et al. (2023) performed an association study for specific combining ability in mixtures. They again analyzed variation in biomass productivity of *A. thaliana* genotype mixtures grown in pots, where 98 accessions were combined with each of the 10 tester genotypes in a full factorial design. Through an association analysis focusing on the previously identified QTL region, it was possible to narrow down the locus responsible for overyielding in Sav-0 and Uk-1 mixtures. Specifically, the strongest association was within *SUCROSE PROTON SYMPORTER 8* (*AtSUC8*) gene, which codes for a root-expressed proton-sucrose symporter. Sanger sequencing and sequence comparisons among natural accessions of *A. thaliana* identified several potential polymorphisms within the coding sequences of *AtSUC8* that may affect protein sequence and therefore protein function. Further analyses of the identified genetic polymorphisms are necessary to establish clear causal links, and to identify the respective physiological or morphological traits responsible for positive mixture effects. Genetic and biochemical analyses, however, suggested that variation at the *AtSUC8* locus may be important for adaptation to soils that exhibit differences in pH. This observation supports a hypothesis that evolutionary divergence and specialization along (abiotic) environmental factors could have led to genetic differences that now cause overyielding within mixtures. This shows that genetic studies may reach beyond identifying specific genes and 'knowing their names': they can reveal possible links between ecological observations and evolutionary processes. Alternatively, they could also provide new ideas on how to devise simple predictive methods for crop mixtures (see Wuest et al. 2021 for details).

While systematic pairing can facilitate genetic studies of PPI, such designs also come with some drawbacks (**Fig. 2**). For example, due to their combinatorial nature, experiments can quickly become very large, which is likely a problem for field crop research. This issue could be solved by sub-sampling, i.e. by only growing a subset of all possible combinations (Forst et al. 2019). At the same time, systematic pairing designs also generate datasets with whose several different aspects of PPIs can simultaneously be examined. For example, the study of Montazeaud et al. (2023) was also based on the data from the factorial combinations of 98 *A. thaliana* genotypes with 10 tester lines, but the analytical emphasis was on the question of how individual plant genotypes exert influences on their neighbors. They applied an existing quantitative genetic framework for this analysis, quantifying so-called indirect genetic effects (IGEs), i.e. the effect of neighboring genotypes and their genes on focal plant's growth. Even though the fraction of total phenotypic variance explained by IGEs was small (2.7% of the total phenotypic variance in above-ground plant biomass), a GWAS analysis revealed significant associations of IGE with 11 loci, together explaining 85% of the total IGE variability. Furthermore, population genetic analyses could identify potential demographic and ecological factors that determine variation in IGEs. In another instance, the same dataset was used to compare the performance of genotypes across different mixtures with their performance in a monoculture, to identify potentially cooperative alleles (Wuest et al. 2022). Cooperative alleles improve monoculture productivity particularly under planting high densities, where increased resource allocation to competitive traits normally maximizes individual fitness but reduces the performance of the population as a whole (Denison et al. 2003, Weiner et al. 2017). In the genetic study, a GWAS identified a chromosomal region where allelic variation had a large effect on cooperation, and consequently on the productivity under high densities. At the same time, the authors found that genotypes carrying the more cooperative allele were also more pathogen-resistant, suggesting a possible evolutionary scenario about why this allele may be maintained in natural populations. In summary, the systematic combination of genotypes in diallel or factorial designs represents effective ways to analyze various aspects of PPI and the underlying genetics, even though such designs quickly become very large.

Case Study 2—Reduced Herbivore Damage in a Randomized Mixture of Plant Genotypes in the Field

Instead of systematic pairing, a widely applicable way is to focus on neighbor interactions in a spatially randomized arrangement of many accessions (**Fig. 2B**). The advantage of randomized pairing lies in its scalability to any randomized cultivation that arranges many accessions on a large spatial scale. The application of GWAS to spatially randomized arrangements of genotypes may be feasible in crops and plantations, because breeders often perform extensive field trials where new breeding varieties are cultivated in a spatially randomized manner, such as a randomized block design. These randomized cultivations are often conducted at an individual level in perennial fruit trees such as apples and grapevines (Flutre et al. 2022, Jung et al. 2022) or at a population level for cereal crops such as barley and wheat (Ordon and Friedt 2019, Zhao et al. 2021). While designed to score genetic differences among individuals, such trials can be analyzed to determine inter-individual or inter-plot interactions to identify potential mixing partners.

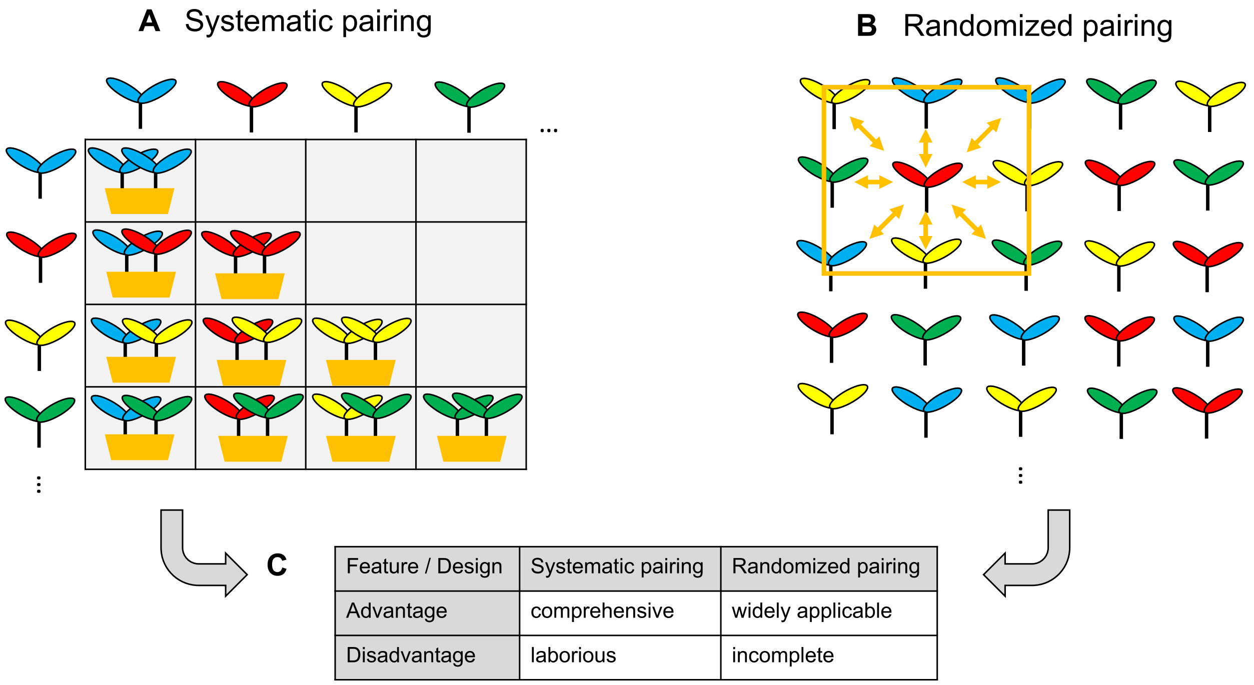
Based on the randomized arrangement design, Sato et al. (2021b) proposed a novel GWAS method named 'Neighbor GWAS' that incorporated the effects of neighbor genotypic similarity on a focal plant's trait. This method was inspired by the Ising model of magnetics, which has been widely applied to spatial patterns in ecology such as forest gap dynamics (Schlicht and Iwasa 2004) and habitat fragmentation (Bascompte and Sole 1996). The Neighbor GWAS method (Sato et al. 2021b) employed the Ising model to quantify neighbor allelic interactions at each locus in a randomized mixture of plant genotypes. In this method, GWAS of neighbor interactions can be performed by mapping the locus-wise effect of allelic similarity on target traits. This estimated effect of allelic similarity on target traits distinguishes between positive and negative interactions between two alleles (Sato et al. 2021b). In addition to the sign of allelic interactions, symmetric and asymmetric interactions infer how balanced dimorphism i.e. allelic mixture increases population-level yield or resistance (Sato et al. 2023). With combinations of positive or negative and symmetric and asymmetric interactions, the total effects of allelic mixtures on population-level yield can be partitioned into those from complementarity or from the probability of having high-yielding genotypes (Takahashi et al. 2018). This line of theoretical basis is given by frequency-dependent selection on one locus with two alleles (Schutz et al. 1968, Schutz and Usanis 1969, Schneider 2008, Sato et al. 2023) and evolutionary game theory (Takahashi et al. 2018). This evolutionary theory of allelic interactions among neighboring individuals is relevant to various population-level properties, such as overyielding (Takahashi et al. 2018) and associational resistance (Underwood et al. 2014).

In field trials, researchers usually score multiple traits, such as herbivore damage, disease infection, flowering time and yield, and estimate the heritability of these traits before conducting GWAS (Zhao et al. 2011, Horton et al. 2014, Pang et al. 2020, Flutre et al. 2022, Jung et al. 2022, Sato et al. 2024). As a test case, Sato et al. (2024) recorded all insect herbivores that harbored 200 *A. thaliana* accessions grown in eight replicated blocks in a field garden. Similar to the analysis of SNP heritability (Yang et al. 2010), they analyzed neighbor interactions and quantified the genetic variation explained by neighbor genotype effects on herbivore damage and abundance. This variance component analysis revealed that a 6% variation in herbivore damage was explained by incorporating the genotypes of the nearest neighbors. Such an influence of the nearest neighbors on the abundance of mobile herbivores was also significant, whereas that of sedentary herbivores was not (Sato et al. 2024). Even when the effective range of these neighbor interactions differs among target traits and their responsible agents, the Neighbor GWAS model allows us to estimate the optimal spatial scales by repeatedly calculating the proportion of phenotypic variation explained by neighbor genotypes within a certain range (Sato et al. 2021b). The variance component analysis of neighbor genotypic effects provides a way to identify promising traits and an effective spatial scale to be analyzed using GWAS in a randomized arrangement.

While the Neighbor GWAS distinguishes between positive and negative interactions at a single SNP level, this can also be applied for a multi-locus analysis of polygenic traits that are often used in crops and field-grown plants (e.g. Brault et al. 2021, Scott et al. 2021, Riehl et al. 2023). In field-grown *A. thaliana*, Sato et al. (2024) did not find any large-effect SNPs responsible for neighbor genotypic effects on the herbivore damage, but could narrow down key SNPs using genome-wide sparse regression. These key SNPs included genes involved in jasmonic acid biosynthesis *LOX2* and *LOX6* as candidates. *LOX*s are known to affect volatile production (Matsui and Engelberth 2022), which play multifunctional roles in plant–plant communications and herbivore attraction (Schuman et al. 2015, Dahlin et al. 2018, Takabayashi 2022). These results highlight the capability of quantitative genetic analysis of polygenic traits that exhibit significant heritability without large-effect QTLs. The applicability of the Neighbor GWAS method to polygenic traits and large-scale field experiments would be suitable for the study of field-grown cultivars.

In randomized pairing, potential interactions among all genotype pairs can be estimated using the genotype of each pair. Using key SNPs, Sato et al. (2024) applied genomic prediction to estimate the best and worst pairs. This idea is based on the concept of genomic selection, wherein the genetic ability of each variety is predicted using genome-wide polymorphism data (Meuwissen et al. 2001). Such a genomic selection approach enables the prediction of elite varieties prior to actual phenotyping for breeding (Jannink et al. 2010, Yabe et al. 2018). By applying the idea of genomic selection for PPIs, Sato et al. (2024) estimated the effects of mixed planting for genotype combinations that were missing in a randomized mixture. To validate the estimation, they planted three candidate pairs of *A. thaliana* in a mixture and monoculture, and indeed detected an 18–30% reduction in herbivore damage in the mixture. These results show that the genomic prediction of PPIs helps identify key pairs out of many genotypes (the process on the left of **Fig. 1B**) in a randomized arrangement.

The potential limitation of randomized pairing is that only a certain fraction of all possible combinations is realized in randomized cultivation. This problem might make genomic prediction less reliable and lead us to overlook important genotype pairs. Once candidate pairs are identified, their actual



Feature / Design	Systematic pairing	Randomized pairing
Advantage	comprehensive	widely applicable
Disadvantage	laborious	incomplete

Fig. 2 Experimental design for GWAS of intraspecific plant–plant interactions. (A) Systematic pairing adopted to study complementary growth in controlled environments (Wuest et al. 2022, 2023, Montazeaud et al. 2023). (B) Randomized pairing adopted to study reduced pest damage in field environments (Sato et al. 2021b, 2024). (C) Summary of the advantages and disadvantages of each approach.

effects should be verified by comparing phenotypes between the monoculture and mixture. These key pairs can then be subjected to QTL mapping in the same manner as that used by Wuest et al. (2023). To enable QTL mapping of intraspecific PPIs, an interval mapping method called 'Neighbor QTL' is available for the randomized pairing design (Sato et al. 2021a). Given that systematic and randomized pairings have both advantages and disadvantages (**Fig. 2C**), we need to validate the results based on further field and laboratory experiments, such as transplant experiments, QTL mapping and mutant analysis.

Perspective

PPIs are ubiquitous in nature and in crop fields. Despite their importance, relatively few genetic studies have examined them due to the many challenges in studying such complex traits by means of quantitative genetics. Thus far, we have shown two case studies in which GWAS and relevant methods have been applied to study intraspecific PPIs in the model plant *A. thaliana*. We have shown that PPIs and their consequences on populations need not be irreducibly complex, and that some designs can be very effective for such purposes. In this section, we discuss how the genetics of plant-plant interactions can reveal important insights into higher levels of biological systems, such as populations and communities, and drive new applications in agriculture and nature.

Population-level: cooperative crops or mixtures for increased yield and resistance in agriculture

The quantitative genetic approaches to intraspecific PPIs are particularly applicable to agricultural fields where humans cultivate and manage a single plant species over a large space. In this agricultural practice, breeders and farmers can increase yield by reducing competition, whereby we could draw lessons from crop breeding, e.g. as performed by breeding efforts that fueled the Green Revolution in rice and wheat. Hereby, high-yielding cultivars were developed by optimizing plant populations grown under new management practices that rely on increased applications of fertilizers (Vogel et al. 1956, De Datta et al. 1968). The breeding of less competitive ideotypes contributed to the optimization of crop productivity per area by making plants more cooperative (Tsunoda 1959, Jennings 1964, Donald 1968), which was inspired by the eco-physiological theory of optimal canopy structure and function (Monsi and Saeki 1953; reviewed by Hirose 2004). Breeders therefore reduced plant stature and made leaf angles more vertical by introducing semi-dwarfing alleles to rice and wheat cultivars, which reduced light competition under dense planting conditions. Since then, selecting genotypes for optimal yield in monoculture populations has affected multiple plant traits that are consistent with the idea that reducing competitive allocation improves yield and stress tolerance of plant populations (Duvick et al. 2003, Feng et al. 2023, Xi et al. 2023). This approach holds the potential for further yield increases, even in crops that have been intensively bred for higher yields over a century and using modern techniques (Tian et al. 2019, Weiner 2019). Following this idea and while studying multiple PPIs through factorial pairing designs and genetics, Wuest et al. (2022) found that a QTL in *A. thaliana* at which the less competitive allele was also associated with increased disease resistance, suggesting a potential trade-off between competitive ability and disease resistance. The yield maximization achieved through weak competition might therefore shift a balance from competition to defense, thereby leading to increased disease resistance and yield simultaneously. The relatively direct molecular links that determine a trade-off between neighbor detection/shade avoidance and plant immunity (Ballaré and Pierik 2017) seem to support this notion.

Reducing competitive interference among crop plants could also be achieved by increasing within-field crop diversity, as discussed in Case Study 1. This would be implemented by genotype mixtures that exhibit some degree of complementarity (e.g. different resource requirements, root foraging behavior, light acquisition strategies, etc.) among plants to reduce competition. This proof-of-concept study highlights an avenue for increasing crop productivity while maintaining genetic diversity. Beyond that, plants incur negative effects from pest organisms as well as competitors in field environments. Pest outbreaks are another serious problem in monocultural fields, in which pesticide treatments impose a huge environmental burden on agricultural lands (Pimentel 1996). Variety mixtures provide a possible solution to the vulnerability of monocultural cultivars to pest organisms, such as disease (Finckh et al. 2000, Zhu et al. 2000, Zeller et al. 2012) and herbivory (Dahlin et al. 2018). Compared with the agents of plant disease, herbivores move more actively between individual plants. The joint use of repellent and attractant semiochemical volatiles, also known as push-pull systems, is successful for maize protection from insect herbivores (Pickett et al. 2014). Such a push–pull system is currently achieved between different plant species, but volatile-mediated pest suppression is also known among cultivars within a crop species (Dahlin et al. 2018). To deal with the different underlying processes among pest organisms, a genomic prediction approach, similar to the one outlined in Case Study 2, would be effective as the initial step to identify key genotype pairs responsible for increased pest resistance in mixtures.

Beyond the work outlined in Case Studies 1 and 2 that utilized *A. thaliana* as a model to set up designs and methods, there have also been attempts to apply GWAS of PPIs to crops (Kikuchi et al. 2017, Montazeaud et al. 2022). For example, using 170 inbred lines, Montazeaud et al. (2022) investigated the yield and disease of durum wheat, *Triticum turgidum* ssp. *durum*, in monocultures and randomly paired mixtures. Mixtures of these durum varieties were more productive and less damaged than monocultures overall. Furthermore, they conducted a GWAS using 117,888 SNPs and detected a significant QTL responsible for a negative effect of allelic richness on yield and disease. These results suggest that QTLs with negative mixture effects should be homogeneous over variety mixtures. This example also illustrates that GWAS of intraspecific PPIs is feasible and useful for crop breeding and management, but the crop genome resources may not be as well suited as the model plant species, specifically for functional studies. In turn, *A. thaliana* provides an excellent study system that can connect field studies and molecular or evolutionary genetic approaches and be used to devise and test experimental methods or designs.

Community-level: cascading effects of plant–plant interactions on pest organisms

Alterations in plant yield or resistance can exert cascading effects on the community of plant-associated organisms, such as arthropods and microbes. Over past decades, the rise of community genetics posited this perspective from genes to community levels (Johnson and Agrawal 2005, Crutsinger et al. 2006, Whitham et al. 2008). While trees and perennial herbs have been intensively studied (Johnson and Agrawal 2005, Crutsinger et al. 2006, Schweitzer et al. 2008, Barker et al. 2019), the concept of community genetics can also be applied to crop species. In this context of community genetics, the genetics of PPIs and *A. thaliana*–insect interactions provide transferable knowledge to pest management in Brassicaceae crops as *A. thaliana* produce major secondary metabolites shared across Brassicaceae linages, i.e. glucosinolates (Brachi et al. 2015, Barbour et al. 2022, Jing et al. 2023). For example, glucosinolate variation within *Brassica oleracea* is known to underpin insect communities, including herbivores and their natural enemies (Poelman et al. 2008). These herbivore communities include specialist pests of Brassicaceae crops, such as the diamondback moth *Plutella xylostella*, the small white butterfly *Pieris rapae* and the cabbage aphid *Brevicoryne brassicae* (Poelman et al. 2009). These herbivore species are further attacked by carnivorous insects such as parasitoid wasps and aphidophabous ladybirds (Poelman et al. 2008), shaping a multitrophic food web of the insect community. Notably, mixtures of *B. oleracea* genotypes increased herbivore diversity but decreased herbivore damage compared with monocultures (Bustos-Segura et al. 2017). This beneficial effect of the mixture on plant resistance was conferred through the diversification of glucosinolate profiles per population (Bustos-Segura et al. 2017). In addition to herbivory and glucosinolates, plant size in these genotype mixtures was larger than that in monocultures (Bustos-Segura et al. 2017), suggesting simultaneous optimization of plant growth and damage by mixed planting. These cascading effects of genotype mixtures on pest communities will be reassessed by means of the genetics of intraspecific PPIs.

The community structures of plant-associated organisms are often considered extended phenotypes of individual plants (Whitham et al. 2003), which can be subjected to quantitative genetic analyses (Johnson and Agrawal 2005). Specifically, these extended phenotypes can be quantified as a diversity index of associated organisms, such as species richness, Shannon entropy, and other diversity indices of community ecology (Johnson and Agrawal 2005), for each individual plant. Once measured as quantitative traits, extended phenotypes can be analyzed following our scheme of quantitative genetic analyses. Using a randomized pairing approach, Sato et al. (2024) quantified arthropod community composition as an extended phenotype of *A. thaliana* accessions and tested whether the extended phenotypic variation could be explained by genome-wide neighbor effects. This study revealed that the genotypes of neighboring plants significantly influenced the total number of insect species (i.e. species richness), including herbivores and carnivores. Some herbivores among these species were influenced by neighboring genotypes while others were not (Sato et al. 2024), indicating species-specific effects of neighboring genotypes on herbivores. To obtain functional insights, normal GWAS can be performed on the component species of the community. Xu et al. (2023) performed a GWAS of aphid abundance and found an association with a putative ribosomal gene (AT3G13882) that was also linked to delayed growth in *A. thaliana*. These findings showcase a way to understand the cascading effects of intraspecific PPIs on the community composition and diversity of associated organisms. While these examples again show that the genome resources of *A. thaliana* provide a rich platform for genetic studies on PPIs, they also underline the notion that we are only beginning to realize their potential.

The cascading effects of intraspecific PPIs are expected to be prominent in crop fields, but these effects are also likely to occur in any terrestrial ecosystem where one or a few plant species governs a food web and biomass flow. Such ecosystem functioning of plant genetic diversity has been reported in the dominant plant species called foundation species, including perennial herbs (Crutsinger et al. 2006, Johnson et al. 2006) and trees (Whitham et al. 2008). Examples of ecosystem functioning include significant changes in soil conditions (Schweitzer et al. 2008), biomass production (Genung et al. 2012) and food web structures (Barbour et al. 2016). When positive PPIs occur within a foundation species, these impacts are profound at the ecosystem level in nature or agriculture. In natural ecosystems, tree species produce a large fraction of biomass and harbor diverse organisms and exert large impacts of intraspecific PPIs, if any, on surrounding ecosystems (Whitham et al. 2008). In the context of indirect genetic effects, for example, studies on *Populus* trees reported the impacts of neighboring genotype-by-genotype interactions on the biomass of plants and associated microorganisms (Shuster et al. 2006, Schweitzer et al. 2008). In managed ecosystems, crops and plantations can be considered foundation species that are artificially cultivated across a large area. Cascading effects of crop intraspecific PPIs are therefore expected to be substantial and range from the population to the ecosystem level. When our strategy is applied for foundation species, these analyses may illustrate the ecological significance of PPIs at the ecosystem level in nature and agriculture. This way of ecosystem management will become feasible owing to the increasing availability of functional genomics in community ecology (Stange et al. 2021).

Future challenges

The proof-of-concept using *A. thaliana* illuminates further issues as well as potential solutions when applying our strategies to crops and other plant species. Specifically, we anticipate two obstacles in the contexts of ecology and genetics. First, the ecological obstacle is the size and generation time of individual plants. Although thousands of individual plants were cultivated in our case studies, cultivating large crops and trees requires much larger space than *A. thaliana*. In addition to plant size, generation time should be longer in crops than in *A. thaliana*. These practical issues require much more effort in field trials to conduct GWAS of PPIs than standard GWAS, although this problem could be partly solved by the randomized pairing approach proposed in this review. Second, the genetic obstacle lies in the complex genomic structure of crops and other plant species. It is well-known that many species of cultivated plants are polyploids that possess parental homeologs (in allopolyploids: Shimizu 2022) and duplicated genes (in autopolyploids: Parisod et al. 2010). The genomes of these cultivated plants are much larger than those of *A. thaliana*, such as an allohexaploid wheat cultivar with a 15-Gb genome (Shimizu et al. 2021). Unlike GWAS, genomic prediction may be feasible as long as SNP-based pedigree can be estimated, but its reliability is based on the quality and resolution of genotyping (Meuwissen et al. 2001). We expect that this genetic issue will be resolved by emerging sequencing and bioinformatics technologies, which will enable GWAS and genomic prediction of PPIs.

Concluding remarks

Our review presents a strategy to understand the genetic basis of PPIs and their outcomes at higher levels of biological systems. We have shown that effective designs exist to study intraspecific PPIs in particular, and that such studies provide ideas for more widely applicable genetic studies on molecular mechanisms and ecological outcomes of PPIs in general. The rich genomic resources and molecular genetic data available for the model plant *A. thaliana* contribute to integrating reductionist and holistic studies in a single species (**Fig. 1**), in which GWAS helps identify key genotype pairs or loci responsible for positive ecological outcomes (**Fig. 2**). Further experiments that include crosses and functional analyses can dissect the genetic architecture of PPIs at the single-gene level. Now that genome resources are increasingly available for crops and other plant species (Mochida and Shinozaki 2010, Sundell et al. 2015, Shimizu et al. 2021), future studies may apply similar strategies in cultivated species. At the same time, developing a better picture of the many aspects of PPIs and their wider impacts on ecological and evolutionary processes will require interdisciplinary research across biological scales, ranging from genes to processes occurring at the level of communities and ecosystems.

Data Availability

No new datasets were generated or analyzed in this study.

Funding

Japan Science and Technology Agency (JST, grant no. JPMJPR17Q4 to Y.S.), Japan Society for the Promotion of Science (JSPS, JP23K14270 to Y.S.), Swiss National Science Foundation (SNSF, CRSK-3_221418 to Y.S.), University Research Priority Program of Global Change and Biodiversity (UPPP GCB) at the University of Zurich and SNSF (grant no. 310030_192537 to S.E.W.) and Agroscope.

Acknowledgements

The authors thank Germain Montazeaud (INRAE), Pascal Niklaus (University of Zurich), and Kentaro K. Shimizu (University of Zurich) for insightful discussions during the study.

Author Contributions

Y.S. and S.E.W. conceptualized, wrote, and revised the manuscript.

Disclosures

The authors have no conflicts of interest to declare.

References

Alonso-Blanco, C., Andrade, J., Becker, C., Bemm, F., Bergelson, J., Borgwardt, K.M., et al. (2016) 1,135 genomes reveal the global pattern of polymorphism in *Arabidopsis thaliana*. *Cell* 166: 481–491.

Atwell, S., Huang, Y.S., Vilhjálmsson, B.J., Willems, G., Horton, M., Li, Y., et al. (2010) Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature* 465: 627–631.

Ballaré, C.L. and Pierik, R. (2017) The shade-avoidance syndrome: multiple signals and ecological consequences. *Plant Cell Environ*. 40: 2530–2543.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. and Szendrei, Z. (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu. Rev. Ecol. Evol. Syst*. 40: 1–20.

Barbour, M.A., Fortuna, M.A., Bascompte, J., Nicholson, J.R., Julkunen-Tiitto, R., Jules, E.S., et al. (2016) Genetic specificity of a plant–insect food web: implications for linking genetic variation to network complexity. *Proc. Natl. Acad. Sci. U.S.A*. 113: 2128–2133.

Barbour, M.A., Kliebenstein, D.J. and Bascompte, J. (2022) A keystone gene underlies the persistence of an experimental food web. *Science* 376: 70–73.

Barker, H.L., Riehl, J.F., Bernhardsson, C., Rubert-Nason, K.F., Holeski, L.M., Ingvarsson, P.K., et al. (2019) Linking plant genes to insect communities: identifying the genetic bases of plant traits and community composition. *Mol. Ecol*. 28: 4404–4421.

Barry, K.E., Mommer, L., Van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y., et al. (2019) The future of complementarity: disentangling causes from consequences. *Trends Ecol. Evol*. 34: 167–180.

Bascompte, J. and Sole, R.V. (1996) Habitat fragmentation and extinction thresholds in spatially explicit models. *J. Anim. Ecol*. 65: 465–473.

Becker, C., Berthomé, R., Delavault, P., Flutre, T., Fréville, H., Gibot-Leclerc, S., et al. (2023) The ecologically relevant genetics of plant–plant interactions. *Trends Plant Sci*. 28: 31–42.

Bourke, P.M., Evers, J.B., Bijma, P., Van Apeldoorn, D.F., Smulders, M.J.M., Kuyper, T.W., et al. (2021) Breeding beyond monoculture: putting the ‘intercrop’ into crops. *Front. Plant Sci*. 12: 734167.

Brachi, B., Meyer, C.G., Villoutreix, R., Platt, A., Morton, T.C., Roux, F., et al. (2015) Coselected genes determine adaptive variation in herbivore resistance throughout the native range of *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. U.S.A*. 112: 4032–4037.

Brault, C., Doligez, A., Cunff, L., Coupel-Ledru, A., Simonneau, T., Chiquet, J., et al. (2021) Harnessing multivariate, penalized regression methods for genomic prediction and QTL detection of drought-related traits in grapevine. *G3:Genes|Genomes|Genet*. 11: jkab248.

Bronstein, J.L. (2009) The evolution of facilitation and mutualism. *J. Ecol*. 97: 1160–1170.

Brooker, R.W. (2006) Plant–plant interactions and environmental change. *New Phytol*. 171: 271–284.

Brooker, R.W., George, T.S., Homulle, Z., Karley, A.J., Newton, A.C., Pakeman, R.J., et al. (2021) Facilitation and biodiversity–ecosystem function relationships in crop production systems and their role in sustainable farming. *J. Ecol*. 109: 2054–2067.

Bustos-Segura, C., Poelman, E.H., Reichelt, M., Gershenzon, J., Gols, R. and Scherber, C. (2017) Intraspecific chemical diversity among neighbouring plants correlates positively with plant size and herbivore load but negatively with herbivore damage. *Ecol. Lett*. 20: 87–97.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., et al. (2002) Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.

Clauw, P., Ellis, T.J., Liu, H. and Sasaki, E. (2024) Beyond the standard GWAS—a guide for plant biologists. *Plant Cell Physiol.*

Cossani, C.M. and Sadras, V.O. (2021) Symmetric response to competition in binary mixtures of cultivars associates with genetic gain in wheat yield. *Evol. Appl*. 14: 2064–2078.

Costa E Silva, J., Potts, B.M., Gilmour, A.R. and Kerr, R.J. (2017) Genetic-based interactions among tree neighbors: identification of the most influential neighbors, and estimation of correlations among direct and indirect genetic effects for leaf disease and growth in *Eucalyptus globulus*. *Heredity* 119: 125–135.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. and Sanders, N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313: 966–968.

Dahlin, I., Rubene, D., Glinwood, R. and Ninkovic, V. (2018) Pest suppression in cultivar mixtures is influenced by neighbor-specific plant-plant communication. *Ecol. Appl*. 28: 2187–2196.

De Datta, S.K., Tauro, A.C. and Balaoing, S.N. (1968) Effect of plant type and nitrogen level on the growth characteristics and grain yield of indica rice in the tropics. *Agron. J*. 60: 643–647.

Denison, R.F., Kiers, E.T. and West, S.A. (2003) Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? *Q. Rev. Biol*. 78: 145–168.

Donald, C.M. (1968) The breeding of crop ideotypes. *Euphytica* 17: 385–403.

Duvick, D.N., Smith, J.S.C. and Cooper, M. (2003) Long-term selection in a commercial hybrid maize breeding program. *In Plant Breeding Reviews*. Edited by Janick, J. pp. 109–151. John Wiley & Sons, Ltd: New York, USA.

Ebeling, A., Klein, A., Schumacher, J., Weisser, W.W. and Tscharntke, T. (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117: 1808–1815.

Erb, M. (2018) Volatiles as inducers and suppressors of plant defense and immunity—origins, specificity, perception and signaling. *Curr. Opin. Plant Biol*. 44: 117–121.

Exposito-Alonso, M., 500 Genomes Field Experiment Team, Burbano, H.A., Bossdorf, O., Nielsen, R. and Weigel, D. (2019) Natural selection on the *Arabidopsis thaliana* genome in present and future climates. *Nature* 573: 126–129.

Feng, T., Zhu, Y.-H., Chai, N., Zhang, X.-T., Du, Y.-L., Turner, N.C., et al. (2023) Increased grain yield in modern genotypes of spring wheat for dryland cultivation in northwest China is associated with the decreased allocation of carbon to roots. *Field. Crops Res.* 303: 109114.

Finckh, M.R., Gacek, E.S., Goyeau, H., Lannou, C., Merz, U., Mundt, C.C., et al. (2000) Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie* 20: 813–837.

Flutre, T., Le Cunff, L., Fodor, A., Launay, A., Romieu, C., Berger, G., et al. (2022) A genome-wide association and prediction study in grapevine deciphers the genetic architecture of multiple traits and identifies genes under many new QTLs. *G3:Genes|Genomes|Genet.* 12: jkac103.

Forst, E., Enjalbert, J., Allard, V., Ambroise, C., Krissaane, I., Mary-Huard, T., et al. (2019) A generalized statistical framework to assess mixing ability from incomplete mixing designs using binary or higher order variety mixtures and application to wheat. *Field. Crops Res.* 242: 107571.

Frachon, L., Libourel, C., Villoutreix, R., Carrère, S., Glorieux, C., Huard-Chauveau, C., et al. (2017) Intermediate degrees of synergistic pleiotropy drive adaptive evolution in ecological time. *Nat. Ecol. Evol.* 1: 1551–1561.

Frachon, L., Mayjonade, B., Bartoli, C., Hautekèete, N.-C., Roux, F. and Wright, S. (2019) Adaptation to plant communities across the genome of *Arabidopsis thaliana*. *Molecul. Biol. Evol.* 36: 1442–1456.

Genung, M.A., Bailey, J.K. and Schweitzer, J.A. (2012) Welcome to the neighbourhood: interspecific genotype by genotype interactions in *Solidago* influence above- and belowground biomass and associated communities. *Ecol. Lett.* 15: 65–73.

Griffing, B. (1956) Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463–493.

Grime, J.P. and Pierce, S. (2012) *The Evolutionary Strategies that Shape Ecosystems*. Wiley-Blackwell, Chichester.

Groux, R., Stahl, E., Gouhier-Darimont, C., Kerdaffrec, E., Jimenez-Sandoval, P., Santiago, J., et al. (2021) Arabidopsis natural variation in insect egg-induced cell death reveals a role for LECTIN RECEPTOR KINASE-I.1. *Plant Physiol.* 185: 240–245.

Gujas, B., Alonso-Blanco, C. and Hardtke, C.S. (2012) Natural *Arabidopsis brx* loss-of-function alleles confer root adaptation to acidic soil. *Curr. Biol.* 22: 1962–1968.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., et al. (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123–1127.

Hirose, T. (2004) Development of the Monsi-Saeki theory on canopy structure and function. *Ann. Bot.* 95: 483–494.

Horton, M.W., Bodenhausen, N., Beilsmith, K., Meng, D., Muegge, B.D., Subramanian, S., et al. (2014) Genome-wide association study of *Arabidopsis thaliana* leaf microbial community. *Nat. Commun.* 5: 5320.

Horton, M.W., Hancock, A.M., Huang, Y.S., Toomajian, C., Atwell, S., Auton, A., et al. (2012) Genome-wide patterns of genetic variation in worldwide *Arabidopsis thaliana* accessions from the RegMap panel. *Nat. Genet.* 44: 212–216.

Huang, T., Döring, T.F., Zhao, X., Weiner, J., Dang, P., Zhang, M., et al. (2024) Cultivar mixtures increase crop yields and temporal yield stability globally. A meta-analysis. *Agron. Sustainable Dev.* 44: 28.

Jactel, H., Moreira, X. and Castagneyrol, B. (2021) Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. *Ann. Rev. Entomol.* 66: 277–296.

Jannink, J.-L., Lorenz, A.J. and Iwata, H. (2010) Genomic selection in plant breeding: from theory to practice. *Brief. Function. Genom.* 9: 166–177.

Jennings, P.R. (1964) Plant type as a rice breeding objective. *Crop Sci.* 4: 13–15.

Jennings, P.R. and De Jesus, J. (1968) Studies on competition in rice I: competition in mixtures of varieties. *Evolution* 22: 119–124.

Jing, Y., Watanabe, M., Aarabi, F., Fernie, A.R., Borghi, M. and Tohge, T. (2023) Cross-species metabolomic analyses in the brassicaceae reveals common responses to ultraviolet-b exposure. *Plant Cell Physiol.* 64: 1523–1533.

Johnson, M.T.J. and Agrawal, A.A. (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* 86: 874–885.

Johnson, M.T.J., Lajeunesse, M.J. and Agrawal, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* 9: 24–34.

Jung, M., Keller, B., Roth, M., Aranzana, M.J., Auwerkerken, A., Guerra, W., et al. (2022) Genetic architecture and genomic predictive ability of apple quantitative traits across environments. *Hortic. Res.* 9: uhac028.

Keddy, P.A. (2001) Competition. Springer, Dordrecht, the Netherlands.

Kikuchi, S., Bheemanahalli, R., Jagadish, K.S.V., Kumagai, E., Masuya, Y., Kuroda, E., et al. (2017) Genome-wide association mapping for phenotypic plasticity in rice. *Plant Cell Environ.* 40: 1565–1575.

Li, J., Mo, X., Wang, J., Chen, N., Fan, H., Dai, C., et al. (2009) BREVIS RADIX is involved in cytokinin-mediated inhibition of lateral root initiation in *Arabidopsis*. *Planta* 229: 593–603.

Li, L., Tilman, D., Lambers, H. and Zhang, F. (2014) Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytol.* 203: 63–69.

Libourel, C., Baron, E., Lenglet, J., Amsellem, L., Roby, D. and Roux, F. (2021) The genomic architecture of competitive response of *Arabidopsis thaliana* is highly flexible among plurispecific neighborhoods. *Front. Plant Sci.* 12: 741122.

Loreau, M. and Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Lynch, M., Walsh, B., et al. (1998) Genetics and Analysis of Quantitative Traits. Sinauer Sunderland, MA.

Marhava, P., Bassukas, A.E.L., Zourelidou, M., Kolb, M., Moret, B., Fastner, A., et al. (2018) A molecular rheostat adjusts auxin flux to promote root protophloem differentiation. *Nature* 558: 297–300.

Matsui, K. and Engelberth, J. (2022) Green leaf volatiles—the forefront of plant responses against biotic attack. *Plant Cell Physiol.* 63: 1378–1390.

McGale, E. and Sanders, I.R. (2022) Integrating plant and fungal quantitative genetics to improve the ecological and agricultural applications of mycorrhizal symbioses. *Curr. Opin. Microbiol.* 70: 102205.

Meuwissen, T.H.E., Hayes, B.J. and Goddard, M.E. (2001) Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157: 1819–1829.

Mochida, K. and Shinozaki, K. (2010) Genomics and bioinformatics resources for crop improvement. *Plant Cell Physiol.* 51: 497–523.

Monsi, M. and Saeki, T. (1953) Uber den lichtfaktor in den pflanzengesellschaften und seine bedeutung fur die stoffproduktion. *Jap. J. Bot.* 14: 22–52.

Montazeaud, G., Flutre, T., Ballini, E., Morel, J., David, J., Girodolle, J., et al. (2022) From cultivar mixtures to allelic mixtures: opposite effects of allelic richness between genotypes and genotype richness in wheat. *New Phytol.* 233: 2573–2584.

Montazeaud, G., Helleu, Q., Wuest, S.E. and Keller, L. (2023) Indirect genetic effects are shaped by demographic history and ecology in *Arabidopsis thaliana*. *Nat. Ecol. Evol.* 7: 1878–1891.

Mutic, J.J. and Wolf, J.B. (2007) Indirect genetic effects from ecological interactions in *Arabidopsis thaliana*. *Mol. Ecol.* 16: 2371–2381.

Naeem, S., Bunker, D.E., Hector, A., Loreau, M. and Perrings, C. (2009) Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective. Oxford University Press, Oxford.

Nallu, S., Hill, J.A., Don, K., Sahagun, C., Zhang, W., Meslin, C., et al. (2018) The molecular genetic basis of herbivory between butterflies and their host plants. *Nat. Ecol. Evol*. 2: 1418–1427.

Norrington-Davies, J. (1967) Application of diallel analysis to experiments in plant competition. *Euphytica* 16: 391–406.

Ordon, F. and Friedt, W. Eds. (2019) *Advances in Breeding Techniques for Cereal Crops*, 1st edn. Burleigh Dodds Science Publishing, London.

Pang, Y., Liu, C., Wang, D., St. Amand, P., Bernardo, A., Li, W., et al. (2020) High-resolution genome-wide association study identifies genomic regions and candidate genes for important agronomic traits in wheat. *Molecul. Plant* 13: 1311–1327.

Parisod, C., Holderegger, R. and Brochmann, C. (2010) Evolutionary consequences of autopolyploidy. *New Phytol*. 186: 5–17.

Pélissier, R., Ballini, E., Temple, C., Ducasse, A., Colombo, M., Frouin, J., et al. (2023) The genetic identity of neighboring plants in intraspecific mixtures modulates disease susceptibility of both wheat and rice. *PLoS Biol*. 21: e3002287.

Pickett, J.A., Woodcock, C.M., Midega, C.A. and Khan, Z.R. (2014) Push–pull farming systems. *Curr. Opin. Biotechnol*. 26: 125–132.

Pimentel, D. (1996) Green revolution agriculture and chemical hazards. *Sci. Total Environ*. 188: S86–S98.

Poelman, E.H., Dam, N.M., Loon, J.J.A., Vet, L.E.M. and Dicke, M. (2009) Chemical diversity in *Brassica oleracea* affects biodiversity of insect herbivores. *Ecology* 90: 1863–1877.

Poelman, E.H., Loon,van, J.J.A. and Dicke, M. (2008) Consequences of variation in plant defense for biodiversity at higher trophic levels. *Trends Plant Sci*. 13: 534–541.

Reynolds, M.P., Acevedo, E., Sayre, K.D. and Fischer, R.A. (1994) Yield potential in modern wheat varieties: its association with a less competitive ideotype. *Field. Crops Res*. 37: 149–160.

Riehl, J.F.L., Cole, C.T., Morrow, C.J., Barker, H.L., Bernhardsson, C., Rubert-Nason, K., et al. (2023) Genomic and transcriptomic analyses reveal polygenic architecture for ecologically important traits in aspen (*Populus tremuloides* Michx). *Ecol. Evol*. 13: e10541.

Rodrigues, A., Santiago, J., Rubio, S., Saez, A., Osmont, K.S., Gadea, J., et al. (2009) The short-rooted phenotype of the *brevis radix* mutant partly reflects root abscisic acid hypersensitivity. *Plant Physiol*. 149: 1917–1928.

Sato, Y., Shimizu-Inatsugi, R., Takeda, K., Schmid, B., Nagano, A.J. and Shimizu, K.K. (2024) Reducing herbivory in mixed planting by genomic prediction of neighbor effects in the field. *Nat. Commun.* 15: 8467.

Sato, Y., Takahashi, Y., Xu, C. and Shimizu, K.K. (2023) Detecting frequency-dependent selection through the effects of genotype similarity on fitness components. *Evolution* 77: 1145–1157.

Sato, Y., Takeda, K. and Nagano, A.J. (2021a) Neighbor QTL: an interval mapping method for quantitative trait loci underlying plant neighborhood effects. *G3:Genes|Genomes|Genet*. 11: jkab017.

Sato, Y., Yamamoto, E., Shimizu, K.K. and Nagano, A.J. (2021b) Neighbor GWAS: Incorporating neighbor genotypic identity into genome-wide association studies of field herbivory. *Heredity* 126: 597–614.

Schlicht, R. and Iwasa, Y. (2004) Forest gap dynamics and the ising model. *J. Theor. Biol*. 230: 65–75.

Schneider, K.A. (2008) Maximization principles for frequency-dependent selection I: the one-locus two-allele case. *Theoretical. Popul. Biol*. 74: 251–262.

Schuman, M.C., Allmann, S. and Baldwin, I.T. (2015) Plant defense phenotypes determine the consequences of volatile emission for individuals and neighbors. *eLife* 4: e04490.

Schutz, W.M., Brim, C.A. and Usanis, S.A. (1968) Inter-genotypic competition in plant populations I. Feedback systems with stable equilibria in populations of autogamous homozygous lines. *Crop Sci*. 8: 61.

Schutz, W.M. and Usanis, S.A. (1969) Inter-genotypic competition in plant populations II. Maintenance of allelic polymorphisms with frequency-dependent selection and mixed selfing and random mating. *Genetics* 61: 875–891.

Schweitzer, J.A., Bailey, J.K., Fischer, D.G., LeRoy, C.J., Lonsdorf, E.V., Whitham, T.G., et al. (2008) Plant–soil–microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms. *Ecology* 89: 773–781.

Scott, M.F., Fradgley, N., Bentley, A.R., Brabbs, T., Corke, F., Gardner, K.A., et al. (2021) Limited haplotype diversity underlies polygenic trait architecture across 70 years of wheat breeding. *Genome Biol*. 22: 137.

Shimizu, K.K. (2022) Robustness and the generalist niche of polyploid species: genome shock or gradual evolution? *Curr. Opin. Plant Biol*. 69: 102292.

Shimizu, K.K., Copetti, D., Okada, M., Wicker, T., Tameshige, T., Hatakeyama, M., et al. (2021) De novo genome assembly of the Japanese wheat cultivar Norin 61 highlights functional variation in flowering time and *Fusarium*-resistant genes in east asian genotypes. *Plant Cell Physiol*. 62: 8–27.

Shindo, C., Bernasconi, G. and Hardtke, C.S. (2008) Intraspecific competition reveals conditional fitness effects of single gene polymorphism at the *Arabidopsis* root growth regulator *BRX*. *New Phytol*. 180: 71–80.

Shuster, S.M., Lonsdorf, E.V., Wimp, G.M., Bailey, J.K. and Whitham, T.G. (2006) Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. *Evolution* 60: 991–1003.

Stange, M., Barrett, R.D.H. and Hendry, A.P. (2021) The importance of genomic variation for biodiversity, ecosystems and people. *Nat. Rev. Genet*. 22: 89–105.

Subrahmaniam, H.J., Libourel, C., Journet, E.-P., Morel, J.-B., Muños, S., Niebel, A., 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.

Sundell, D., Mannapperuma, C., Netotea, S., Delhomme, N., Lin, Y.-C., Sjödin, A., et al. (2015) The plant genome integrative explorer resource: PlantGen IE.org. *New Phytol*. 208: 1149–1156.

Tahvanainen, J.O. and Root, R.B. (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10: 321–346.

Takabayashi, J. (2022) Herbivory-induced plant volatiles mediate multitrophic relationships in ecosystems. *Plant Cell Physiol*. 63: 1344–1355.

Takahashi, Y., Tanaka, R., Yamamoto, D., Noriyuki, S. and Kawata, M. (2018) Balanced genetic diversity improves population fitness. *Proc. R. Soc. B*. 285: 20172045.

Tian, J., Wang, C., Xia, J., Wu, L., Xu, G., Wu, W., et al. (2019) Teosinte ligule allele narrows plant architecture and enhances high-density maize yields. *Science* 365: 658–664.

Tilman, D. and Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature* 367: 363–365.

Tilman, D., Wedin, D. and Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718–720.

Tsuchimatsu, T., Kakui, H., Yamazaki, M., Marona, C., Tsutsui, H., Hedhly, A., et al. (2020) Adaptive reduction of male gamete number in the selfing plant *Arabidopsis thaliana*. *Nat. Commun*. 11: 2885.

Tsunoda, S. (1959) A developmental aanlysis of yielding ability in varieties of field crops.: II. The assimilation-system of plants as affected by the form, direction and arrangement of single leaves. *Japanese J. Breeding* 9: 237–244.

Turner, K.G., Lorts, C.M., Haile, A.T. and Lasky, J.R. (2020) Effects of genomic and functional diversity on stand-level productivity and performance of non-native *Arabidopsis*. *Proc. R. Soc. B*. 287: 20202041.

Underwood, N., Inouye, B.D. and Hambäck, P.A. (2014) A conceptual framework for associational effects: when do neighbors matter and how would we know? *Q. Rev. Biol*. 89: 1–19.

Vogel, O.A., Craddock, J.C., Muir, C.E., Everson, E.H. and Rohde, C.R. (1956) Semidwarf growth habit in winter wheat improvement for the Pacific Northwest. *Agron. J*. 48: 76–78.

Wang, M., Roux, F., Bartoli, C., Huard-Chauveau, C., Meyer, C., Lee, H., 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.

Weiner, J. (2019) Looking in the wrong direction for higher-yielding crop genotypes. *Trends Plant Sci*. 24: 927–933.

Weiner, J., Du, Y., Zhang, C., Qin, X. and Li, F. (2017) Evolutionary agroecology: individual fitness and population yield in wheat (*Triticum aestivum*). *Ecology* 98: 2261–2266.

Whitham, T.G., DiFazio, S.P., Schweitzer, J.A., Shuster, S.M., Allan, G.J., Bailey, J.K., et al. (2008) Extending genomics to natural communities and ecosystems. *Science* 320: 492–495.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., et al. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84: 559–573.

Wolf, J.B., Mutic, J.J. and Kover, P.X. (2011) Functional genetics of intraspecific ecological interactions in *Arabidopsis thaliana*. *Philos. Trans. R. Soc. Lond. B. Biol. Sci*. 366: 1358–1367.

Wuest, S.E. and Niklaus, P.A. (2018) A plant biodiversity effect resolved to a single chromosomal region. *Nat. Ecol. Evol*. 2: 1933–1939.

Wuest, S.E., Peter, R. and Niklaus, P.A. (2021) Ecological and evolutionary approaches to improving crop variety mixtures. *Nat. Ecol. Evol*. 5: 1068–1077.

Wuest, S.E., Pires, N.D., Luo, S., Vasseur, F., Messier, J., Grossniklaus, U., et al. (2022) Increasing plant group productivity through latent genetic variation for cooperation. *PLoS Biol*. 20: e3001842.

Wuest, S.E., Schulz, L., Rana, S., Frommelt, J., Ehmig, M., Pires, N.D., et al. (2023) Single-gene resolution of diversity-driven overyielding in plant genotype mixtures. *Nat. Commun*. 14: 3379.

Xi, Y., Wang, D., Weiner, J., Du, Y.-L. and Li, F.-M. (2023) Time to onset of flowering, water use, and yield in wheat. *Agronomy* 13: 1217.

Xu, C., Sato, Y., Yamazaki, M., Brasser, M., Barbour, M.A., Bascompte, J., et al. (2023) Genome-wide association study of aphid abundance highlights a locus affecting plant growth and flowering in *Arabidopsis thaliana*. *R. Soc. Open Sci*. 10: 230399.

Yabe, S., Hara, T., Ueno, M., Enoki, H., Kimura, T., Nishimura, S., et al. (2018) Potential of genomic selection in mass selection breeding of an allogamous crop: an empirical study to increase yield of common buckwheat. *Front. Plant Sci*. 9: 276.

Yang, J., Benyamin, B., McEvoy, B.P., Gordon, S., Henders, A.K., Nyholt, D.R., et al. (2010) Common SNPs explain a large proportion of the heritability for human height. *Nat. Genet*. 42: 565–569.

Zeller, S.L., Kalinina, O., Flynn, D.F.B. and Schmid, B. (2012) Mixtures of genetically modified wheat lines outperform monocultures. *Ecol. Appl*. 22: 1817–1826.

Zhang, D.-Y., Sun, G.-J. and Jiang, X.-H. (1999) Donald's ideotype and growth redundancy: a game theoretical analysis. *Field. Crops Res*. 61: 179–187.

Zhao, K., Tung, C.-W., Eizenga, G.C., Wright, M.H., Ali, M.L., Price, A.H., et al. (2011) Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. *Nat. Commun*. 2: 467.

Zhao, Y., Thorwarth, P., Jiang, Y., Philipp, N., Schulthess, A.W., Gils, M., et al. (2021) Unlocking big data doubled the accuracy in predicting the grain yield in hybrid wheat. *Sci. Adv*. 7: eabf9106.

Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., et al. (2000) Genetic diversity and disease control in rice. *Nature* 406: 718–722.

Plant Cell Physiol. 00(00): 1–13 (2024) doi:https://doi.org/10.1093/pcp/pcae092, Advance Access publication on 10 September 2024, available online at https://academic.oup.com/pcp