

## Letters

### Kin recognition or phenotype matching?

In their paper 'Photoreceptor-mediated kin recognition in plants', Crepy & Casal (2015) present a beautiful series of experiments on *Arabidopsis thaliana* proving the existence of neighbor recognition without direct contact between plants through the perception of the vertical red : far-red (R : FR) and blue light profiles. This recognition elicits a leaf-position response that decreases shading of same accession neighbors and increases fitness despite increasing self-shading. The response is shape dependent and, in the Col accession, the same response is obtained by placing a green filter vertically, close to the plants.

Crepy & Casal (2015) discuss their results in the context of kin selection, in which altruism might be selected for as long as it is directed toward kin, and for which kin recognition, that is the ability to assess the shared ancestry (and thus genetic relatedness) with another individual, is one possible prerequisite (Hamilton, 1964). Mechanisms of kin recognition are typically separated into direct (kin are recognized because they express some trait or set of traits directly linked to their genotype) and indirect (kin are recognized based on properties of the circumstances rather than of the individuals themselves) mechanisms (Waldman, 1988). Phenotype matching is a mechanism by which individuals may be able to identify kin, provided that there is a correlation between phenotypic similarity and genetic similarity (Waldman, 1988; Hare *et al.*, 2003). In this case, any cooperation behavior directed towards a similar looking individual has a good chance to be directed towards a kin and thus to be selected through kin selection. It is thus sometimes called kin recognition, and used as such (the 'armpit effect', Dawkins, 1982), although this is not strictly true. What the paper shows is phenotype matching, but we are not convinced that this is strict kin recognition. Indeed, phenotype matching is a possible implementation of kin recognition but, depending on the proxy used, it may also serve for many other kinds of assessments. Specifically, it is likely that two plants exhibiting the same light profile (a proxy for morphology) will have similar competitive abilities regarding cross-shading. Because the outcome of a competition with similar opponents is hardly predictable, such a behavior could be seen as cooperative (i.e. benefiting both opponents) rather than altruistic (costly to one but beneficial to the other opponent) as directing leaves away from neighboring plants decreases the probability of both shading and being shaded by the neighbor. We believe that this alternative hypothesis should be investigated along with the hypothesis of kin recognition. Nonetheless, this phenotype assessment mechanism (without direct contact) is completely novel and opens exciting perspectives in the field of plant interactions.

In the case of the R : FR and blue light profiles of a plant discussed in Crepy & Casal (2015), evidence from three of the experiments (Expts 5, 6 and 7; Crepy & Casal, 2015), shows an appreciable error rate in the ability of *A. thaliana* plants to actually assess the genetic relatedness to their neighbors. In Expt 5, plants of the Columbia accession grown close to a green filter have a higher fraction of leaves orientated away from the filter compared to a clear (control) filter, indicating the importance of the light signal to elicit the leaf reorientation response. There is however no reason for the green filter to display a light signal matching specifically to that produced by the Columbia accession. The signal of the filter is vertically uniform and this would trigger the observed response of any neighbor according to our competition hypothesis.

In Expt 6, plants of one accession (*Landsberg erecta*, Ler) are grown alongside other plants from the same accession, but 7 d younger. No shade avoidance response is detected, meaning that the plants did not detect their neighbors as kin (p. 334: 'The rows formed by alternate plants with an age difference of 7 d failed to show the leaf-position response (Fig. 6). Neither the eldest nor the youngest plants rearranged their leaves away from the row of neighbors.') possibly because the younger plants did not shade older plants (thus did not emit the adequate signal) because of their smaller size. An alternative explanation for this result would be that the nonrecognition of younger/older kin neighbors is adaptive because older neighbors will be more competitive because of their size difference, and younger plants exhibit an altruistic behavior by not emitting the signal eliciting the costly response in older plants. However, the actual altruistic behavior would be that older plants rearrange their leaf position so as not to shade the younger plant. A simpler explanation, is that of light signal matching regarding competitive abilities of the neighbors rather than kin recognition, because young and old plants simply differ in their competitive profile (the older plants always win the shading competition).

Expt 7 (discussed on p. 335) uses *sav3* mutants which are affected in a gene involved in the synthesis of auxin and are unable to reorient their leaf growth in response to low R : FR that is, they are impeached in their response mechanism. Wild-type and *sav3* mutants of the same accession were grown in alternation within the same row. These wild-type plants had an intermediate response between that of wild-type plants grown in pure rows and that of mutants grown in pure rows (leaf position ratio: wild-type pure =  $1.50 \pm 0.07$ ; wild-type in mixture with mutant =  $1.30 \pm 0.08$ ; mutant pure =  $1.05 \pm 0.03$ ; mutant in mixture with wild-type =  $1.09 \pm 0.05$ ; values extracted from Fig. 7(a) or given on p. 335;  $P < 0.05$  for all comparisons except between mutant pure and mutant in mixture with wild-type which is not significant). Strict kin recognition should have prompted a very similar response from the wild-type (having both the signal and the response mechanism) towards other wild-type plants as towards the mutants (impeached for the response but not for the signal), as both are from

the same accession. A possible explanation for this intermediate response is that the *sav3* mutation also affects the R : FR profile (i.e. the signal) emitted by plants. However no information in that respect is given by the authors, and this experiment would then be an argument more in favor of the competitive ability matching hypothesis.

The conclusion of Crepy & Casal (2015) is that 'This mechanism of kin recognition involves phenotype matching' and, specifically for Expt 6 that 'kin recognition requires matching body shapes'. As for now, kin does not seem a requirement for photoreceptor-mediated recognition in plants. Yet note that the Ler accession, which has an erect growth (Fig. 3) has the best fitness when grown in mixture (Fig. 8) while the RLD accession has a prostrate growth and has a poor fitness in mixture. This suggests that some accessions are simply better competitors than others, and not that there is 'an indication of mutual benefit and cooperation' (Bais, 2015, p. 4).

A formal proof of kin recognition would be to show that the response is sensitive not only to shape but also to kinship, for example, that plants of similar shape but genetically unrelated do not show the leaf-position response or a reduced response compared to kin in a wide range of situations (shapes and relatedness values). However, a leaf position response in the absence of relatedness for a few situations would not invalidate the kin recognition hypothesis, as some error in kin recognition is still compatible with the evolution of altruism through kin selection. The response should thus be measured in a broader genetic and ecologically more realistic context (Bergelson & Roux, 2010). The relatedness values used in this study are extremely high (relatedness values *c.* 1, as individuals from the same *A. thaliana* accession are mostly genetically identical). It would be interesting to compare the response of individuals towards relatives to that of individuals towards strangers (i.e. unrelated individuals) using a range of relatedness values, for example, their sibs, half-sibs, etc. issued preferentially from outcrossed individuals from natural populations. Indeed, Hamilton's rule (Hamilton, 1964) predicts that the response should decrease (or display a threshold) with relatedness.

Plant evolutionary biology has lagged behind animal evolutionary biology in several aspects where strategy and behavior were concerned. One of the objections for kin selection to actually occur in plants is that the kin recognition mechanisms were thought to be impossible in the plant kingdom (i.e. lack of sensors). This has recently been challenged by experimental studies showing differential response of root growth depending on the relatedness of neighbors (Dudley & File, 2007; Murphy & Dudley, 2009), providing a major opportunity to explore new hypotheses and perspectives. Crepy & Casal's (2015) work is an attempt to find a

recognition mechanism that does not involve direct contact. The fact that plants can recognize the shape of their neighbors and rearrange their leaf position in consequence is novel and very exciting. It could be a cooperative or an altruistic behavior in a species where populations are viscous, the other mechanism described by Hamilton (1964) allowing for kin selection, that is, where dispersal is rare enough for neighbors in a population to be closely related. In this case, an altruistic behavior towards a neighbor of similar shape has a high probability to be directed towards a kin and Hamilton's rule could be validated. Further experiments are required to show that the neighbor recognition mechanism through the vertical R : FR and blue light profiles identified by Crepy & Casal (2015) might be one such behavior.

## Acknowledgements

The authors thank three anonymous referees for valuable insight during the review process.

Irène Till-Bottraud<sup>1,2\*</sup> and Pierre de Villemereuil<sup>1,2</sup>

<sup>1</sup>Laboratoire d'Ecologie Alpine (LECA), University of Grenoble Alpes, F-38000 Grenoble, France;

<sup>2</sup>CNRS, LECA, F-38000 Grenoble, France

(\*Author for correspondence: tel +33 4 76 51 45 24; email Irene.till@ujf-grenoble.fr)

## References

- Bais HP. 2015. Shedding light on kin recognition response in plants. *New Phytologist* 205: 4–6.
- Bergelson J, Roux F. 2010. Towards identifying genes underlying ecologically relevant traits in *Arabidopsis thaliana*. *Nature Reviews Genetics* 11: 867–879.
- Crepy MA, Casal JJ. 2015. Photoreceptor-mediated kin recognition in plants. *New Phytologist* 205: 329–338.
- Dawkins R. 1982. *The extended phenotype*. San Francisco, CA, USA: Freeman.
- Dudley SA, File AL. 2007. Kin recognition in an annual plant. *Biology Letters* 3: 435–438.
- Hamilton WD. 1964. Genetical evolution of social behaviour. *Journal of Theoretical Biology* 7: 1–16.
- Hare JF, Sealy SG, Underwood TJ, Ellison KS, Stewart RLM. 2003. Evidence of self-referent phenotype matching revisited: airing out the armpit effect. *Animal Cognition* 6: 65–68.
- Murphy GP, Dudley SA. 2009. Kin recognition: competition and cooperation in *Impatiens* (Balsaminaceae). *American Journal of Botany* 96: 1990–1996.
- Waldman B. 1988. The ecology of kin recognition. *Annual Review of Ecology and Systematics* 19: 543–571.

**Key words:** *Arabidopsis thaliana*, kin selection, light signal, neighbor recognition, phenotype matching, shade avoidance.