



## Commentary

### Shedding light on kin recognition response in plants

Kin recognition, a well understood phenomenon in animals, has also more recently been illustrated in plants (Dudley & File, 2007; Biedrzycki & Bais, 2010; Biedrzycki *et al.*, 2010; Bhatt *et al.*, 2011). The work done on *Cakile edentula* showed an increase in root growth in the presence of strangers compared with kin, demonstrating that these plants have the ability to distinguish kin from nonkin and alter their growth in response. In parallel, Biedrzycki *et al.* (2010) showed for the first time that a model system, *Arabidopsis thaliana* (CHA-25), has the ability to recognize kin and strangers. Further, the data by Biedrzycki *et al.* (2010) demonstrated that recognition is mediated through a root-derived cue. The surprising observation of plants recognizing kin has also garnered some controversy (Klemens, 2008; Masclaux *et al.*, 2010; Willis *et al.*, 2010), and the lack of a precise molecular mechanism underpinning the kin recognition response in plants has led to a debate questioning the occurrence of kin recognition in plants. In this issue of *New Phytologist*, Crepy & Casal (pp. 329–338) followed a systematic approach of analyzing kin recognition in the model system *A. thaliana*. Crepy & Casal showed that plants recognized their kin neighbors by horizontally reorienting leaf growth compared with the interactions with the nonkin members. The authors also showed that the mechanism that led to reorientation of the leaf with kin members was regulated by *phytochrome B* and *cryptochrome 1*. The work by Crepy & Casal provides the first molecular evidence of the way in which plants respond to kinship. The proposed work will provide the foundations for the genetic and biochemical mechanisms responsible for kin recognition in *A. thaliana* and will not only shed light on competitive interactions between kin and strangers in this model species, but will also facilitate understanding of how these processes may occur in crop species.

---

*‘Crepy & Casal showed that plants interacting with kin plants yielded more seeds compared with plants interacting with nonkin members, a clear indication of mutual benefit and cooperation.’*

---

Plants depend on their dynamic root systems to provide nutrients and water to the rest of the plant, often competing with

other plants for these necessities. Lateral root growth in plants has been shown to be a very plastic and nutrient-dependent process (Malamy & Ryan, 2001; Biedrzycki *et al.*, 2010). Recently Biedrzycki *et al.* (2010) showed that root morphology of very young seedlings of *A. thaliana* responds to identity, supporting the contention that kin recognition can be a major force in the evolution of plants. By contrast, it has been argued that kin recognition is a manifestation of self-/nonself-recognition (Falik *et al.*, 2005). Biedrzycki *et al.* (2010), showed that root exudates mediate the kinship response in *A. thaliana*. Various other studies have analyzed the belowground factors for kinship recognition in different plant species (Dudley & File, 2007; Bhatt *et al.*, 2011; Fang *et al.*, 2013). The question of how plants recognize kin or strangers can be approached through the genetic and molecular tools available with *Arabidopsis*. Interestingly, the paper by Crepy & Casal analyzed the aboveground interactions in a kin recognition process; this is one of the first reports to show an aboveground behavior response in plants exposed to kin members.

Plants recognize cues to avoid self-incompatibility and self-fertilization (Sanabria *et al.*, 2008), and they have also developed mechanisms to sense pathogens, mutualists, and parasitic plants through signals derived from roots (Keyes *et al.*, 2007). However, even more subtle forms of recognition and sensing at the plant organ level have been identified (de Kroon, 2007) – for example, roots show responses to the neighboring roots’ genotype (Mahall & Callaway, 1996) and species (Huber-Sannwald *et al.*, 1997; Dudley & File, 2007; Semchenko *et al.*, 2007; Biedrzycki *et al.*, 2010; Bhatt *et al.*, 2011). While these studies demonstrate how plants use roots or root-derived cues to discriminate between self/nonself and kin/nonkin, there is no evidence that dictates the precise mechanism by which plants show this recognition behavior. Semiochemicals and volatile organic compounds (VOCs) have been suggested to be the potential cues that mediate the plant–plant response, but no genetic mechanism or chemicals have yet been elucidated to precisely regulate kin-/nonkin-recognition in plants.

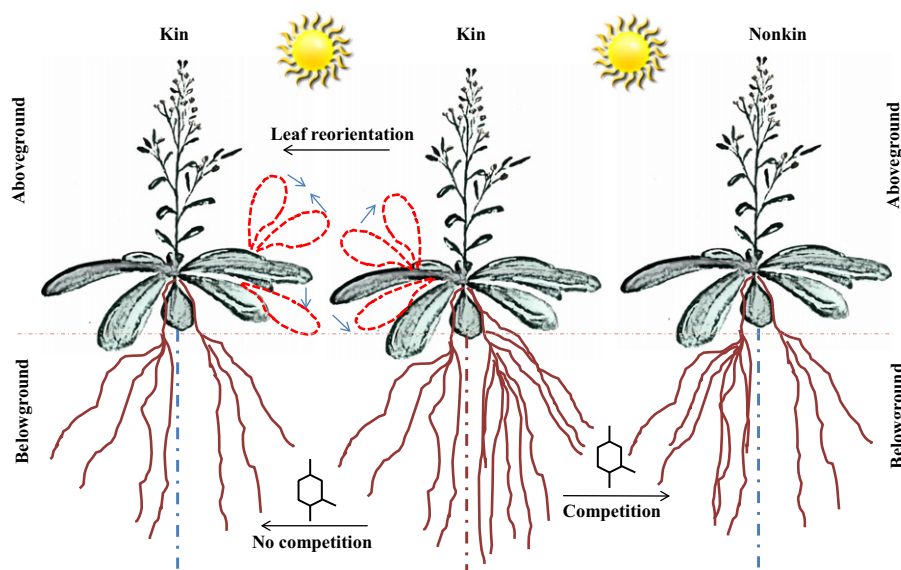
It is known that plants compete for space and nutrient acquisition. Studies focusing on belowground communications have shown that plants allocate more roots to sequester nutrients and that root allocation increases during kin–nonkin interactions compared with kin–kin interactions (Biedrzycki & Bais, 2010; Biedrzycki *et al.*, 2010). Other lines of study involving different plant species have also shown that plants compete with nonrelated species more aggressively than with related kin members (Dudley & File, 2007; Murphy & Dudley, 2009). The recent findings that belowground interactions may have implications for plant recognition have garnered attention but have also been criticized for caveats related to the experimental procedures (Klemens, 2008). Contrary to the findings of Biedrzycki *et al.* (2010), work by Masclaux *et al.* (2010) showed competitive

ability in *A. thaliana* accessions, negating the kinship response. Masclaux *et al.* (2010) evaluated aerial parts of the plants to show competitive ability within the accessions. The quantitative evaluation of the cooperative relationship is difficult as it also accounts for competitive interactions to sequester the common pool of nutrients.

The foliar parts of plants behave differently during crowding and encroaching interactions from neighbors (Casal, 2012). Light sharing and shade avoidance are common features that plants experience during interactions with other plants (Casal, 2012). The changes in red to far-red (R:FR) ratios and low blue light interactions indicate plant canopy shade resulting in various growth modifications in aerial parts of the plants including reorientation of the leaves (Casal, 2012, 2013). Growth modifications in the form of reorientation of leaves both 'horizontally' and 'vertically' are called 'shade-avoidance reactions' (Casal, 2013). The presence of neighboring plants modifies the light environment and is perceived through phytochrome B (phyB) and cryptochrome 1 (cry1) (Keller *et al.*, 2011; Casal, 2012). It is argued that photosensory receptors such as phytochrome and cryptochrome are able to perceive airborne signals generated by neighbors. There is a significant amount of work that has been performed to understand the functional importance of photosensory receptors in light signaling in plant communities (Casal, 2013), but the impact of photosensory receptors to perceive and recognize kin and nonkin interactions is not yet elucidated. Crepy & Casal employed a systematic approach of utilizing the power of genetics in the model system *A. thaliana* and showed the involvement of *phyB*, *cry1* and *shade avoidance 3 (sav3)* in recognizing kin signals. It is often argued that photosensory signal-mediated aerial growth change, including leaf orientation, add fitness costs to the plant (Casal, 2013). Concomitantly, Crepy & Casal showed that plants interacting with kin plants yielded more seeds compared with plants interacting with nonkin members, a clear indication of mutual benefit and cooperation.

The article by Crepy & Casal provides one of the first insights into the mechanism of kin recognition in plants. The article also shows cooperation within the plants interacting with kin. This is not the first time that plants showed an altruistic behavior while interacting with kin; other reports in different plant species have also shown an underground trait of minimal root allocation for kin–kin interactions (Dudley & File, 2007; Biedrzycki *et al.*, 2010). The conception that kin behavior is altruistic is controversial, as most of the experiments showing kin interactions have not negated the possibility of a competitive environment. Plants used in the study by Crepy & Casal were only allowed to sense their neighbors through aerial interactions, thereby negating any root–root competition (Fig. 1). The results clearly indicate that mutants impaired in photosensory receptors failed to rearrange their leaves under kin–kin interactions compared with the wild-type plants.

Plants are sessile organisms, and are incapable of selecting the genotype of their neighbors. Over time, plants have evolved to produce a plethora of small-molecular-weight compounds as signaling and defense molecules (Bais *et al.*, 2006). Another report on kin interaction indicates the involvement of a root-derived signaling molecule for kin recognition (Biedrzycki *et al.*, 2010) (Fig. 1). Although Crepy & Casal avoided root interactions in their study, it could be argued that volatiles-derived through leaves may still hold a key to modulating orientation and reorientation of leaves. An experiment completely negating involvement of volatiles may be needed to confirm that only sensory receptors override the kin recognition process in plants. Interestingly, it is also known that changes in root interactions may also impact on shoot plasticity (Dudley & File, 2007; Biedrzycki *et al.*, 2010), so it would be interesting to do the same experiments described in Crepy & Casal under root interaction environments. The implications of the work done by Crepy & Casal are multi-fold as it would be very important for commercial agricultural settings, where similar genotype species are grown in close proximity and may have tradeoffs which may ultimately impact overall productivity.



**Fig. 1** A schematic showing the aboveground and belowground interactions in plants experiencing kin and nonkin members. Crepy & Casal (in this issue of *New Phytologist*, pp. 329–338), showed that plants interacting with kin members reoriented leaves compared with interactions with nonkin members.

## Acknowledgements

H.P.B. thanks Dr Carla Spence for helpful comments on the draft of this manuscript.

Harsh P. Bais<sup>1,2</sup>

<sup>1</sup>Delaware Biotechnology Institute, Newark, DE 19711, USA;

<sup>2</sup>Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19716, USA  
(tel +1 302 831 4889; email hbais@udel.edu)

## References

- Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology* 17: 233–266.
- Bhatt MV, Khandelwal A, Dudley SA. 2011. Kin recognition, not competitive interactions, predicts root allocation in young *Cakile edentula* seedling pairs. *New Phytologist* 189: 1135–1142.
- Biedrzycki ML, Bais HP. 2010. Kin recognition in plants: a mysterious behaviour unsolved. *Journal of Experimental Botany* 61: 4123–4128.
- Biedrzycki ML, Jalany TA, Dudley SA, Bais HP. 2010. Root exudates mediate kin recognition in plants. *Communicative and Integrative Biology* 3: 28–35.
- Casal JJ. 2012. Shade avoidance. *The Arabidopsis Book* 10: e0157.
- Casal JJ. 2013. Photoreceptor signaling networks in plant responses to shade. *Annual Review of Plant Biology* 64: 403–427.
- Crepy MA, Casal JJ. 2014. Photoreceptor-mediated kin recognition in plants. *New Phytologist* 205: 329–338.
- Dudley SA, File AL. 2007. Kin recognition in an annual plant. *Biology Letters* 3: 435–438.
- Falik O, Reides P, Gersani M, Novoplansky A. 2005. Root navigation by self inhibition. *Plant, Cell & Environment* 28: 562–569.
- Fang SQ, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN. 2013. Genotypic recognition and spatial responses by rice roots. *Proceedings of the National Academy of Sciences, USA* 110: 2670–2675.
- Huber-Sannwald E, Pyke DA, Caldwell MM. 1997. Perception of neighbouring plants by rhizomes and roots: morphological manifestations of a clonal plant. *Canadian Journal of Botany—Revue Canadienne De Botanique* 75: 2146–2157.
- Keller MM, Jaillais Y, Pedmale UV, Moreno JE, Chory J, Ballare CL. 2011. Cryptochrome 1 and phytochrome B control shade-avoidance responses in *Arabidopsis* via partially independent hormonal cascades. *Plant Journal* 67: 195–207.
- Keyes WJ, Palmer AG, Erbil WK, Taylor JV, Apkarian RP, Weeks ER, Lynn DG. 2007. Sernagenesis and the parasitic angiosperm *Striga asiatica*. *Plant Journal* 51: 707–716.
- Klemens JA. 2008. Kin recognition in plants? *Biology Letters* 4: 67–68.
- de Kroon H. 2007. Ecology – how do roots interact? *Science* 318: 1562–1563.
- Mahall BE, Callaway RM. 1996. Effects of regional origin and genotype on intraspecific root communication in the desert shrub *Ambrosia dumosa* (Asteraceae). *American Journal of Botany* 83: 93–98.
- Malamy JE, Ryan KS. 2001. Environmental regulation of lateral root initiation in *Arabidopsis*. *Plant Physiology* 127: 899–909.
- Masclaux F, Hammond RL, Meunier J, Gouhier-Darimont C, Keller L, Reymond P. 2010. Competitive ability not kinship affects growth of *Arabidopsis thaliana* accessions. *New Phytologist* 185: 322–331.
- Murphy GP, Dudley SA. 2009. Kin recognition: competition and cooperation in *Impatiens* (Balsaminaceae). *American Journal of Botany* 96: 1990–1996.
- Sanabria N, Goring D, Nurnberger T, Dubery I. 2008. Self/nonself perception and recognition mechanisms in plants: a comparison of self-incompatibility and innate immunity. *New Phytologist* 178: 503–513.
- Semchenko M, John EA, Hutchings MJ. 2007. Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. *New Phytologist* 176: 644–654.
- Willis CG, Brock MT, Weinig C. 2010. Genetic variation in tolerance of competition and neighbour suppression in *Arabidopsis thaliana*. *Journal of Evolutionary Biology* 23: 1412–1424.

**Key words:** competition, cryptochrome 1, kin recognition, kin–kin interactions, kin–nonkin interactions, phytochrome b, red to far-red (R : FR) ratio, shade avoidance.

New Phytologist  
Tansley Medal  
For excellence in plant science



Full details, terms and conditions at  
[www.newphytologist.org/tansleymedal](http://www.newphytologist.org/tansleymedal)

### Calling all early-stage career scientists! Deadline for submissions for 2015: 1 December 2014

Win £2000 (GBP) and have your work highlighted in *New Phytologist*, one of the world's leading plant science journals (2013 Impact Factor 6.545).

- The *New Phytologist* Tansley Medal is awarded annually in recognition of an outstanding contribution to research in plant science
- This is a global competition open to all plant scientists in the early stages of their career and includes both student and post-doctoral researchers with up to five years experience, excluding career breaks, since gaining/defending their PhD

- Selection is based on a two-stage process:

- **Stage 1** Submit your CV, a personal statement and reference:  
Deadline: 1 December 2014
- **Stage 2** Submission of a single-authored short review intended for publication:  
Deadline: 31 March 2015
- All competition articles that are accepted after peer review will be published in *New Phytologist* and the Tansley Medal winner selected by the judges from these final papers.