Commentary

Decisions, decisions, decisions: plant roots detect and respond to complex environmental cues

The ability to detect and react in ecologically meaningful ways to variation in the environment can affect the abundance, distribution and fitness of organisms. This is axiomatic for most animals, but figuring out how and why plants behave in this way is more difficult and requires patience (Hodge, 2009). However, the benefits of complex responses to the environment are no different for plants than animals – finding and assessing the availability of resources, avoiding harm from competitors or predators, or locating a mate. In this context, our understanding of adaptive plant behavior has been steadily expanding. In this issue of *New Phytologist* in an article entitled 'Neighbouring plants modify maize root foraging for phosphorus: coupling nutrients and neighbours for improved nutrient-use efficiency', Zhang *et al.* (2020; pp. 244–253) make an important contribution to this expansion. They report that plant roots can respond in complex and conditional ways to *combinations* of abiotic and biotic stimuli. Specifically, Zhang *et al.* found that the 'foraging strategy of maize roots is an integrated function of heterogeneous distribution of nutrients and neighbouring plants, thus improving nutrient acquisition and maize growth'. In addition to species-specific root proliferation patterns in response to either neighbors or nutrient patches, Zhang *et al.* found that the roots of maize were less abundant, and spent less time, in phosphorus (P) patches with other maize plants in the neighborhood, than in P patches with faba bean neighbors.

We know that the roots of some plant species can respond to their neighbors and move away or towards them (Schenk *et al.*, 1999; Gersani *et al.*, 2001; Schenk, 2006; Hodge, 2009; Depuydt, 2014), communicate stressful conditions to conspecific neighbors (Falik *et al.*, 2012) and detect and grow towards high concentrations of resources (Jackson & Caldwell, 1996; McNickle *et al.*, 2009). We also know that the outcome of such root behavior can determine overlap among species and affect competitive outcomes (Armas & Pugnaire, 2011). And together, our previous understanding suggests that plants might have the ability to negotiate even more complex combinations of signals in their environment (see Hodge, 2009). But, we have had very few examples indicating that plants have the capacity to process *both* biotic and abiotic information simultaneously, much as we process the need for coffee at the same time and place as the length of the queue. In earlier research, Cahill *et al.* (2010) explored the root responses of *Abutilon theophrasti* to resource distribution in soils and intra-specific competition, in an effort to evaluate possible additive responses of roots to different environmental signals or 'whether plants used novel behaviors' to complex cues. They found that plants integrated information about resources and neighbors in a nonadditive manner. Zhang *et al.* support this previous research, expand it to inter-specific interactions, and show that integrating complex signals might 'increase the benefits, while minimizing the costs, of a set of responses'. To be precise, they found that maize roots acquired P made available by faba bean where roots overlapped, which reduced the cost of proliferating roots to find those same resources.

> *'. . . foraging strategy of maize roots is an integrated function of heterogeneous distribution of nutrients and neighbouring plants, thus improving nutrient acquisition and maize growth.'*

The complex recognition and responses demonstrated by Zhang *et al.* may also provide insight into our conceptually evolving perspective on chemical interactions among plants. For decades, chemical, or allelopathic, interactions have been considered in the straightforward context of toxic suppression of neighbors. Instead, recently we have seen evidence for modes of action that may be related more to communication rather than direct chemical toxicity. Evidence for the 'Biochemical Recognition Hypothesis' (see Renne *et al.*, 2004) indicates that the recognition of chemicals released by some species other plant's chemicals may elicit effects on neighbors that could be misinterpreted as toxic effects. For example, Renne *et al.* (2014) compared the effects of leachates from species native to either Argentinean or North American grasslands on seedling emergence. Two Argentinian species showed decreases in seedling emergence in response to leachate from species from North America, but for no species that were also native to Argentina. Leachate origin did not affect seedling biomass, suggesting that recognition was likely to be a more important mechanism than toxicity. Similarly, the germination of small seeds of the dimorphically seeded *Aegilops truncalis* has been shown to be inhibited by the presence of large sibling seeds on the same mother plant (Dyer, 2004). This does not happen in the absence of large sibling seeds suggesting chemical communication, or biochemical recognition, between small and large seeds (see Smith *et al.*, 2019).

Interestingly, Zhang *et al.* also provide new insight into another body of research, the diversity-ecosystem function aspect of intercropping. Intercropping is the ancient practice of growing two or more crop species in the same plots at the same time, and intercropping is now an important agricultural practice that can

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increase productivity and sustainability. Li *et al.* (2007), experimenting with the same species as in Zhang *et al.*, found that intercropped maize grew better and produced more grain biomass when planted with faba bean than when planted with wheat, and that maize roots intermingled with faba bean roots, but not with those of wheat. Results from Zhang *et al.* indicate that this field-based, diversity-based agricultural phenomenon is governed, at least in part, by complex and integrated responses to both neighbors and resources. However, signaling in maize–faba bean intercrops appears to be yet more complex. Li *et al.* (2016) used permeable and impermeable root barriers in the field to show that maize promotes nodulation and symbiotic nitrogen fixation by faba bean. This was promoted by maize root exudates. Root exudates from other grain crops did not do this, suggesting that the kind of complex communication reported by Zhang *et al.* might be species-specific and bidirectional.

Might root recognition and responses be even more complex? A number of studies have shown that the genetic relatedness of conspecific neighbors can affect root behavior (Dudley & File, 2007; Semchenko *et al.*, 2007; Yang *et al.*, 2015). For example, Semchenko *et al.* (2014) found that root exudates can communicate genetic relatedness and the species identity of neighbors, and that responses to these signals affected whole root systems. Fang *et al.* (2013) found that root systems of the same genotype of rice plants grew toward each other and overlapped more in spaces than roots of different genotypes, which tended to avoid each other. Linking such genetically based root recognition and responses has the potential to shed even more light on how complex belowground behavior by plants might affect co-existence, competitive exclusion, niche differentiation, size-asymmetric competition, territoriality (Schenk *et al.*, 1999), inter- and intra-specific diversity effects on ecosystem function, and community organization.

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