Editorial

Plant interactions with other organisms: molecules, ecology and evolution

The plant sciences, during much of the 20th century, evolved as a group of disciplines that sought to explain plant responses to factors of the abiotic environment, such as water, mineral nutrients and light. In the last two decades, there have been major advances in our understanding of how plants interact with a growing list of other components of their biotic environment, including other plants, animal consumers and detritivores, pollinators, and beneficial and pathogenic microorganisms. This progress has rendered a much richer picture of plant function in real life than the one produced by traditional models of physiological responses to simple variations in abiotic factors. Simultaneously, this progress has revealed major gaps in our understanding of the evolution of plant adaptation, the molecular mechanisms that mediate phenotypic plasticity in complex biotic scenarios, and the ecosystem consequences of these interactions.

The overarching goal of the 32nd New Phytologist Symposium (NPS), 'Plant interactions with other organisms: molecules, ecology and evolution', was to bring together researchers working on various aspects of plant interactions with the biotic world. Despite the fact that exciting advances have been made in individual subfields, which captured the attention of specialists in each particular discipline, there has been little communication across disciplinary and scale boundaries for synthesizing our conceptual understanding of how plants interact with components of the biotic environment. This Special Issue features articles from the invited speakers of the 32nd NPS, and represents a collection that describes progress in a broad cross-section of disciplines. All articles are written keeping in mind the multidisciplinary nature of the audience. This combination of research papers, review papers and commentaries aims to provide a multifaceted view of the field of plant biotic interactions, which we hope will be appealing not only to the specialist but also to anyone interested in plant biology and ecology.

Stops on the molecular road map

A classic area of research in plant interactions has focused on the study of plant defenses against pathogens and herbivorous organisms. Plant pathology is an extremely active area of research, with obvious implications for agriculture, and the powdery mildew disease of barley has been a model system in the discipline for many years, owing to the economic importance of losses caused by the fungus *Blumeria graminis* on barley crops. Loss-of-function mutant alleles of the *Mildew resistance locus o* (*Mlo*) gene confer broad-spectrum resistance to almost all known isolates of the pathogen, and *mlo* resistance continues to be extensively used in the field. A synthesis of our progress in the understanding of *mlo*-mediated disease resistance in barley and Arabidopsis is provided in a timely review by Acevedo-Garcia *et al.* (in this issue, pp. 273–281), with a discussion of current views regarding MLO function.

One of the unifying concepts that emerged in the last decade is that plant interactions with heterotrophic organisms are often modulated by two key plant hormones: jasmonic acid (JA) and salicylic acid (SA) (Pieterse *et al.*, 2012). JA plays a key role in orchestrating plant defenses against herbivores and several pathogens (Browse, 2009). A major discovery by Clarence (Bud) Ryan's group in the early 1970s was that defense responses in plants can be induced by tissue damage in a systemic way within the organism, meaning in tissues and organs not directly affected by the damage event that activated the plant defense system (Green & Ryan, 1972). The nature of the systemic signals, however, has remained elusive. In this issue, Ted Farmer *et al.* (pp. 282–288) outline a creative model that proposes that the rapid changes caused by wounding in xylem hydrostatic pressure travel through the vasculature and lead to activation of JA signaling in distal tissues through a clade 3 GLR-dependent mechanism (see also Editors' choice).

Jasmonic acid signaling is finely regulated by internal and external factors (Robert-Seilaniantz *et al.*, 2011; Pieterse *et al.*, 2012). Low red : far-red (R : FR) ratios, which signal a high risk of competition in plant canopies acting through the photoreceptor phytochrome B (phyB), repress JA signaling and JA-induced defenses (Ballaré, 2014). This down-regulation of JA signaling by low R : FR ratios presumably helps plants to redirect resources from defense to rapid growth to overtop potential competitors when they face intense competition from other plants. Two papers in this Special Issue from the Ballaré laboratory address links between phyB and plant immunity from different perspectives (Cargnel *et al.*, pp. 342–354; Leone *et al.*, pp. 355–367). Leone *et al.* (pp. 355–367) propose a model in which phyB regulation of JA signaling is the result of changes in the abundance of DELLA and JASMONATE ZIM domain (JAZ) transcriptional repressors, along with changes in the activity of PIF and MYC transcription factors (see Commentary by Pieterse *et al.*, pp. 261–264). The metabolomic link between phyB and plant immunity was explored by Cargnel *et al.* (pp. 342–354) using the well-studied Arabidopsis–*Botrytis cinerea* pathosystem. The authors conclude that inactivation of phyB by low R : FR ratios increases plant susceptibility to the fungus by repressing the synthesis of Trp-derived secondary metabolites (indolic glucosinlates and camalexin; Cargnel *et al.*, pp. 342–354). The effects of plant proximity on R : FR ratio and plant responses to the light cue can be complex; therefore simulation models can be useful tools for handling this complexity. In a Letter in this issue, Bongers *et al.* (pp. 268–272) introduce the concept of functional–structural plant (FSP) models, and outline how they may be used to improve our understanding of plant responses to competition.

Of course, not all microorganisms are pathogenic and major strides have been made in the last decade in our understanding of plant interactions with 'beneficial' microorganisms. Indeed, many microorganisms can help the plant to fight disease. For example, the rhizobacteria *Pseudomonas fluorescens* WCS417 induces a systemic immune response in Arabidopsis that is effective against a broad spectrum of pathogens (induced systemic resistance, ISR), but the mechanisms that control this effect are not well understood. In this issue, Zamioudis *et al.* (pp. 368–397) report a significant advance in this field by uncovering the role of β-glucosidase BGLU42 as an important novel component that acts downstream of the transcription factor MYB72 in the signaling pathway that leads to activation of ISR. Another well-studied beneficial interaction between plants and rhizobacteria is the symbiotic association between legume roots and rhizobia. Gary Stacey and coworkers discuss fascinating recent advances in the understanding of the mechanism of signaling between legume roots and rhizobia mediated by lipochitooligosaccharides (Liang *et al.*, pp. 289–296).

Volatility of communication

The explosion of interest in volatile communication among or within plants has resulted in an intense focus of research since the discovery that the emission of plant volatile compounds in response to insect herbivory could represent an indirect antiherbivore defense (Dicke & Sabelis, 1988). It is now understood that there are innumerable ways in which volatile compounds can be used as communication signals between plants and other organisms and between parts of the same plant. As Karban *et al.* (pp. 380–387) demonstrate in their paper, we may be underestimating the sophisticated nature of this communication in a semiarid shrub ecosystem. These authors show that related individuals tend to have a similar 'cocktail' of the relative proportion of various volatile compounds, called chemotypes, and that this similarity is heritable. This recognition of chemotypes may lend increased herbivore resistance when these volatile compounds are detected as coming from a related individual. An unconventional look at the open questions regarding this topic can be found in the research review by Martin Heil (pp. 297–306), who discusses the view that the main targets of herbivore-induced volatile compounds are the emitting plant themselves. He argues that volatile plant molecules play important roles as direct resistance agents in and around the wound site, and they serve as signals to prepare distal parts of the same plant for upcoming damage. A novel way in which plants may communicate through volatile signals with other organisms is proposed in the review by Austin *et al.* (pp. 307–314), who suggest that these same unique combinations of volatile signals that come from green leaves may extend to the litter, signaling attraction or inhibition of soil fauna to specific microsites in the forest floor and thus affecting decomposition.

Surprising interactions and outcomes

Several papers in this Special Issue have surprises in store, outcomes that we might not expect based on our current understanding of plant interactions, particularly when limited to one interactor. In their research review, Marcel Dicke and coworkers argue that most studies on plant–herbivore interactions have treated herbivores as individual entities; yet, herbivores consist of communities themselves, carrying associated organisms such as parasites and symbionts, which may have important effects on the herbivore and its interactions with the host plant (Zhu *et al.*, pp. 315–321). They discuss several fascinating examples of how herbivore-associated organisms can affect the behavior and physiology of their herbivore host, and also interfere with plant signal-transduction pathways, repressing the expression of plant defenses.

The idea that more must be better for beneficial interactions may not hold in two important cases in this Special Issue. In terms of pollination, Aizen *et al.* (pp. 322–328) demonstrate in their review that having more pollinators does not always bring benefits, especially in the case of nonnative bee species and floral damage. They suggest that the presence of high numbers of alien pollinators, particularly the widely introduced *Apis mellifera*, do double-duty in their negative effects by reducing the reproductive success of native species while promoting nonnative plant success. A second case from a very different study system is the importance of context for beneficial interactions on facilitation effects in alpine cushion plants. Schöb *et al.* (pp. 386–396) demonstrate a delicate balance between beneficial impacts and negative feedbacks on the benefactor plants depending on the local biotic and climate conditions in this cold and inhospitable habitat, which affect the intensity of the facilitation effects.

When thinking about global change, the last place to look for nutrient subsidies may be the herbivores, but the study by Meehan *et al.* (pp. 397–407), examining the interactive effects of ozone and elevated CO_2 on nutrient cycling, offers a further surprise. It appears that nutrient-rich frass from increased herbivore feeding in elevated CO_2 treatments results in an injection of labile nitrogen to the soil surface that, while small in terms of total nutrient content, may have important consequences as a result of its stimulation of nitrogen turnover in these human-impacted ecosystems.

Plants affecting the soil

The soil environment, and in particular soil physical characteristics and nutrient availability, has long been recognized as a key factor in determining ecosystem structure and biogeochemical cycling in terrestrial ecosystems (Jenny, 1980; Vitousek *et al.*, 1995). Equally, plant species and their associated traits have important consequences for carbon and nutrient turnover (Hobbie, 1992; Cornwell *et al.*, 2008), which can ultimately determine nutrient availability for plant growth. Nevertheless, the importance of the biotic interactions between soil organisms and plant species, both above and below ground, could play a much larger role than we previously thought. Several articles in this Special Issue address the importance of plant interactions with organisms below ground. One plant–soil interaction that has been of particular interest to ecologists is the plant–soil feedback (PSF). PSF can be observed as a result of the fact that over time, negative and positive feedbacks can develop which lead to positive or inhibitory effects on plant growth as plants affect soil biota (Bever *et al.*, 1997; Callaway *et al.*, 2004). Baxendale *et al.* (pp. 408–423) explored the importance of plant functional traits as a modulator of PSFs, and found that plant traits were quite important predictors for plant response to soils conditioned by other species, and in particular in multispecies grasslands that are likely to be encountered in natural ecosystems.

There has been relatively little research devoted to how viruses may interact with plants in natural ecosystems, although in agronomic ecosystems it has long been recognized that the intensity of viral infection can be related to nutrient availability in soil (see Commentary by Smith, pp. 265–267). A novel perspective is provided by Lacroix *et al.* (pp. 424–433), who explore not only the response of viral infection to N and P supply, but also how two competing virus species can interact under different nutrient conditions. It is the multiple interactions of the two viruses in the context of variable N and P supply that ultimately determine the consequences of this interaction for plant growth.

Finally, the identification of a home-field advantage for decomposition, meaning that plant litter will decompose more quickly in its site of origin (Vivanco & Austin, 2008), has been observed in several terrestrial ecosystems, but the mechanisms behind this phenomenon are not well understood. Austin *et al.* (pp. 307–314) explore how biotic interactions may play key roles in determining plant litter–decomposer affinity effects, through the green leaf phyllosphere, below-ground symbioses and soil faunal interactions. These affinity effects between the soil biota and the plants growing above them may have important consequences for determining plant and soil community structure and may contribute to the coexistence of species in undisturbed ecosystems.

An evolutionary perspective

There are still many open questions regarding how plant interactions with other organisms are shaped by evolutionary forces over time. Two provocative reviews address this issue in interesting ways. The review by Gary Stacey and coworkers focuses on recognition by plant cell receptors of microbial lipochitooligosaccharide (LCO) signals (Liang *et al.*, pp. 289–296), and the multiple roles of this recognition in mediating plant–microbe interactions. The authors discuss the fascinating possibility that the perception of LCOs, which act as Nod and Myc factors in legume–rhizobium and plant–arbuscular mycorrhiza symbioses, respectively, might have evolved from the same basic mechanism that activates innate plant immunity against pathogenic microorganisms, which is triggered upon perception of by plasma membrane receptors of related chitooligosaccharide molecules.

A second review examines the nature of plant resistance and what we may have lost along the way of agricultural domestication. Reviewing the evidence for insect resistance in teosintes, de Lange *et al.* (pp. 329–341) demonstrate that for many of the identified insect pests, present-day representatives of what were thought to be the wild ancestors of maize have superior resistance to several herbivore and pathogenic species. Because of our singular focus on increasing yields in modern crops, there may have been collateral damage during the process of domestication for resistance to pathogens and herbivores that once formed a part of the genetic composition of teosintes. This interesting review highlights the role of human interference in affecting plant interactions with herbivorous organisms.

Moving forward

In their book, *Induced responses to herbivory*, published in 1997, two of the participants of the Buenos Aires 32nd NPS, Rick Karban and Ian Baldwin, referred to the topic of biotic interactions with the following consideration:

> *Plant physiologists have played a relatively minor role in the development of this field. Given that the phenomena are fundamentally physiological, this observation is surprising. We predict that in ten years there will be two separate volumes of plant physiology textbooks: the volume that is already written, which covers interactions of plants with the abiotic world, and the one that is currently being written, which will cover interactions of plants in response to the biotic world.* (Karban & Baldwin, 1997)

While plant physiology textbooks have not yet been divided into two volumes, it is clear that the field of biotic interactions has experienced dramatic growth since the publication of this book, some of which is reflected in the collection of articles included in this Special Issue of *New Phytologist*. More excitingly, rather than two separate textbooks or perspectives, we are contemplating a whole world of new interactions between plant physiological responses to abiotic factors and plant responses to biotic interactors, which we are beginning to understand at the molecular level and in a broad ecological context. Crosstalk between key signaling molecules and pathways, for example, is emerging as a major topic in plant biology (Pieterse *et al.*, 2012), and this crosstalk is thought to play a central role in the mechanisms used by plants to optimize their phenotype in the face of multiple challenges from the abiotic and biotic world (Robert-Seilaniantz *et al.*, 2011; Pieterse *et al.*, 2012; Ballaré, 2014). From the ecologist's perspective, the fact that we have begun to open the microbial 'black box' in the soil with an identification of who the microbial community is and its functional significance (Fierer & Jackson, 2006; Strickland *et al.*, 2009) provides enormous opportunities for incorporating genomic information into ecological studies of biotic interactions.

While it might sound like something of a cliché, the way forward to broaden our understanding of how plants interact with other organisms really requires more integration across disciplinary scales. Both ecologists and plant biologists need to step out of their disciplinary comfort zone and consider both the mechanistic basis for these interactions and their ecological relevance in the 'real' world. This collection represents experimentation and reviews on the ways in which plants interact with other organisms, and novel perspectives on the mechanistic control of these interactions. It seems that everyone who is fascinated by plant science will find something of interest in this Special Issue on plant interactions with other organisms: molecules, ecology and evolution.

Acknowledgements

We wish to thank the New Phytologist Trust for providing funding for the organization of the Buenos Aires 32nd NPS, which facilitated many exciting discussions on research topics covered in this Special Issue. We also thank Michael Panagopulos of the New Phytologist Trust and our graduate students, post-docs and junior researchers (Adelia González-Arzac, Ignacio Cerrudo, Miriam Izaguirre, Melisa Leone, Carlos Mazza, Laura Martínez, Luis Pérez, and Lucía Vivanco) for their unrelenting enthusiasm and hard work in the organization of the meeting. We extend a special thanks to Sarah Lennon of *New Phytologist* for her invaluable input and patience during the preparation of this issue. Research in the Austin and Ballaré laboratories is supported by grants from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), ANPCyT (Agencia Nacional de Promoción Científica y Tecnológica) and UBACyT (Universidad de Buenos Aires Ciencia y Técnica).

Amy T. Austin[1,2]* and Carlos L. Ballaré[1,2]

[1]IFEVA, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad de Buenos Aires, Buenos Aires, Argentina; [2]IIB-INTECH, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de San Martín, Buenos Aires, Argentina

(*Authors for correspondence: tel +54 11 4524 8070; email austin@ifeva.edu.ar, ballare@ifeva.edu.ar)

References

Acevedo-Garcia J, Kusch S, Panstruga R. 2014. *Magical mystery tour*: MLO proteins in plant immunity and beyond. *New Phytologist* **204**: 273–281.

Aizen MA, Morales CL, Vázquez DP, Garibaldi LA, Sáez A, Harder LD. 2014. When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytologist* **204**: 322–328.

Austin AT, Vivanco L, González-Arzac A, Pérez LI. 2014. There's no place like home? An exploration of the mechanisms behind plant litter-decomposer affinity in terrestrial ecosystems. *New Phytologist* **204**: 307–314.

Ballaré CL. 2014. Light regulation of plant defense. *Annual Review of Plant Biology* **65**: 335–363.

Baxendale C, Orwin KH, Poly F, Pommier T, Bardgett RD. 2014. Are plant–soil feedback responses explained by plant traits? *New Phytologist* **204**: 408–423.

Bever JD, Westover KM, Antonovics J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* **85**: 561–573.

Bongers FJ, Evers JB, Anten NPR, Pierik R. 2014. From shade avoidance responses to plant performance at vegetation level: using virtual plant modelling as a tool. *New Phytologist* **204**: 268–272.

Browse J. 2009. Jasmonate passes muster: a receptor and targets for the defense hormone. *Annual Review of Plant Biology* **60**: 183–205.

Callaway RM, Thelen GC, Rodriguez A, Holben WE. 2004. Soil biota and exotic plant invasion. *Nature* **427**: 731–733.

Cargnel M, Demkura P, Ballare CL. 2014. Linking phytochrome to plant immunity: low red : far-red ratios increase Arabidopsis susceptibility to *Botrytis cinerea* by reducing the biosynthesis of glucosinolates and camalexin. *New Phytologist* **204**: 342–354.

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**: 1065–1071.

Dicke M, Sabelis MW. 1988. How plants obtain predatory mites as bodyguards. *Netherlands Journal of Zoology* **38**: 148–165.

Farmer EE, Gasperini D, Acosta IF. 2014. The squeeze cell hypothesis for the activation of jasmonate synthesis in response to wounding. *New Phytologist* **204**: 282–288.

Fierer N, Jackson RB. 2006. The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences, USA* **103**: 626–631.

Green TR, Ryan CA. 1972. Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. *Science* **175**: 776–777.

Heil M. 2014. Herbivore-induced plant volatiles: targets, perception and unanswered questions. *New Phytologist* **204**: 297–306.

Hobbie SE. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* **7**: 336–339.

Jenny H. 1980. *The soil resource*. New York, NY, USA: Springer-Verlag.

Karban R, Baldwin IT. 1997. *Induced responses to herbivory*. Chicago, IL, USA: University of Chicago Press.

Karban R, Wetzel WC, Shiojiri K, Ishizaki S, Ramirez SR, Blande JD. 2014. Deciphering the language of plant communication: volatile chemotypes of sagebrush. *New Phytologist* **204**: 380–385.

Lacroix C, Seabloom EW, Borer ET. 2014. Environmental nutrient supply alters prevalence and weakens competitive interactions among coinfecting viruses. *New Phytologist* **204**: 424–433.

de Lange ES, Balmer D, Mauch-Mani B, Turlings TCJ. 2014. Insect and pathogen attack and resistance in maize and its wild ancestors, the teosintes. *New Phytologist* **204**: 329–341.

Leone M, Keller MM, Cerrudo I, Ballaré CL. 2014. To grow or defend? Low red: far-red ratios reduce jasmonate sensitivity in Arabidopsis seedlings by promoting DELLA degradation and increasing JAZ10 stability. *New Phytologist* **204**: 355–367.

Liang Y, Tóth K, Cao Y, Tanaka K, Espinoza C, Stacey G. 2014. Lipochitooligosaccharide recognition: an ancient story. *New Phytologist* **204**: 289–296.

Meehan TD, Couture JJ, Bennett AE, Lindroth RL. 2014. Herbivore-mediated material fluxes in a northern deciduous forest under elevated carbon dioxide and ozone concentrations. *New Phytologist* **204**: 397–407.

Pieterse CMJ, Pierik R, Van Wees SCM. 2014. Different shades of JAZ during plant growth and defense. *New Phytologist* **204**: 261–264.

Pieterse CMJ, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees SCM. 2012. Hormonal modulation of plant immunity. *Annual Review of Cell and Developmental Biology* **28**: 489–521.

Robert-Seilaniantz A, Grant M, Jones JDG. 2011. Hormone crosstalk in plant disease and defense: more than just JASMONATE-SALICYLATE antagonism. *Annual Review of Phytopathology* **49**: 317–343.

Schöb C, Callaway RM, Anthelme F, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Xiao S *et al.* 2014. The context dependence of beneficiary feedback effects on benefactors in plant facilitation. *New Phytologist* **204**: 386–396.

Smith VH. 2014. Nutrient supply differentially alters the dynamics of co-infecting phytoviruses. *New Phytologist* **204**: 265–267.

Strickland MS, Lauber C, Fierer N, Bradford MA. 2009. Testing the functional significance of microbial community composition. *Ecology* **90**: 441–451.

Vivanco L, Austin AT. 2008. Tree species alters forest litter decomposition through long-term plant and soil interactions in Patagonia. *Argentina. Journal of Ecology* **96**: 727–736.

Vitousek PM, Turner DR, Kitayama K. 1995. Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology* **76**: 712–720.

Zamioudis C, Hanson J, Pieterse CMJ. 2014. β-Glucosidase BGLU42 is a MYB72-dependent key regulator of rhizobacteria-induced systemic resistance and modulates iron deficiency responses in Arabidopsis roots. *New Phytologist* **204**: 368–379.

Zhu F, Poelman EH, Dicke M. 2014. Insect herbivore-associated organisms affect plant responses to herbivory. *New Phytologist* **204**: 315–321.

Key words: ecology and evolution, facilitation, immunity and interactions, litter decomposition, plant defense, plant volatiles.