Plant–plant communication in variety mixtures plays on disease susceptibility and immunity

Marie-Odile Bancal

Marie-Odile Bancal. Plant–plant communication in variety mixtures plays on disease susceptibility and immunity. Journal of Experimental Botany, Oxford University Press (OUP), 2021, 72 (18), pp.6084-6086. 10.1093/jxb/erab377 . hal-03659342

eXtra Botany

Insight

Plant-plant communication in variety mixtures plays on disease susceptibility and immunity

Marie-Odile Bancal[1,2]
[1]AgroParisTech, University Paris-Saclay, France
[2]INRAE, ECOSYS, UMR 1402, F-78350 Thiverval-Grignon, France
Correspondence: marie-odile.bancal@inrae.fr

This article comments on:
Pélissier R, Buendia L, Brousse A, Temple C, Ballini E , FortF, Violle C, Morel JB. 2021. Plant neighbour-modulated susceptibility to pathogens in intraspecific mixtures. Journal of Experimental Botany 72, XXXX–XXXX.

Keywords: Disease, Immunity, Intraspecific mixture, Neighbour, Plant-plant interactions, Rice, Wheat.

Overview.
Intraspecific mixtures are a well-known means to modulate epidemics in crops, but knowledge on the immunity they induce is scarce. Pélissier et al. (2021) selected pairs of susceptible wheat or rice cultivars cross-modulating disease severity and showed that belowground interactions were involved in communicating infection. Healthy neighbors could initiate significant modulations of transcription of basal immunity genes after pathogen inoculation. No general rule was observed between pathosystems, but the demonstration of the effect of healthy neighbors on disease susceptibility and immunity in adjacent plants is a key finding as we strive to understand health in varietal mixtures.

Biodiversity: an insurance to plant health? In crops, maintaining plant health is crucial, as climate change and decreased availability of pesticides may enhance opportunities for pests and diseases (Barot et al., 2017). A large consensus states that higher natural or cultivated biodiversity increases productivity because functional complementarity and redundancy enhance resilience to environmental fluctuations. In most but not all cases, complex but beneficial biological regulations between trophic or scale levels emerge from ecosystem biodiversity (Tilman, Isbell and Cowles, 2014). Mixing varieties is an easy-to-use and flexible means to adapt annual crops to identified patterns of multi-stress (Grettenberger and Tooker, 2015). Identifying and quantifying the main mechanisms involved as biodiversity increases is a major prerequisite for managing assemblies in agroecology.

Biodiversity attenuates the population response to biotic and abiotic stresses by mobilizing common mechanisms (Tilman, Isbell and Cowles, 2014; Barot et al, 2017; Rolfe, Griffiths and Ton, 2019): escape by phenology or architecture; protection by genetic barriers ("dilution" of susceptible among resistant plants); niche complementarity for resources, microclimate modification; and finally plant immunity. All these mechanisms interplay directly or indirectly to achieve a better crop fitness. The result depends on whether competitive or facilitative mechanisms dominate and on the environmental conditions (Tilman, Isbell and Cowles, 2014; Rolfe, Griffiths and Ton, 2019). While these mechanisms support similar ranges of yield gains, crop management considerations generally favor genetic complementarity and/or remote enhancement of immunity responses in variety mixtures (Grettenberger and Tooker, 2015; Gibson and Nguyen, 2020), even though asymmetric access to resources may occur (Pélissier, Violle and Morel, 2021).

Variety mixtures rely mainly on complementarity between susceptible and resistant genotypes to the more frequent and damaging pests/diseases (Grettenberger and Tooker, 2015; Barot et al., 2017). Alternatively, remote plant immunity involves manipulating a sequence of events from the recognition of a danger/stranger, its transduction and the associated induced physiological responses (Rolfe, Griffiths and Ton, 2019; Pélissier, Violle and Morel, 2021).

Near neighbor crop communications, as premunition of exposure to pathogens and/or priming by emission of a defense-related compound, were long ago identified. From the 2000s, the key role of immunity in population health largely extended to plant-plant interactions during infection. Plants interact either directly through chemical exchanges i.e. exudates and volatile organic compounds (VOCs), or indirectly through the microbiome, a network of above or belowground microorganisms so closely associated to plants that it behaves like a meta-organism, a holobiome (Shafiri et Ryu, 2021; Trivedi et al., 2020).

Pests or pathogens largely induce host-plant immunity by well-known phytohormones including salicylic acid, ethylene and jasmonic acid (Benvenuoto et al., 2020; Trivedi et al., 2020; Shafiri et Ryu, 2021), all of which may prime neighbors (Ninkovic, Markovic and Rensing, 2021). Interestingly, kin and stranger recognition also cross talk with defense pathways (Shafiry et Ryu, 2021; Liu et al., 2020), using root exudates (Anten et al., 2021) or leaf volatiles (Karban et al., 2013), diverting carbon towards beneficial anticipation responses (Anten et al., 2021). Inter plant cues and signals have been found central in herbivory (Pélissier, Violle and Morel, 2021). However, the role of plant immunity in regulating disease development in variety mixtures has certainly been understudied. Furthermore, if priming is a well-established mechanism to anticipate stresses, plant-plant communication in healthy conditions was rarely advocated, especially in conspecific plant populations (Ninkovic, Markovic et Rensing. 2020 ; Pélissier, Violle and Morel, 2021).

Do healthy conspecific neighbours enhance plant resistance and immunity? In their paper "**Plant neighbour-modulated susceptibility to pathogens in intraspecific mixtures**", Pélissier et al. (2021) investigated whether mixing pairs of susceptible varieties of wheat or rice may limit severity and increase immunity, even if the focal receiver plant is neighboured by healthy plants. To unravel plant-plant interactions and focus on immunity only, they set up a glasshouse experiment with both susceptible focal and neighbour plants. The experimental design, moreover, limited plant competition for resources and pathogen dispersal. **The originality of the study is the isolation of basal plant immunity from other defence mechanisms to pinpoint the importance of immunity in the health of conspecific plant populations.**

Pélissier *et al.* (2021) found that **it is possible to select pairs of varieties that significantly cross-protected against rust in wheat or blast in rice, compared to monocrops.** Given that the associated varieties were equally susceptible, the mixture advantage does not rely directly on resistance genes to the inoculated pathogens. It confirms previous studies showing biodiversity mainly ameliorates plant health (Gibson and Nguyen, 2020). However, Pelissier *et al.* did not generalize their observation. Inoculation of mixtures with other pathogens, even of close lifestyle, showed either no change or an increased severity in both focal and neighbour plants. Literature previously pointed out the lack of genericity of pathogen responses to biodiversity (Rolfe, Griffiths and Ton, 2019; Liu et al., 2020), rendering its use in field crops submitted to multiple and unpredictable stresses difficult (Landi, 2020; Berens et al., 2019).

Using the same wheat or rice variety pairs, Pélissier et al. (2021) tried to elucidate by which mechanisms conspecific plants interplay. In both cases**, they showed that varieties communicated directly by a belowground chemical interaction between kin roots.** Root physical contact was needed in wheat mixtures, not in rice. Surprisingly, neither the soil microbiome nor the inoculation of neighbours were necessary for this interplay. **The originality of the paper was to state that healthy and inoculated neighbour plants modified focal plant susceptibility to the same extent,** suggesting that specific kin recognition between cultivars was enough to enhance plant health (Gibson and Nguyen, 2020). Indeed, the key role of plant exudates in plant-plant communication was already shown (Rolfe, Griffiths and Ton, 2019; Liu et al., 2020), and the reshaping of microbiome after defence priming was also recently demonstrated (Trivedi et al., 2021). This study moreover suggests that early plant-plant interactions in varietal mixtures may reshape plant health status only due to the proximity of close but distinct genotypes and without priming. This mechanism was not yet exemplified, maybe because it was hidden by longer-term interactions (Trivedi et al., 2021), or because other plant-plant interactions interfere, such as resource competition or multi-stress responses (Landi, 2020; Benvenuoto et al., 2020).

Finally, basal immunity was a good candidate to trigger these processes. In healthy rice plants, the basal immunity was enhanced by mixture; this effect was even strengthened by inoculation, suggesting the changes in susceptibility relate to those in basal immunity. Conversely, in wheat healthy plants' basal immunity was unchanged by mixture, while inoculation modulated differently immunity of each variety. Consequently, changes in basal immunity could not explain changes in wheat mixture susceptibility. **In varietal mixtures, the link between decreased susceptibility and increased basal immunity may not be a general rule.**

Perspectives for crop health management. This is the first study pointing out that mixing close relatives enhances crop health, even without priming, by using root chemical signalling.

Interestingly, this imaginative experimental design evidenced that an underlying communication between healthy kin plants, even if weak, may enhance the population health, by modulating complex network of interactions (Liu et al., 2020). It is a key finding to avoid confusion of effects, while setting up experimental designs involving inter- and intra- specific mixtures under multistresses (Landi, 2020). Furthermore, it opens the way to search for new chemical traits, based on early plant-plant recognition, to assembly varieties.

This study nevertheless opens up some questions. (i) If belowground signals or cues were clearly involved, aerial VOCs may also interplay (Ninkovic, Markovic and Rensing, 2021) what the experimental design did not show, preventing pathogens but not VOCs movements. (ii) Short-term responses to mixtures may be relayed by longer-term soil microbiome changes (Benvenuoto et al., 2020; Rolfe, Griffiths and Ton, 2019). (iii) The variety relatedness, usually high (Grettenberger and Tooker, 2015), was not examined, although being a key information for the future assembly of varieties, even susceptible ones (Gibson and Nguyen, 2020). This last point particularly challenges the link with agricultural practices that largely use complementary resistance profiles in mixtures (Barot et al., 2017). More generally, (iv), these effects must be confirmed under natural conditions, with varietal mixtures subjected to multiple stresses: climate (Benevenuoto et al., 2020; Berens et al., 2019), soil and its biotic history (Shafiri and Ryu, 2021), nutrition (Landi, 2020; Liu et al., 2020) and/or pests (Liu et al., 2020), which all interact with immunity towards a given outcome.

This paper provides a renewed insight into interactions between closely related plants, putting forward an underlying mechanism of ecosystem resilience that future research has investigate in more depth for further applications in agroecology.

Literature cited

Anten, NPR, Chen, BJW. 2021. Detect thy family: Mechanisms, ecology and agricultural aspects of kin recognition in plants. **Plant Cell and Environment 44**: 1059– 1071. https://doi.org/10.1111/pce.14011

Barot, S., Allard, V., Cantarel, A. et al., 2017. Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. **Agronomy for Sustainable Development 37,** 13-33. doi: 10.1007/s13593-017-0418-x

Benevenuto R F., Seldal T., Moe S R., Saona C R., Hegland S J., 2020. Neighborhood Effects of Herbivore-Induced Plant Resistance Vary Along an Elevational Gradient**. Frontiers in Ecology and Evolution 8:117. 8 mai 2020.** doi: 10.3389/fevo.2020.00117

Berens M. L., Wolinska K. W., Spaepen S., Ziegler J., Nobori T., Nair A., Krüler V., Winkelmüller T. M., Wang Y., Mine A., Becker D., Garrido-Oter R., Schulze-Lefert P., Tsuda K., 2019. Balancing trade-offs between biotic and abiotic stress responses through leaf age-dependent variation in stress hormone cross-talk. **Proceedings of the National Academy of Sciences 116 (6)** 2364-2373; doi: 10.1073/pnas.1817233116

Gibson A K. and Nguyen A E., 2020. Does genetic diversity protect host populations from parasites? A meta-analysis across natural and agricultural systems**. Evolution Letters 5-1**: 16–32. doi:10.1002/evl3.206

Grettenberger IM & Tooker JF., 2015. Moving beyond resistance management toward an expanded role for seed mixture in agriculture. **Agriculture, Ecosystems and Environment 208**: 29-36. http://dx.doi.org/10.1016/j.agee.2015.04.019

Karban R, Shiojiri K, Ishizaki S, Wetzel WC, Evans RY. **2013.** Kin recognition affects plant communication and defence. **Proceedings of the Royal Society B: Biological Sciences. Feb 13; 280(1756):**20123062. doi: 10.1098/rspb.2012.3062.

Landi M., 2020. Airborne signals and abiotic factors: the neglected side of the plant communication. **Communicative & Integrative Biology**, **13(1):** 67-73, DOI: 10.1080/19420889.2020.1767482

Liu H, Brettell LE, Qiu Z, Singh BK. 2020. Microbiome-Mediated Stress Resistance in Plants. **Trends in Plant Science 25(8):**733-743. doi: 10.1016/j.tplants.2020.03.014

Ninkovic, V, Markovic, D, Rensing, M. 2021. Plant volatiles as cues and signals in plant communication. **Plant Cell and Environment 44:** 1030– 1043. https://doi.org/10.1111/pce.13910

Pélissier R., Violle C., Morel J-B., 2021. Plant immunity: Good fences make good neighbors? **Current Opinion in Plant Biology 62**, pp.102045. doi: 10.1016/j.pbi.2021.102045

Pélissier R, Buendia L, Brousse A, Temple C, Ballini E , Fort F, Violle C, Morel JB. 2021. Plant neighbour-modulated susceptibility to pathogens in intraspecific mixtures. Journal of Experimental Botany 72, XXXX–XXXX.

Rolfe S.A., Griffiths J., Ton J., 2019. Crying out for help with root exsudates. **Current Opinion in Microbiology 49:**73–82 **.** doi: 10.1016/j.mib.2019.10.003.

Sharifi, R, Ryu, C-M. 2021. Social networking in crop plants: Wired and wireless cross-plant communications. **Plant Cell and Environment 44**: 1095– 1110. doi: 10.1111/pce.13966

Tilman D., Isbell F., Cowles JM. , 2014. Biodiversity and Ecosystem Functioning. **Annual Review of Ecology Evolution and Systematics 45**: 471-493. doi: 10.1146/annurev-ecolsys-120213-091917

Trivedi P., Leach JE., Tringe SG., Sa T., Singh BK., 2020. Plant-microbiome interactions: from community assembly to plant health. **Nature reviews Microbiology_vil18_Nov2020_607-621.** doi : 10.1038/s41579-020-0412-1