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Friends, neighbours and enemies: an overview of the communal and social biology of plants

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Running Head: An overview of plant-plant interactions

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Abstract: Plants were traditionally seen as rather passive actors in their environment, interacting with each other only in so far as they competed for the same resources. In the last 30 years, this view has been spectacularly overturned, with a wealth of evidence showing that plants actively detect and respond to their neighbours. Moreover, there is evidence that these responses depend on the identity of the neighbour, and that plants may cooperate with their kin, displaying social behaviour as complex as that observed in animals. These plant-plant interactions play a vital role in shaping natural ecosystems, and are also very important in determining agricultural productivity. However, in terms of our mechanistic understanding, we have only just begun to scratch the surface, and many aspects of plant-plant interactions remain poorly understood. In this review, we aim to provide an overview of the field of plant-plant interactions, covering the communal interactions of plants with their neighbours as well as the social behaviour of plants toward their kin, and the consequences of these interactions. We particularly focus on the mechanisms that underpin neighbour detection and response, highlighting both progress and gaps in our understanding of these fascinating but previously overlooked interactions.

Keywords: Plant-plant interactions, plant communication, neighbour detection, social biology, plant evolution, plant ecology, root exudates, light signalling, volatile signalling.

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1. Introduction: a communal existence

2 The discoveries of the 19th Century shook apart the idea of nature as a harmonious world. As
3 Darwin showed in his 'lawn plot experiment', a 'struggle for existence' occurs even between
4 humble plants; it is just a very quiet and slow struggle. And yet, when an average person thinks of
5 interactions both within and between species, plant-plant interactions are rarely at the forefront of
6 the mind. Even among plant scientists, interactions between plants and other plants have been
7 traditionally overlooked relative to the interactions of plants and just about any other taxon. Plants
8 were traditionally viewed as passive, affected by their neighbours only through indirect effects on
9 resource availability (Pierik et al, 2013). Until the early 1980s, there was little indication that plants
10 might have interactions every bit as complex as those seen in animals (Vicherova et al, 2020).
11 However, as an ever-increasing body of work is demonstrating, plants do detect, respond to and
12 interact with their neighbours. These interactions are often rather subtle and slow, and as will be
13 described, can also be unintuitive and surprising. These qualities perhaps stem inevitably from the
14 sessile nature of plants. Being motile gives animals the great advantage of being able to decide
15 which individuals to aggregate with, and to avoid competitors and predators. In contrast, a plant
16 cannot choose or change its neighbours. And most likely, it can't kill them either (not quickly,
17 anyway). This changes the game: a plant will often be inadvertently stuck next to problematic
18 neighbours for its entire life; in the vast majority of cases, this is simply not a feature of animal life.
19

20 Thus, for all the pests, pathogens and predators a plant might meet, the biggest and most long-
21 lasting biotic stress it will encounter will probably be its neighbours. Neighbouring plants represent
22 a direct threat to the resources (light, water, mineral nutrients) that a plant must access, and –
23 regardless of how the interaction plays out – it would therefore seem imperative that plants can
24 detect and respond to their neighbours. But can they, and do they? In this review, we aim to
25 provide an overview of our current knowledge of plant-plant interactions, particularly focussing on
26 the question of whether plants can detect and differentially respond to friend, neighbour and
27 enemy.

28

29

30 **2. Plant-plant interactions: theory and controversy**

31 There are a range of interactions that could in theory occur between two neighbouring plants, with
32 different fitness outcomes for the actor (plant A) and the recipient (plant B) (Figure 1). In describing
33 these, we largely adhere to the definitions in the review by West et al (2007) from the original ideas
34 of Hamilton (1964, 1970). Plant A could *compete* for resources with plant B, in the process
35 reducing B's fitness. However, depending on the competitive ability of B, the outcome for the
36 fitness of A might be beneficial, neutral or costly. In a '*selfish*' outcome A benefits at B's expense,
37 for instance if the competition is highly asymmetric, while in a '*spiteful*' outcome there is a fitness
38 cost to both A and B, for instance if the competitors exhaust the resource (the so-called 'Tragedy of
39 the Commons')(Hamilton, 1970). Alternatively, plant A could *cooperate* with plant B, in the process
40 increasing B's fitness. The outcome of this might also be beneficial to plant A ('*mutualism*') – for
41 instance by avoiding spending resources on competition – neutral, or occur at a cost to A
42 ('*altruism*'). In the case of altruism, A might still indirectly benefit if B is a close relative, since this
43 will increase the inclusive fitness of A (i.e. kin selection). Plant A could behave without regard to
44 plant B ('*live and let live*'), but a neutral strategy could still inadvertently have a range of outcomes
45 for plant B. '*Facilitation*' describes beneficial interactions where there is negligible cost or benefit to
46 A but a benefit to B (similar to *byproduct reciprocity* in West et al 2007). Facilitation has been more
47 strictly defined as the positive effect on the environment by one species that improves the fitness of
48 another species (Bertness and Callaway 1992, Bronstein 2009).

49
50 Two implicit assumptions when proposing the existence of these different interactions are that
51 plants can **actively detect and distinguish** their neighbours, and **actively respond** by altering
52 their growth or behaviour relative to a 'no-neighbour' scenario. However, in neither case is there
53 currently conclusive supporting evidence. In part, this is because (as described above) the
54 measurable outcome of interactions between plants does not necessarily reflect any 'intent' on
55 behalf of the plants, making it very difficult to infer whether a plant is following a given strategy, or
56 simply growing with no regard to its neighbours. These unproven assumptions create an
57 interpretational minefield for the whole field of plant-plant interactions, which we refer to hereafter
58 as the '**identity problem**' and the '**response problem**'. In terms of the identity problem, it is now

59 fairly incontrovertible that plants do detect their neighbours (see section 3 below), but it remains
60 less clear whether they can distinguish between their neighbours. While there is certainly
61 experimental evidence that plants can do this, it is primarily phenomenological, and therefore open
62 to interpretation (see section 4). In terms of response problem, there is again experimental
63 evidence that competitive, cooperative and facilitative interactions do occur in plants (see section 5
64 and 6). However, the evidence is rarely conclusive, and there are often other plausible
65 explanations for these observations.

66

67 In writing this review, it is our general thesis that plants do distinguish between, and differentially
68 respond to their neighbours. We will examine the evidence, and compare this to the null hypothesis
69 that *'plants act to increase their fitness without reference to the identity of their neighbours'*. Based
70 on the evidence, we cannot currently reject this hypothesis, but we assess whether parsimony
71 prevents us accepting it, while also considering what evidence would be required to finally reject
72 this hypothesis.

73

74 **3. Mechanisms of neighbour detection**

75 Traditionally, it was assumed that plants could only detect their neighbours passively, by detecting
76 changes in resource (light, water and nutrient) availability caused by other plants. Above-ground,
77 plants have well-described responses to poor light quality or shading, whether plant-generated or
78 not (Roig-Villanova & Martínez-García, 2016). Root growth responses to soil nutrient availability
79 have been extensively characterised (e.g. Shahzad & Amtmann, 2017), and will be inevitably be
80 triggered if neighbouring plants deplete the environment of e.g. nitrate and phosphate (de Kroon et
81 al, 2003; Schenk, 2006; Nord et al, 2011). Furthermore, it is certainly clear that plants can, and do
82 passively respond to the presence of neighbouring plants simply due to the reduced availability of
83 resources in the environment (Schenk, 2006; Pierik et al, 2013). However, it is also now clear that
84 plants have multiple mechanisms by which they can **actively** detect neighbouring plants (Figure 2).
85 Mostly, plants use 'cues' to do this – information that neighbouring plants cannot avoid making
86 available for detection (Karlovsy, 2008; Shelef et al, 2019). In this section, we introduce the main

87 mechanisms of neighbour detection, critique the evidence for more speculative mechanisms, and
88 examine whether these mechanisms might allow plants to distinguish between neighbours.

89

90 **3.1 Light**

91 Plant organs absorb, reflect and scatter incoming solar radiation, reducing its photosynthetically
92 active radiation (PAR), red:far red ratio (R:FR), and blue fluence rate. This creates unique cue of
93 neighbour presence, distinct from fluctuations in ambient light levels and quality. Plants are
94 exquisitely sensitive to these perturbations in light quality, even in the absence of reduction in PAR,
95 because they indicate current or future competition for light (Roig-Villanova & Martínez-García,
96 2016). These responses to altered light quality are particularly associated with direct shading, but
97 because of their extensive scattering of light, plants can use light cues to detect each other over
98 significant distances in the absence of shading (Roig-Villanova & Martínez-García, 2016).
99 Neighbour-generated light cues are detected by the well-known and highly-characterised plant
100 photoreceptors, particular phytochromes, with their strong sensitivity to far-red light. The tips of
101 leaves are the primary site of light cue sensing, reducing the likelihood that self-shading will
102 triggering these responses (Pantazopoulou et al, 2017). These photoreceptor-mediated responses
103 to neighbours represent the most unambiguous evidence of the active nature of plant-plant
104 interactions, and have been well characterised at the ecological, physiological and molecular
105 levels; they are reviewed in more detail elsewhere in this issue (Huber et al, 2020).

106

107 Although light quality is incontrovertibly used as a neighbour cue by plants, it is very simple in
108 nature, and hard to envisage how it could encode specific information about the identity of
109 neighbouring plants. In the case of *Arabidopsis*, arguments have been made to suggest that light
110 signals can allow discrimination between kin and non-kin (Crepy & Casal, 2015; Crepy & Casal,
111 2016), but it would be perhaps fairer to say that light signals can allow plants to distinguish
112 between different morphological states (Till-Bottraud, de Villedieu, 2016). Similarly, light signals
113 can permit some level of neighbour recognition by 'phenotype matching' among tree species. For
114 instance, sycamore trees cast deep shade, tolerate deep shade and have relatively slow growth;
115 silver birch trees by contrast cast a weak shade, are poorly shade tolerant, and have fast growth. In

116 the deep shade of a sycamore tree, the growth of sycamore seedlings is promoted over birch
117 seedlings, but in the light shade of a birch tree, growth of birch seedlings is greater than sycamore
118 seedlings (Gilbert et al, 2001). Only the 'type' of neighbour is being detected in these examples,
119 rather than its specific identity, but this nevertheless demonstrates the potential of light signals to
120 carry complex information.

121

122 **3.2 Touch**

123 Plants are naturally exposed to mechanical forces by a range of factors (e.g. wind, insects,
124 physical obstacles). As such, they have mechanisms that allow them to detect and respond to
125 these mechanical forces, which can be in part characterised as a response to 'touch' (Hamant &
126 Haswell, 2017). The effectiveness of mechanical stimulus depends on length and repetitiveness of
127 the signal and less on the force applied (Anten et al, 2010). In the context of plant-plant
128 interactions, plants are sensitive to even the light touch of neighbouring plants, which provides a
129 rapid indicator of competitor presence (Markovic et al, 2016); these touch stimuli are perceived with
130 high sensitivity by leaf trichomes and root tips (Massa and Gilroy, 2003; Zhou et al, 2017). Plant-
131 generated touch is clearly distinguishable from other mechanical stimuli, since touch, wind and
132 mechanical damage evoke distinct molecular responses (Anten et al, 2010; Markovic et al, 2016).
133 Responses to touch include increasing growth away from neighbouring plants, or acclimation by
134 production of more resistant structures.

135

136 Touch by neighbouring plants seems to play a particularly important role in priming plants for
137 further interactions, and has been found to modify both release of VOCs and of root exudates
138 (Elhakeem et al, 2018, Markovic et al, 2019). In *Arabidopsis*, touch of leaf tips promotes leaf
139 hyponasty, which move the leaves into a position in which they can better detect scattered light
140 signals to 'confirm' the presence of neighbouring plants (de Wit et al, 2012). This highlights the
141 interactive nature of neighbour cue-use, and the ways in which this multimodality can convey
142 complex information. However, touch is a very simple cue and there is currently no reason to
143 suppose that it can convey information about the identity of neighbouring plants.

144

145 **3.3 Chemical signals - VOCs**

146 Plants emit a large range of organic chemicals into the environment, which are usually divided into
147 volatile organic compounds (VOCs) and exudates. VOCs are typically found as free molecules in
148 the gaseous phase, and can be released both above and below ground. In contrast, exudates
149 would typically be secreted by the root system solubilised in water. We will cover volatiles and
150 exudates separately, but they are perhaps best viewed as a continuum of chemical cues released
151 into the environment by plants.

152

153 More than 1000 different plant-emitted VOCs have been identified to date, including highly volatile
154 compounds such as isoprene, monoterpenes, methanol and ethylene, and other more moderately
155 volatile compounds (e.g. terpenes, methyl jasmonate, methyl salicylate and 'green leaf volatiles')
156 (Baldwin, 2010, Heil and Karban 2010; Ninkovic et al. 2019). Plants could therefore theoretically
157 emit a very large number of VOC combinations, which might dynamically reflect both their
158 physiological status and species (Karban et al, 2006; Pichersky et al, 2006; Ueda et al, 2012).
159 Consistent with the ready availability of this 'information', plants can detect and respond to the
160 presence of neighbouring plants through VOC emissions. For instance, an indication of emitter
161 plant proximity can be 'deduced' by a receiver plant due to the fast rate of diffusion of highly volatile
162 compounds relative to moderately volatile ones (Baldwin, 2010; Heil and Karban 2010; Ninkovic et
163 al, 2019). VOC detection and response are reviewed in detail elsewhere in this issue (Ninkovic et
164 al, 2020).

165

166 It has been hypothesised that VOC emission evolved to quickly spread information about herbivory
167 or pathogen attacks, although it is unclear whether this their primary function is to spread this
168 information within the same plant, or between neighbouring plants (Farmer, 2001; Heil and Karban,
169 2010; Morrell and Kessler, 2017). Plants can rapidly spread information systemically to distal
170 organs through vascular-associated calcium signalling (Toyota et al, 2018), but VOCs may act as
171 second system to achieve the same effect. While VOC emissions would attenuate rapidly over
172 longer distances, they would be very efficient over short distances, particularly where the
173 corresponding vascular connection is very long (i.e. between neighbouring branches connected to

174 a distant stem)(Heil & Adame-Álvarez, 2010). Nevertheless, priming of defence responses in
175 related neighbours could also have driven the evolution of VOC emission via effects on inclusive
176 fitness (Shiojiri and Karban, 2008; Karban et al, 2013). The simple nature of common VOC signals
177 would also allow eavesdropping by unrelated neighbours (Karban et al. 2003; Ninkovic et al. 2013).
178 This unintentional sharing of information with unrelated neighbours may not be maladaptive (since
179 reducing overall herbivory/pathogen pressure may benefit the emitting plant), but could also have
180 led to the evolution of VOCs 'chemotypes' in a number of plant species (Gouinguene et al, 2001;
181 Ninkovic et al, 2003; Karban et al, 2014). There is evidence that VOC-mediated herbivory defence
182 is more effective if signalled by related conspecific plants (Karban et al. 2013) even though the
183 emission of VOCs may be reduced in conspecific stands (Kigathi et al. 2013).

184

185 VOCs thus seem like an excellent candidate for a mechanism by which plants not only detect, but
186 distinguish their neighbours. As combinations, VOCs could have sufficient complexity to allow the
187 distinction between neighbours, and there is some evidence that plants can indeed distinguish
188 between neighbours on this basis (Karban et al. 2013). However, it is not clear exactly how plants
189 might be able to do this; neither which VOCs might be involved in distinguishing between
190 neighbours, nor how these volatiles are perceived). Furthermore, it should be noted that currently,
191 VOC detection by plants has mostly been associated with defensive priming, rather than
192 responding to the presence of neighbouring plants *per se*.

193

194 **3.4 Chemical signals - exudates**

195 Plants exude significant quantities of organic molecules into the soil (Bais et al, 2006), which play a
196 wide range of functional roles such conditioning soil by changing its adhesive properties or pH
197 (Vives-Peris et al, 2020). Plants also release signalling molecules that promote the formation of
198 beneficial symbioses with micro-organisms, that suppress pathogens, and which act
199 allelopathically (see section 6) (Rolfe et al, 2019; Ehlers et al, 2020). These compounds may
200 persist in soil due to low rates of oxidation and photodecomposition (Karlovsy, 2008), and alter
201 soil properties in a way perceptible to both contemporary neighbours and future generations,
202 known as plant-soil feedback (Hu et al, 2018; van der Putten et al, 2013). The soil is thus full of

203 potential cues for the presence of neighbouring plants, but to what extent do plants actively detect
204 and respond to these exudates?

205

206 There is reasonable evidence that plants can detect the mix of chemicals exuded by other plants,
207 in the absence of actual neighbouring plants or any nutrient depletion, and can respond with
208 alterations in root architecture and growth (Biedrzycki et al, 2010; Semchenko et al, 2014; Yang et
209 al, 2018; Kong et al, 2018). Gradients of exudates in the soil might thus provide information on the
210 proximity of neighbouring plants, as well as their physiological status, and may thus allow roots to
211 precisely avoid neighbouring roots (Fang et al, 2013). The build-up of exudates near physical
212 obstacles might also explain the ability of roots to avoid these obstacles without touching them
213 (Falik et al, 2005). Since exudates possess much greater complexity than most other mechanisms
214 of neighbour detection, root exudates have regularly been suggested to be key factors in the
215 apparent ability of plants to distinguish self/non-self and kin/non-kin (discussed further below)
216 (Biedrzycki et al, 2010; Semchenko et al, 2014; Yang et al, 2018).

217

218 It is certainly possible that, as combinations, exudates would have sufficient complexity to permit
219 plants to distinguish between neighbours, but it is not currently clear which exudate compounds
220 plants can detect. The candidates suggested so far, such as jasmonic acid and (-)-loliolide, seem
221 likely to be generic signals, involved in triggering broad responses such as allelopathy (Kong et al.
222 2018). Strigolactones are a class of phytohormones that are also exuded into the soil and play a
223 broad signalling role in the rhizosphere, including promoting formation of mycorrhizal associations
224 (Waters et al. 2017). Since they strongly regulate plant growth, strigolactones are obvious
225 candidates to act as plant-plant signals, but currently there is no clear evidence that this occurs,
226 and indeed some evidence to the contrary (Kong et al, 2018). At the moment, root exudates seem
227 the most likely candidates to act in neighbour recognition, but it remains a clear priority for the field
228 to identify which signals are involved, whether they do encode specific information, and if so how.
229 Root exudate detection and response is reviewed in detail elsewhere in this issue (Wang et al,
230 2020).

231

232 **3.5. Acoustic and electrical stimuli**

233 The mechanisms discussed above are unambiguously involved in neighbour detection in plants.
234 Plants have also been proposed to use acoustic and electrical cues to detect and respond their
235 neighbours. Plants generate acoustic vibrations by cavitation of gas bubbles in the xylem, and
236 resulting alterations in vessel diameter (Hölttä et al, 2005; Lashimke et al, 2006), particularly in
237 drought stressed plants (Zweifel and Zeugin 2008). Plants can also detect acoustic vibrations of
238 sufficient magnitude via the mechanosensing pathway that integrates touch and mechanical stimuli
239 (Ghosh et al, 2016, Ghosh et al, 2017). Acoustic vibrations can induce defence responses
240 suggesting a role in promoting resistance to vibration-emitting predators (Appel and Coccoft, 2014;
241 Choi et al, 2017; Kim et al, 2020), and plants can detect pollinator sound frequencies and release
242 pollen or increase nectar in response (De Luca and Vallejo-Marin 2013; Veits et al, 2019). Thus,
243 theoretically, plants have been suggested to detect their neighbours through acoustic cues
244 (Gagliano and Mancuso 2012; Rodrigo-Moreno et al. 2017), but these studies are controversial,
245 and there is currently no clear evidence for acoustic neighbour detection.

246

247 Plants generate electrophysiological action and variation potentials throughout the plant body,
248 though their function is unclear (Davies, 2006; Fromm, 2006; Stahlberg et al, 2006). One recent
249 suggestion is that continuous electrical signalling could allow communication between organs (de
250 Toledo et al, 2019, Sukhov et al, 2019). Electric stimuli have been shown to be conducted through
251 the soil, exchanged between neighbouring plants, and to invoke electrical signals in the receiver,
252 whether con- or heterospecific (Volkov and Shtessel, 2017; Volkov and Shtessel, 2018; Volkov et
253 al, 2019). In principle, electrical cues could be used to detect neighbours, and moreover to assess
254 the competitive abilities of neighbours, since there is a relationship between electrical activity and
255 the physiological state of plant. Electric signal generation can be triggered by many external
256 stimuli, for example wounding and touch stimuli (Szechyńska-Hebda et al, 2010; Mousavi et al,
257 2013; Degli Agosti, 2014), and a rapidly improving understanding of electric signals has revealed
258 specific patterns connected to water status (Comparini et al, 2020), salt stress (Wang et al, 2019)
259 and infection by pathogens (Simmi et al, 2020). However, at the moment, there is no evidence that

260 plants do use electrical signals for neighbour detection, though it is an interesting possibility, and
261 more work to understand its relevance is definitely warranted.

262

263 **3.6. Via fungal intermediaries**

264 Symbiotic associations between plant roots and fungi are extremely common, with arbuscular
265 mycorrhizal symbiosis present in over 70% plant species (Cosme et al, 2018). As such, plants
266 inevitably become interconnected *via* mycorrhizal fungi in a 'common mycorrhizal network' (CMN)
267 of multiple con- and heterospecific shareholders. Therefore, it has been hypothesised that CMN
268 might transfer interplant signals *via* the hyphal external surface, cytoplasmic streaming or electrical
269 signal conduction (Barto et al, 2012; Johnson and Gilbert, 2015). For instance, it has been
270 suggested that signalling molecules, including jasmonic acid, can be transferred through CMN,
271 allowing priming of neighbouring plants to pathogen infection (Song et al, 2010) and aphid or
272 caterpillar herbivory (Babikova et al, 2013; Song et al, 2014). However, while there is certainly
273 evidence that mycorrhizal colonization improves disease resistance, though might be due to
274 nutrient support rather than priming effects (Delavaux et al, 2017). Thus far, the only well
275 documented and widely accepted impact of CMN is the effect on plant competitiveness by nutrient
276 transfer and growth promotion (Parniske, 2008; Smith and Smith, 2012; Delavaux et al, 2017).
277 Furthermore, in general, it should be noted that CMN add no information to the system, but are
278 simply proposed as a more efficient means of transmitting chemical cues between plants.

279

280 **4. Distinguishing between neighbours**

281 As highlighted above, a very important problem in the field is whether plants can distinguish
282 between their neighbours. Work in this area can be broadly divided into two separate but related
283 questions; can plants distinguish their own body from those of neighbouring plants (self/non-self
284 recognition) and can plants distinguish between different neighbouring plants on the basis of
285 relatedness (kin/non-kin recognition)? These areas are reviewed in detail elsewhere in this issue,
286 (Anten & Chen, 2020), but we aim to provide a concise discussion here.

287

288 **4.1. Self/non-self recognition**

289 The self/non-self recognition question arises because all the neighbour detection cues discussed
290 above can also be generated by the plant itself. How can a plant therefore specifically respond to
291 the presence of a neighbour (i.e. by competing or not competing) unless it is able to distinguish
292 between signals arising from itself and its neighbours? How do plants 'filter out' cues generated by
293 their own body and avoid competing with themselves? Work on self/non-self discrimination has
294 particularly focussed on interactions between the root systems of plant, because that is where the
295 most obvious evidence for (apparent) competition or non-competition between plants is found. A
296 variety of evidence has been obtained for self/non-discrimination via the root systems, in a
297 relatively short burst of activity.

298

299 One set of work used a system in which two plants with 'split roots' share two pots, or are grown
300 separately in one pot (Gersani et al, 2001; Maina et al, 2002; Falik et al, 2003; O'Brien et al, 2005).
301 Under these conditions, 'sharer' plants apparently competed with each other and over-proliferated
302 roots relative to 'owners'. However, these results were subsequently heavily criticised, because of
303 the failure to take into account confounding variables; although the sharer and owner plants have
304 access to the same amount of nutrients, sharer plants have access to twice the soil volume -- and
305 soil volume in itself has a very strong effect on plant growth (Hess & de Kroon, 2007; Semchenko
306 et al, 2007; Poorter et al, 2012). A subsequent series of studies showed no evidence for over-
307 proliferation in the presence of neighbours (Semchenko et al, 2007; Lankinen, 2008; Markham &
308 Halwas, 2011; Nord et al, 2011; Meier et al, 2013; McNickle & Brown 2014), leading to suggestions
309 that plants essentially ignored the presence of neighbours in determining root growth, and only
310 responded to nutrient availability (Nord et al, 2011; McNickle & Brown, 2014) -- but again, the effect
311 of soil volume was largely ignored. When all variables are properly accounted for, the presence of
312 neighbouring plants reduces the growth of roots in pea - an effect in the opposite direction to that
313 originally proposed (Chen et al, 2015).

314

315 In a second approach, clonally-propagating plants, such as strawberry, clover and buffalo grass
316 were used to test the idea further (Holzapfel & Alpert 2003; Gruntman & Novoplansky, 2004; Falik

317 et al, 2006). These plants produce 'ramets' (new clonal individuals) which remain physiologically
318 connected. In a two-ramet system, physiological disconnection resulted in more root growth in both
319 ramets than if they remained connected, which was taken as evidence for the plants now
320 recognizing each other as non-self, and competing. Again, these studies have been criticised for
321 their experimental design (Hess & de Kroon, 2007), but also defended as providing evidence for
322 "self/non-self recognition ...[that] cannot be denied" (Chen et al, 2012). In truth, these experiments
323 provide no direct evidence for neighbour detection; they simply show that two small plants grow
324 differently to one larger twin plant. The inference that this is due to self/non-self discrimination is a
325 matter of interpretation, rather than firm experimental evidence.

326

327 Overall, perhaps the largest problem with self/non-self recognition is that no convincing mechanism
328 has been identified that could account for it. Self/non-self recognition inevitably invokes the
329 existence of additional contextual signals from either self or non-self that permit discrimination of
330 the origin of cues (Chen et al, 2012). This is theoretically possible, since different species release
331 different molecules into the environment, but *as defined*, self/non-self recognition requires even
332 genetically identical plants to be able to distinguish the origin of cues. It is very difficult see how
333 identical plants can possibly generate distinct cues that allow unambiguous self/non-self
334 discrimination. Thus, a variety of intricate mechanisms involving internal oscillations and/or electric
335 signals have been suggested to explain self/non-self recognition, but there is no convincing
336 experimental evidence for these (Chen et al, 2012; Depuydt, 2014).

337

338 **4.2. Kin/non-kin recognition**

339 Over the last decade, interest in the self/non-self question has very clearly diminished, and
340 attention has focussed much more strongly on question of whether plants can distinguish kin from
341 non-kin (Dudley et al, 2013). Kin/non-kin recognition suggests that plants have a mechanism that
342 allows them to distinguish closely related neighbours (kin) from all other neighbours (non-kin)
343 (Callaway & Mahall, 2007; Chen et al, 2012). Again, work on kin/non-kin discrimination has
344 particularly focussed on interactions between the root systems of plant, because that is where the
345 most obvious evidence for competition or non-competition between plants is found. However, the

346 phenomenon is not necessarily restricted to the roots; potential examples from the shoot system
347 have already been mentioned (Crepy & Casal, 2015; Karban et al, 2013) and there may be
348 interactions above and below ground, with root contact being required for recognition but a
349 response being expressed in shoots (Murphy & Dudley, 2009).

350

351 As with self/non-self recognition, the initial studies which apparently demonstrated kin/non-kin
352 recognition (Andalo et al, 2001; Donohue, 2003; Dudley & File, 2007) were also subject to criticism
353 for problems in experimental design and statistical approach (Chen et al, 2012). However,
354 subsequent studies have provided more firm evidence of kin/non-recognition, although again, this
355 is primarily phenomenological (Bhatt et al, 2011; Marler et al, 2013; Palmer et al, 2016; Takigahira
356 & Yamawo, 2019). In these experiments, plants are generally found to reduce their root growth (i.e.
357 to 'cooperate') in the presence of kindred plants, but not (or less so) in the presence of non-kin
358 plants. For instance, in rice plants grown together in transparent agar columns, the root systems of
359 plants of the same variety remain completely segregated (the roots systems never touch each
360 other), which does not occur when the plants are from different varieties (Fang et al, 2013). This is
361 a striking result, which is very difficult to explain without the existence of some kin-recognition
362 mechanism. Further work in rice supports the existence of kin-recognition across a spectrum of
363 relatedness (Yang et al, 2018). Furthermore, plants of the same ecotype in *Arabidopsis* have been
364 proposed to display reduction in root growth that is not present between ecotypes (Biedrzycki et al
365 2010). This study was challenged on the basis that there is no difference in gene expression in
366 plants grown with members of the same ecotype versus different ecotypes (Masclaux et al, 2010),
367 but this does not preclude kin recognition in *Arabidopsis*; it may simply mean that the kin group
368 operates at a different taxonomic level than the ecotype.

369

370 Although the phenomenological evidence is firmer, there is currently no clear mechanistic
371 explanation for kin/non-kin recognition. However, it is generally easier to conceptualise how
372 kin/non-kin recognition might work than self/non-self recognition. The work described in the
373 previous section shows that plants can detect their neighbours through a range of different
374 mechanisms, and that some of these have sufficient complexity to permit identity recognition. In

375 this context, most attention has focussed on root exudates, and there is certainly some evidence
376 that these can invoke kin- or non-kin responses, but it is not clear which molecules might do so
377 (Biedrzycki et al, 2010; Semchenko et al, 2014; Yang et al, 2018). Different species certainly
378 release different profiles of exudates, and thus the presence of 'foreign' molecules could certainly
379 trigger a competitive response. However, an alternative model would be that plants release a
380 molecule that positively identifies them as kin, and down-regulate their growth when exposed to
381 this molecule (whether self-generated or not); in the absence of this signal, normal growth
382 responses occur. Furthermore, such a molecule might be recognised with decreasing efficiency by
383 increasingly distant kin, resulting in the observed spectrum of responses as a function of
384 relatedness.

385

386 Although we do not yet understand its basis, the evolution of kin-recognition and cooperative
387 responses would be readily explicable via well-established effects on inclusive fitness (Hamilton
388 1964; Mitteldorf et al, 2000). Indeed, given their reproductive systems, we might expect kin
389 cooperation to be especially strong among land plants. While animals have evolved multiple
390 strategies to avoid inbreeding and therefore rarely have a relatedness (R) of greater than 0.5 (full-
391 sibling) (Pusey & Wolf, 1996), many plants reproduce clonally or asexually (R = 1), or with some
392 degree of self-pollination (R ~1). Similarly, poor dispersal of offspring in many plants will result in
393 local populations with a high degree inbreeding, except where self-incompatibility mechanisms are
394 present (Barrett & Harder, 2017).

395

396 **4.3. Species recognition**

397 In addition to kin recognition, it is also possible that plants can distinguish between members of the
398 same species and those of different species (Mahall & Callaway, 1991; Krannitz & Caldwell, 1995;
399 Novoplansky, 2009). Given that conspecifics usually compete for the same ecological niche, being
400 able to detect neighbour species identity could be adaptive. For example, in experimental plots of
401 multiple tropical tree species, coarse roots were shorter but denser in trees growing near
402 conspecifics than heterospecifics, interpreted as a strategy to minimize competition without
403 sacrificing nutrient acquisition (Madsen et al, 2020). However, in other experiments, there is no

404 evidence for differential responses to conspecific versus heterospecific neighbours (Jacob et al,
405 2017). An intriguing (but purely theoretical) possibility is that species detection might occur by the
406 same mechanisms as kin-recognition, since conspecifics are to some extent kindred, even if only
407 very distantly. Members of the same species might be recognised as ‘distant kin’, triggering weaker
408 or different responses than close kin. Given the low dispersal of many species, plants are likely to
409 be closely related to any conspecifics that are also their neighbours (Semchenko et al, 2013). In
410 such populations with “high viscosity”, kin selection could occur without any requirement for a
411 discrimination system (Hamilton 1964), though it would be highly unlikely that individuals never
412 encountered distantly related/unrelated neighbours. Thus, a kin-recognition system may not need
413 to discriminate kin very precisely to still confer a selective benefit via inclusive fitness, which could
414 allow the same system to be used for both kin- and species-recognition. This may be particularly
415 the case in basal land plant lineages (mosses, liverworts, hornworts) which are particularly
416 characterized by short-range dispersal through asexual reproduction, leading to continuous
417 assemblies of closely related individuals (Frey and Kürschner 2011; Partridge and Harvey 1988;
418 Renzaglia et al. 2000; Taylor et al. 2005). Within species, related mosses co-operatively avoid
419 overgrowth, (Proust et al, 2011), whereas heterospecific mosses seem to actively compete in
420 response to light and VOC cues from neighbours (Vicherová et al. 2020). While species-level
421 recognition remains largely uncharacterised, it is an intriguing prospect deserving more attention.

422

423 **4.4. A model for neighbour identification**

424 If plants cannot distinguish between themselves and their neighbours, then they cannot possibly
425 respond differentially to their neighbours. Understanding the ‘identity problem’ is thus at the crux of
426 the whole field of plant-plant interactions, and its future direction. Tantalizingly, the current
427 evidence suggests that they can indeed distinguish between their neighbours. Certainly, we cannot
428 accept our null hypothesis that plants make no reference to the identity of neighbours, although it is
429 perhaps not yet safe to reject it outright. But how exactly might plants distinguish between their
430 neighbours? In our view, the phenomenological evidence for self/non-self recognition is too weak,
431 and the mechanistic explanations too convoluted to persist with that model. Conversely, kin/non-kin
432 recognition has better phenomenological support, and avoids some of the theoretical problems

433 inherent in self/non-self recognition. It is also easier to see a clear selective advantage for the
434 evolution of kin/non-kin discrimination via effects on inclusive fitness, and mechanistic explanations
435 could be straightforward, even if currently obscure. Furthermore, kin/non-kin recognition
436 circumvents much of the requirement for a self/non-self recognition system. The self/non-self
437 system was invoked to allow plants to respond differently to their own cues with respect to those of
438 their neighbours. However, in the case of kin plants, the need to respond differently to 'self' may be
439 very much less, since plants should not compete with their kin any more than they should compete
440 with themselves; the most important non-self plants to detect are those that are also non-kin.

441

442 Nevertheless, when responding to plant-generated cues, it is no doubt useful for plants to be filter
443 out self-generated cues. We have already encountered evidence for spatially specific cue-
444 responses designed to filter out self-generated cues (e.g. light sensing in leaf tips), and for
445 multimodal cue-use (e.g. touch sensitisation of light, volatile and exudate signalling). We thus
446 propose that plants use spatially restricted, multimodal processing to distinguish between self and
447 non-self generated cues on a probabilistic basis, supported by a kin/non-kin recognition system to
448 distinguish between the neighbours thereby identified (Figure 3). Whether this model is correct or
449 not, a clear challenge for the field is to solidify our understanding of plant identity-recognition by a
450 much deeper understanding of the mechanisms by which plants recognise the presence of other
451 plants.

452

453 **5. Responding to neighbours**

454 So far, we have seen that plants can certainly detect their neighbours, and can probably distinguish
455 between their neighbours on the basis of relatedness. But can plants use this information to
456 differentially respond to neighbours, adopting different strategies depending on neighbour and
457 context? In this section, we examine some of the observed outcomes of plant-plant interactions
458 (Figure 4), and examine to what extent these can be viewed as deliberate strategies by plants.

459

460 **5.1 Competition**

461 Competition between organisms is a potent ecological and evolutionary driver (Aschehoug et al
462 2016), and evidence for competition between neighbouring plants comes from both formal
463 experimentation and ecological observation. Competition could theoretically occur within the shoot
464 or root system, but experimentally most attention has been paid to the possibility of competition
465 between root systems. Plants have been proposed to over-proliferate either roots or shoots in the
466 presence of a neighbour, a competitive response that in theory increases resource capture at the
467 expense of the neighbour (Gersani et al, 2001). However, if the neighbour responds in kind, both
468 plants increase their expenditure on growth without actually gaining more resources, or may
469 collectively exhaust resources in a 'tragedy of the commons' scenario, which is an evolutionary
470 stable state (Novoplansky, 2009; Smveka & Herben, 2017). However the results from formal
471 experimentation (e.g. Gersani et al, 2001) have been criticised for problems in experimental design
472 (see above)(Hess & Kroon, 2007; Semchenko et al, 2007), and the apparent over-proliferation
473 explained as a consequence of altered nutrient availability or increased pot volume (Hess & Kroon,
474 2007; Semchenko et al, 2007; Nord et al, 2011).

475
476 Whether individuals take a competitive strategy can be context dependent; the same factors may
477 promote competition under some scenarios but not others. The stress gradient hypothesis posits
478 that there will be greater competition in benign conditions and facilitation in stressful ones
479 (Bertness and Callaway 1994). Various studies on plant-plant interactions have found support for
480 this idea (e.g. meta-analysis by He et al 2013, but see Rysavy et al 2016). The stress gradient
481 hypothesis might be particularly relevant to plants found in might be particularly relevant in stressful
482 environments prone to exposure, temperature variation and drought (Eränen and Kozlov, 2008).
483 Shifts may occur during the lifetime of an individual plant, for example where seedling
484 establishment is improved by the presence of others, but adults suffer lower reproduction from
485 competition (Lara-Romero et al, 2016). In some cases, less stress-tolerant genotypes are less
486 negatively affected by competition (e.g. Zhang and Tielborger, 2019). This trade-off between stress
487 tolerance and competitive ability might contribute to the maintenance of polymorphisms in these
488 traits. Theoretically, neighbour competition should be stronger between conspecifics (social
489 competition), their niche requirements being more similar than those of heterospecific neighbours,

490 but so far the evidence for this is mixed (Ehlers and Bilde 2019). Overall, whether competitive
491 strategies depend on the identity of the competitors, beyond asymmetry in competitive ability,
492 remains to be resolved.

493

494 **5.2 Cooperation and facilitation between heterospecifics**

495 Avoiding unnecessary competition for resources with a neighbouring plant likely increases the
496 fitness of many plants, even if this also inadvertently benefits neighbouring plants. The simplest
497 strategy towards an unrelated plant would be a completely neutral strategy ('live and let live'),
498 though this obviously might not be an active strategy. Alternatively, a plant might cooperate with its
499 neighbour by reducing its growth to avoid competition (Semchenko et al, 2010; Wang et al, 2020),
500 though there is not abundant firm evidence for such effects (Novoplansky, 2009). In some species
501 pairs, complex root growth patterns, such as segregation and avoidance, occur during their
502 interaction (Figure 4). These could be deliberate non-competitive responses, since they are
503 specific to the species pairs (Cahill & McNickle, 2011), but might also be inadvertent responses
504 rather than an active strategy (in effect, a form of facilitation). The phenomenon of 'crown shyness',
505 in which tree shoot systems of certain species do not spatially overlap with other members of the
506 same species (Goudie et al, 2008), is also a possible cooperative response, although the genesis
507 of this phenomenon is unclear and might not involve neighbour detection.

508

509 The evidence for facilitation is rather stronger, and there are many examples of such effects
510 between neighbouring plants (see McIntire & Fajardo, 2014; Li et al, 2014; Schöb et al., 2018). For
511 instance, neighbours can ameliorate stressful conditions or create novel niches for other plants.
512 For instance, facilitation is viewed as a key explanation for the over-yielding observed in
513 intercropping systems such as maize/faba bean (Li et al, 2014). In phosphorus impoverished
514 steppe grassland, some species can benefit from phosphorous-mobilizing heterospecific
515 neighbours, but only if the non-mobilizing species can express sufficient plasticity in root growth
516 (Yu et al, 2020). 'Nurse' plants enable seedling establishment, especially in very harsh conditions
517 such as arid environments (Loayza et al. 2017). Plants could also share in 'public goods', such as
518 attraction and maintenance of pollinator populations throughout the season (Dudley, 2015). This

519 can be particularly important for plants with low density populations in which mating can be
520 problematic (Allee effects); neighbours can provide reproductive benefits by attraction of pollinators
521 (Lachmuth et al 2016). Other hypothesised examples of public goods include synchronous flower
522 production ('co-flowering') that increases the attractiveness of displays (Torices et al, 2018) and
523 synchronous production of seeds ('masting') which swamp predators (Dudley, 2015). It should be
524 noted that although the evidence for facilitation is generally good, it does not provide support for
525 the concept of active plant-plant interactions, since facilitative effects can occur in the absence of
526 neighbour detection.

527

528 **5.3 Social interactions**

529 In cooperative and altruistic social responses, plants would be expected to downregulate root or
530 shoot growth in the presence of a related conspecifics, which may ultimately benefit the
531 reproductive success of both participants (Dudley, 2015). These effects could benefit fitness both
532 directly (via the reduction of competition for both plants) and indirectly (via the increased success
533 of both plants). Again, most of the formal experimentation has focussed on root system responses,
534 and suggests that plants respond to close kin (or their exudates) by reducing root growth, and
535 maintaining spatial segregation (Biedrzycki et al, 2010; Fang et al, 2013; Semchenko et al, 2014).
536 It is also worth noting that when sharer/owner experiments are repeated with all variables
537 controlled for (see above), sharers actually reduce their root growth relative to owners (Chen et al,
538 2015). Kin recognition-driven cooperation has been proposed to reduce investment in competitive
539 traits (Cahill et al, 2010; Bhatt et al, 2011; File et al, 2012; Fang et al, 2013), improve resource
540 capture (Lepik et al, 2012) and increase fitness (Donohue, 2003; Biernaskie, 2011; Torices et al.
541 2018; Yang et al, 2018). However, a broad criticism of these studies is that they rarely measure the
542 full extent of individual inclusive fitness (Ehlers and Bilde 2019). In general, the direct evidence for
543 social cooperation is again rather mixed, but some of the kin-induced alterations are very difficult to
544 explain without invoking some form of cooperation between plants.

545

546

547

548 **6. Allelopathy**

549 In some ways, allelopathy has the inverse problem to competition and cooperation; the
550 experimental evidence for the phenomenon is very clear, but the benefits to plants are much less
551 clear. Conventionally, allelopathy is defined as the release chemicals which reduce the growth,
552 development, survival and reproduction of competitors (Figure 4). In plants, allelopathic
553 compounds are exuded into the rhizosphere (Kato-Noguchi et al, 2010; Kong et al, 2018), emitted
554 aboveground as VOCs (Kong et al, 2004), deposited in pollen (Roshchina et al, 2009), or may also
555 be non-specifically released during litter decomposition (Rice 2012). Allelochemicals vary in mode
556 of uptake and mechanism of action, and their effectiveness may vary depending on spatio-
557 temporal factors such as activation (Weston and Duke, 2003; Rice, 2012; He et al, 2019; Gaofeng
558 et al 2018). There is little debate that allelochemicals have phytotoxic potential, but the evidence
559 that they accumulate to sufficiently high levels to cause phytotoxicity under natural conditions is not
560 strong (Zeng, 2014). Allelopathic chemicals should also have autotoxic effects on the source plant,
561 a paradox that has been long debated (Smith 1979; Rice, 2012). The highest concentration of
562 allelochemicals should be observed close to allelopathic plants, selecting for tolerance to their own
563 allelochemicals (Fitter 2003), which has recently been connected with suppression of defence
564 mechanisms, implying a high cost of allelopathic behaviour (Xu et al, 2015; Li et al, 2019; Liu et al,
565 2019). Furthermore, allelopathic compounds may also have hormetic effects; at sub-toxic
566 concentrations, they may actually induce stress tolerance and stimulate of growth of neighbouring
567 plants (Agathokleous and Calabrese, 2019; Stebbing, 2003). Thus, we can reasonably ask what
568 the benefits of plant allelochemicals are -- and what this might tell us about plant-plant interactions.

569
570 There are two non-mutually exclusive answers to this question. Firstly, allelochemicals might be
571 exuded for a different function, with their phytotoxicity only being a secondary and/or rarely
572 expressed property. For instance, some allelochemicals may enhance nutrient uptake by the
573 exuding plant; (Tharayil et al, 2009; Zhang et al, 2020), or function in the recruitment or
574 maintenance of beneficial soil microbes, although tests of this hypothesis so far have returned
575 ambiguous results (Stinson, 2006; Callaway et al, 2008; Cipollini et al, 2008; Mishra et al, 2013). At
576 natural concentrations, allelochemicals might function as signals to neighbouring plants (rather

577 than toxins), or might allow detection of obstacles in soil, triggering root navigation (Falik et al,
578 2005; Semchenko et al, 2008; Fang et al, 2013; Agathokleous and Calabrese, 2019).

579

580 Secondly, allelochemicals might be exuded primarily for competitive reasons, and their
581 costs/drawbacks offset by some other mechanism. For instance, it has been suggested that
582 allelochemicals act indirectly on competitors by preventing nutrient uptake, or altering soil
583 microbiome composition, rather than needing to be exuded at directly phytotoxic (and autotoxic)
584 concentrations (Zeng, 2014). Another possibility is that the costs of are reduced by minimising the
585 expression of the trait. Deployment of allelochemicals seems to be tightly connected to neighbour
586 detection, and particularly non-kin neighbours. Active exudation can be triggered by the presence
587 of neighbours, detected through common signals such as (-)-loliolide, jasmonic and salicylic acids
588 (Li et al, 2016; Kong et al, 2018; Uesugi et al, 2019). Furthermore, allelopathy may only be
589 expressed at certain developmental stages when it is the greatest advantage, particularly during
590 seedling establishment (Kong et al, 2018). This may give plants an early competitive advantage
591 over neighbours that can be maintained without allelochemical release; thus, the costs of
592 allelopathy may only be transiently incurred.

593

594 The most straightforward interpretation of current evidence brings us tantalizingly close to
595 concluding that allelopathy is not just a competitive trait, but one induced in response to the identity
596 of the neighbouring plants. As such, allelopathy could represent the keystone in the argument that
597 plants do differentially detect and respond to their neighbours. And yet, like other key questions in
598 the field, the evidence is currently not conclusive enough, and other interpretations remain
599 possible.

600

601 **7. Conclusion & Perspectives**

602 As the work reviewed here shows, plants are active participants in their interactions with each
603 other, interactions that are every bit as complex as those seen between other organisms. Plants
604 can detect their neighbours through a range of mechanisms (section 3), communicate with their
605 neighbours, and attempt to manipulate their growth and function (section 6). We cannot yet be

606 completely certain that plants can distinguish between the identity of their neighbours (section 4),
607 and respond differentially depending on this identity (section 5), but the evidence currently supports
608 those ideas. Admittedly, this evidence for this is primarily phenomenological, and based on
609 observation of plants growing together; as we have seen, alternative explanations of these studies
610 are usually possible.

611

612 Critical to moving the field forward is to demonstrate the mechanistic basis by which plants may
613 differentially detect and respond to neighbours (Figure 3). This requires investigating how plants
614 integrate the potential cues and whether acting on complex social information requires a
615 multimodal system (Dore et al 2018). If kin-recognition could be detected at the molecular level, for
616 instance -- as a consequence of ligands binding to receptors -- or if different gene expression
617 patterns could be observed in plants exposed to kin and non-kin -- then much of the theoretical
618 tension in the field would be resolved. This information would also be key to revealing whether
619 plants are sensitive to the spectrum of genetic relatedness from self to heterospecifics, and to what
620 extent life history and ecology have driven the evolution of these mechanisms. For example, do
621 mating and dispersal systems that produce highly genetically structured populations correlate with
622 more finely tuned mechanisms? We therefore advocate that the direction of future travel should
623 certainly be towards an increased molecular understanding of plant-plant interactions, but in a
624 holistic way that integrates observation and deeper eco-evolutionary understanding of these
625 interactions in natural environments.

626

627 The study of plant-plant interactions has major implications for understanding and sustainably
628 improving crop yields. Crop systems represent an obvious break from natural biological systems,
629 particularly in their radical reorganization of plant communities into monocultures of closely related
630 plants. Plant-plant interactions are hugely important in the functioning of crop species, because the
631 drive to maximize yield from a minimum of land creates a situation where the collective yield of the
632 group is much more important than the yield of the individual. Highly competitive plants with high
633 individual fitness therefore likely make poorer crops than individuals with intermediate fitness
634 (Weiner et al, 2017). Due to modern breeding and utilization of inbred varieties, crops have

635 effectively undergone 'group selection' for traits that enable them to yield highly at a field level, and
636 to maintain consistency even in stressful conditions (Weiner et al, 2017; Blum, 2018). This artificial
637 selection has likely radically altered the dynamics of plant-plant interactions in crop species
638 compared to their wild relatives and indeed, compared to traditional landraces. For instance,
639 competitive above- and belowground interactions were shown to be less pronounced for example
640 within modern wheat cultivars compared to traditional landraces (Zhu et al, 2019). Since the Green
641 Revolution, crops have also been inadvertently bred for 'density resistance', the ability to perform
642 better under high sowing densities, by reducing inhibition that is caused solely by the presence of
643 neighbouring plants (i.e. that is not caused by resource limitations) (Choe et al, 2016). The role of
644 plant-plant interactions in determining optimal crop densities is reviewed elsewhere in this issue
645 (Postma et al, 2020). Interactions between crops and weeds, and between pairs of crops in
646 intercropping systems are further examples of the importance of plant-plant interactions in
647 agricultural systems. Thus, by better understanding the nature of plant interactions, we can also
648 aim to improve crop systems.

649

650 Overall, it is exciting time for the field, with a wealth of new data continuing to dispel the notion that
651 plants are passive actors in their environment. In hindsight, it seems unlikely that plants have
652 flourished in all terrestrial ecosystems for 500 million years without being able to actively detect
653 and respond to other plants – whether friend, neighbour or enemy.

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FIGURE LEGENDS

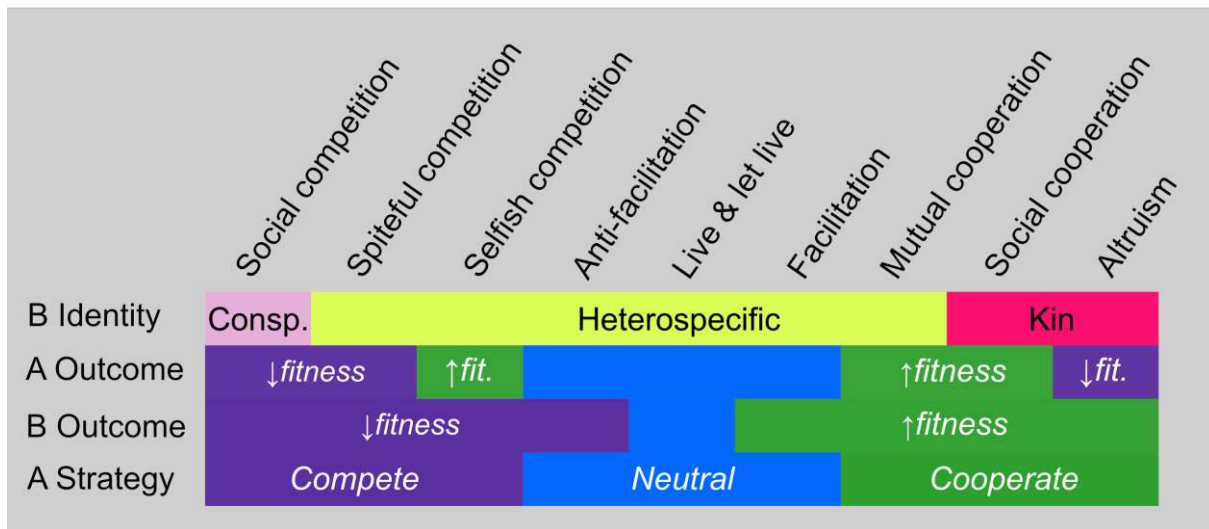


Figure 1: Plant-plant interactions

Matrix showing the possible types of plant-plant interactions, depending on the strategy of the actor (A), the identity of the recipient (B), and the actual fitness outcomes for both A and B. Social interactions are those occurring with members of the same species (consp. – consp.), either related (kin) or unrelated. These may have different properties from equivalent interactions with heterospecifics because of the symmetry of the competition, or because the actor ultimately benefits from the increased fitness of the recipient by increased inclusive fitness (kin selection). Facilitation is an inadvertent benefit to the recipient caused by plant A's impact on the environment; in theory, plant A could also inadvertently reduce the recipient's fitness (anti-facilitation).

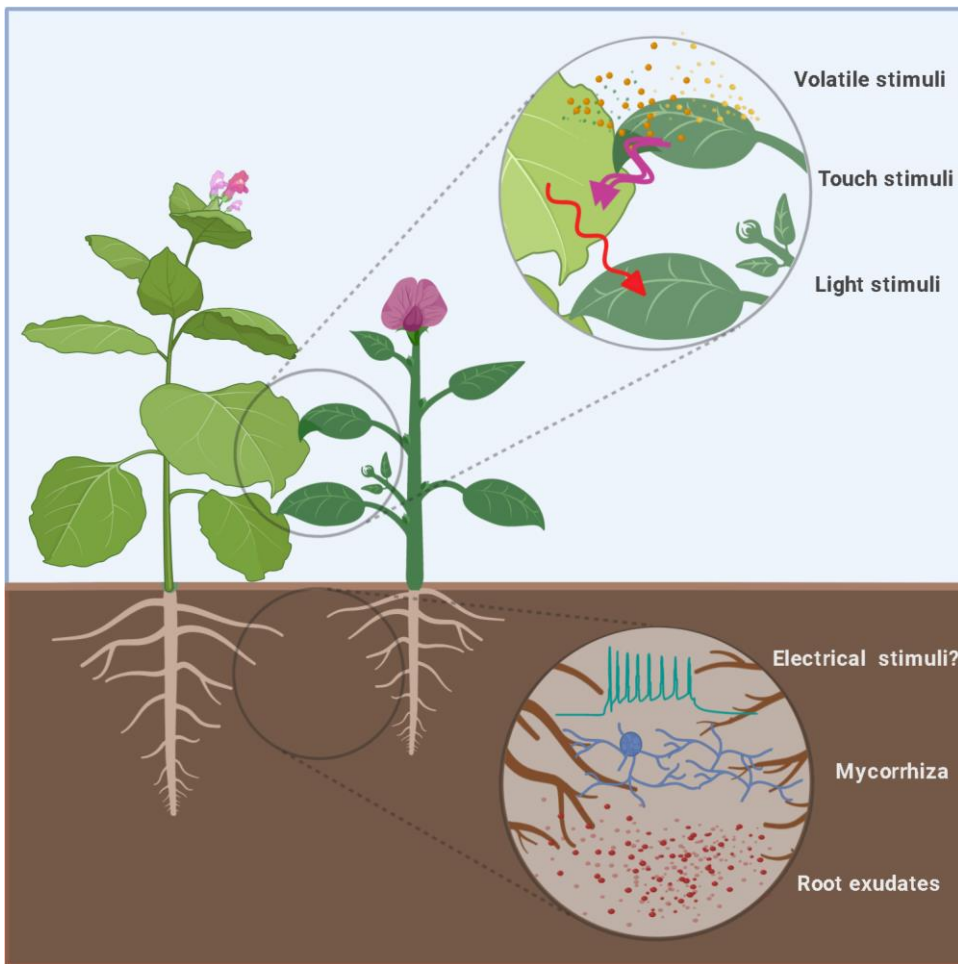


Figure 2: Mechanisms of neighbour detection

A range of above and below ground mechanisms may allow plants to detect the presence of neighbours. Whilst evidence suggests that plants do use multiple cues for neighbour detection (see Section 3), a general understanding of which cues carry sufficient information for discrimination between species or relatives remains elusive.

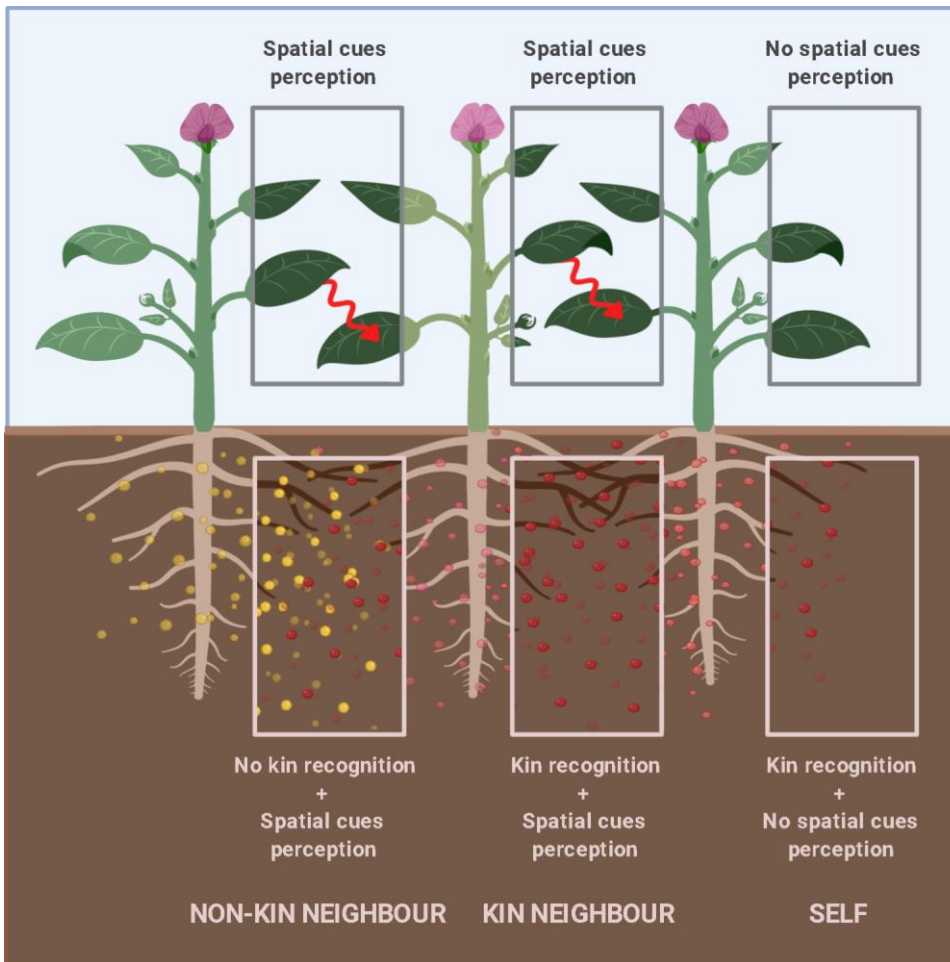


Figure 3: A possible model for neighbour discrimination with respect to kin- and self-recognition in plants.

We suggest that plants could show a range of responses to neighbours based on discrimination using the integration of various cues. Plants exude a 'kin-recognition' signal from their roots, but not the root tips (red/yellow circles). On the right-hand side, the plant's root tips detect its own kin-recognition signal at a low concentration, and detects no other spatial cues (light, touch, volatiles) for neighbour presence, thus perceiving that its roots are encountering 'self'. In the middle, the two plants detect each other's kin recognition signals at high concentration, and the presence of a kin neighbour is confirmed by above-ground spatial cues; both plants thus perceive that their roots are encountering 'kin'. On the left-hand side, the non-kin plant root tips only detect their own kin-recognition signal at a low concentration. Aboveground spatial cues indicate the presence of a neighbour, so the plant perceives that its roots are encountering a non-kin neighbour.

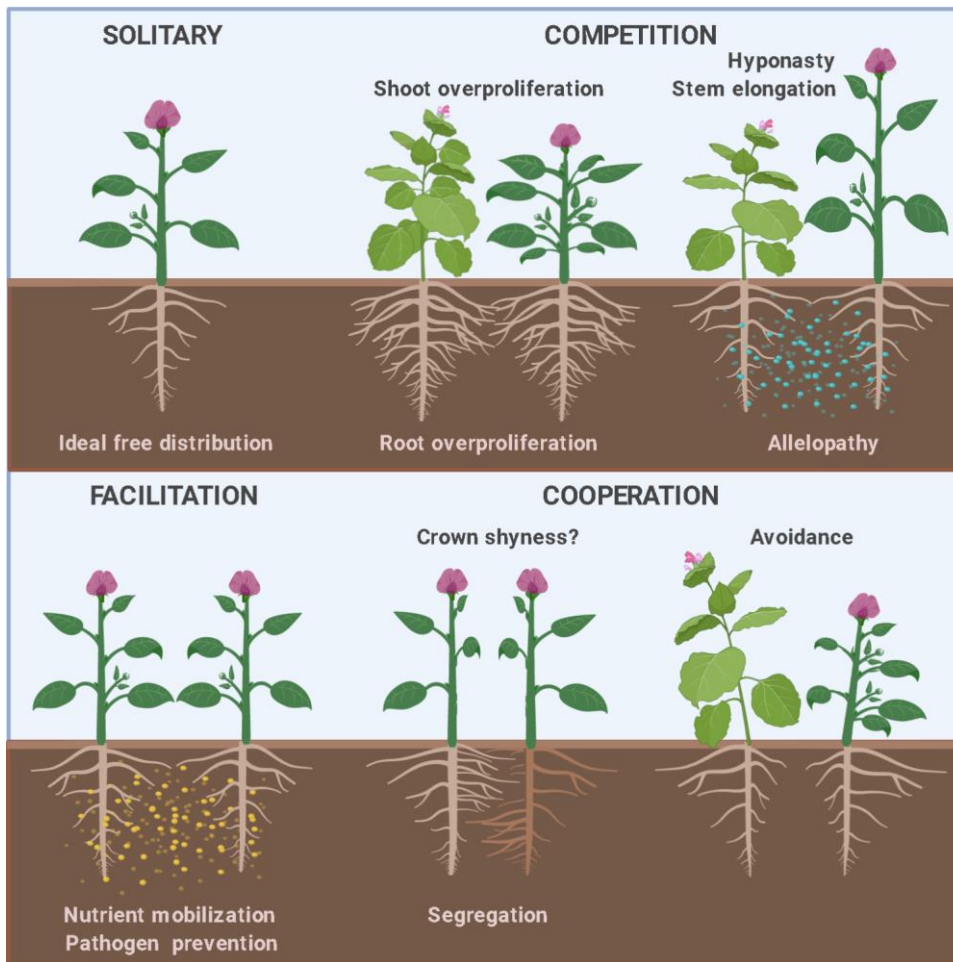


Figure 4: Responses to neighbouring plants

A summary of possible outcomes in interactions between neighbouring plants, relative to the solitary growth pattern. When unconstrained by neighbours (solitary) plants may organise their growth in relation to resource availability in an “Ideal Free Distribution”. When faced with a near neighbour, interactions may take a number of forms. Competitive outcomes involve increased root growth, with the possible release of allelopathic exudates or volatile organic compounds, and increased stem elongation and altered organ positioning and size. Cooperation between conspecifics (perhaps often close relatives) may involve a reduction in root and shoot growth, enhanced spatial segregation of organs to avoid overlapping resource capture, or release of public goods such as nutrients or anti-pathogen molecules. Facilitation between heterospecifics may be manifested in a range of ways that are non-competitive or actively anti-competitive, and might involve avoidance or segregation of root and shoot systems, synchronous flower or seed production.