Kin recognition in plants: a mysterious behaviour unsolved

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Chemical communication plays an integral part in the rhizosphere and in larger ecological processes. The idea of kin recognition and perception of kin-specific chemical signals have long been recognized in microbial and animal models. By contrast, general chemical communication between plants has been well established, especially with regard to the negative communication between plants of two different species. Recent studies have shown that plants, too, have the ability to recognize other plants in their surroundings based on relatedness and identity. To date, the fields of plant kin recognition are met with several inconsistencies of data and conflicting results. Little molecular evidence has been provided for root secretions and, to date, no molecular evidence for understanding kin recognition has been presented, leaving many questions in the field unanswered. This review attempts to provide a background to this intriguing topic and to encourage further studies to decipher kin interactions in plants.

Biologists have long accepted that diverse animal species have evolved means to recognize and interact with other members of their species, often specifically kin members to enhance their survival. More recently, studies have shown that various microbes, some of the simplest life forms, also have the ability to recognize their kin. So why is it surprising that studies have shown that plants, too, can recognize and interact with their kin? Although they are not mobile, plants are not passive organisms. It is for this immobility that they have evolved many biochemical mechanisms to sense and respond to abiotic factors in their environment such as changes in light, temperature, humidity, and soil pH. Plants are also known to sense and respond to biotic stresses such as herbivory and pathogen attack. In addition to these plant–insect and plant–microbe interactions, plant–plant interactions have been well documented ranging from negative interactions such as allelopathy to positive interactions such as the release of volatile compounds as a warning to other plants (Bais et al., 2006; Dicke and Baldwin, 2010). Plant–plant interactions can be interspecies or intraspecies communications; a perfect example of interspecies communication comes from plant species which use chemicals to inhibit the growth of other plants. The most elegant example is the recent work on the chemical effects of garlic mustard (Alliaria petiolata), an invasive understorey forb in North American forests (Stinson et al., 2006; Wolfe et al., 2008). Garlic mustard secretes benzyl isothiocyanate, which inhibits the growth of mycorrhizal fungi that support tree diversity. Recent studies also suggest that other invasive plants, such as Canada goldenrod (Solidago canadensis), Centaurea stoebe, and narrow-leaf cattail (Typha angustifolia), may produce allelochemicals that inhibit native plants directly (Bais et al., 2003; Perry et al., 2005; Abhilasha et al., 2008; He et al., 2009; Jarchow and Cook, 2009; Thorpe et al., 2009; Tharayil and Trubessiweir, 2010). Perhaps we can examine interactions to reveal a more specific recognition and examine behaviour between plants that are closely related versus plants that are unrelated within the same species?

Recently, Dudley and File (2007) reported that an annual plant, Cakile edentula, exhibited kin recognition, as the plants produced more roots when grown in pots with strangers (plants of the same species, but grown from seeds collected from different mother plants) versus being grown with kin plants (plants grown from seeds collected from the same mother plant) (Dudley and File, 2007). It has not been established, however, if the difference in root growth between plants grown with kin or grown with strangers is due to altruism between kin or increased competition between strangers (Dudley and File, 2007; Callaway and Mahall, 2007). Since this was the first study to highlight such a specific interaction in plants, reactions to this pioneering work were divided (Klemens, 2008). Despite the differing opinions of scientists in the field, the work of Dudley and File (2007) has inspired interest in plant kin interactions, resulting in a handful of recent studies (Dudley and File, 2007).

The following aims to present a brief background in the general field of kin recognition studies in order specifically to draw attention to advances in kin recognition in plants and to stimulate increased research in this budding area.

Kin recognition: the basics

The natural world is harsh and the ability to recognize kin can give an organism an advantage to survive and reproduce. Kin recognition, having many nuanced definitions,
can be described as the ability to differentiate related members of the species from non-related members, ‘regardless of the mechanism or evolutionary function’ and has primarily been described in animal species (Penn and Frommen, 2010). One of the most common kin recognition mechanisms is phenotype matching (also known as the ‘arm pit effect’). Phenotype matching occurs when an individual compares phenotypic cues from another in the population to their own to determine kinship. The primary example of phenotype matching is demonstrated in the major histocompatibility complex (MHC) which is known to control the immune response. However, the MHC has shown some bearing on mating preferences in frogs, fish, mice, and humans, through the promotion of heterozygosity and therefore promoting kin avoidance (Penn and Potts, 1998; Penn et al., 2002; Penn and Frommen, 2010). The concept of recognition alleles (also known as ‘Green beard genes’) which is very similar to phenotype matching recognition, describes unique genes that are able to recognize other individuals carrying the same gene within a population and behave altruistically towards the individuals (Brown and Buckling, 2008; Penn and Frommen, 2010). Green beard genes have been most highly represented in microbes. Both slime mould (Dictyostelium discoideum) and yeast (Saccharomyces cerevisiae) carry the Green beard genes csaA and FLO1, respectively; these genes allow for binding of cells that carry the same gene, while preventing cheaters from taking advantage of their survival tactic (Meidjibadi et al., 2006; Smukalla et al., 2008). Since a Green beard gene is considered to be unique, it is highly likely that another individual carrying this gene would be related as general population sizes and dispersal may be low for many organisms (Brown and Buckling, 2008; Penn and Frommen, 2010).

For the above kin recognition mechanisms to occur, several events between individuals of a species must transpire. First, some type of kinship signal such as a marker or cue must be expressed or produced by a ‘sender’. These signals are highly variable between different species, for example, ants have been found to recognize their young through secreted chemicals, whereas many bird species such as penguins and bank swallows recognize their young through unique calls (Waldman, 1988). Second, a ‘receiver’ from the population must perceive or detect the kinship signal and determine if the signal and receiver are a match. Finally, a decision is made by the receiver whether to take an action that will result in the differential treatment of kin, this is known as kin discrimination or kin bias (this may be subject to the cost of the action in a given environment or stress situation; see Hamilton’s rule below) (Hamilton, 1964; Hauber and Sherman, 2001; Liebert and Starks, 2004; Starks, 2004; Lihoreau and Rivault, 2008; Penn and Frommen, 2010).

From this recognition an interaction is frequently motivated by co-operative or altruistic behaviours. Altruistic behaviours aim to benefit a population as a whole, however, at a cost to individual(s) within a given population. According to Hamilton (1964), an altruistic trait will evolve when the benefits to related individuals (dependent upon the degree of relatedness) outweighs the direct costs to the individual (Hamilton’s rule: $r \times b > c$; $b$ is the benefit, $r$ is the relatedness of the individual, and $c$ is the cost of the altruistic trait expression) (Hamilton, 1964; Platt and Bever, 2009). The common frog (Rana temporaria) has been found to grow larger when raised with kin versus being raised in mixed populations in a low tadpole density (favourable conditions) however, when the tadpole density increased (unfavourable conditions) there was no change in the size between frogs reared with kin versus mixed populations (Pakkasmaa and Laurila, 2004). Under these stressful conditions, the cost of survival was too high for expression of kin discrimination. Therefore, the survival benefits of kin discrimination must have a greater effect on the population versus the costs of the recognition and subsequent bias for it to be evolutionarily successful. Also, important as it is for kin recognition to allow altruistic interactions, it is equally important for many species to recognize kin to prevent competitive interactions between closely related individuals.

So what general knowledge can we take from animal and microbe kin interactions and transfer it to aid in the understanding of plant species kin interactions? First, kin recognition does not need to imply a mechanism, simply be observed, and kin recognition does not always lead to kin bias. Second, kin recognition requires a signal in one individual and a receptor in another member of the population for kinship to be determined. Next, kin recognition does not have to imply a positive or altruistic interaction. Finally, kin recognition and kin bias/discrimination mechanisms are as diverse as the number of species and kin bias may only be expressed by individuals under favourable survival conditions.

**Interspecies plant-plant communications**

Studies in kin recognition in animals have been described for many decades, however, kin recognition in plants has only recently come to the attention of biologists and many are sceptical that plants could possess such a sophisticated trait. Plants, however, have been evolving for millions of years and are subject to many of the same situations as animal species, such as competition for resources and production of offspring, and have evolved many advanced mechanisms for survival that are described below.

Parasitic plants, often completely dependent on their host for survival, have evolved mechanisms for sensing and locating their hosts. Sorghum, maize, and pearl millet secrete strigolactones into the soil which attract the parasitic Striga to their location (Awad et al., 2006; Runyon et al., 2006; Lopez-Raez and Bouwmeester, 2008). In addition, Cuscuta pentagona has the ability to recognize volatile organic compounds (VOCs) from the host tomato and, as a result, directs its growth accordingly in order to locate the host plants (Runyon et al., 2006). In addition, some plant species participate in more positive interaction with nearby plants, such as in warning other members of their population.
during a time of stress. Maize (*Zea mays*) has been shown to emit (Z)-3-hexen-1-ol (Z-3-ol) in response to leaf damage which may help to prime surrounding plants in order to prevent a herbivore attack (Rutherford and Kleier, 2005; Heil and Bueno, 2007; Heil and Karban, 2010). These examples of interspecific and intra plant–plant interactions illustrate how the emission of a chemical signal from one plant in a community can determine the growth patterns or chemical production in another plant.

Pollen self-incompatibility is a phenomenon well described in plants and allows plants to somewhat control their partners in genetic contribution to offspring by preventing fertilization when male and female gametes share the same haplotypes. This mechanism is controlled by a single gene (S locus) with multiple alleles where pollen expressing the same allele as the stigma is rejected either through ribonuclease or protein interactions, depending on the species (McClure et al., 1989; Jordan et al., 2000; Snowman et al., 2002). Often the rejected pollen was contributed by a related plant sharing the allele or by the plant itself; therefore, negative effects of inbreeding can be avoided. This recognition method is highly represented in angiosperms with estimates of up to 50% of the flowering plants (Igic and Kohn, 2006). In addition, it has been shown in *Arabidopsis thaliana* (plants that are self-compatible) that non-random mating occurs, favouring offspring that were fathered by a contributor from a different accession rather than the same accession as that of the mother (Carlson et al., 2009). Therefore, despite the fact that plants are sessile, they do not necessarily have to produce offspring with any random pollen that happens to land on the pistil.

As mentioned previously, plants interact with other plant species through a variety of mechanisms including allelopathy, in which one plant will secrete a chemical into the soil to prevent growth or to kill another plant. Recently, it was discovered that the extremely invasive *Phragmites australis* secretes gallic acid into the surrounding soil as a phytotoxin to kill nearby native plants (Rudrappa et al., 2007, 2009). It has also been speculated that *P. australis* secretions can recruit rhizobacteria to aid in their phytotoxicity (Rudrappa and Bais, 2008; Bains et al., 2009). A recent study shows again that biochemical processes are highly important for promoting plants’ ability to recognize and respond to other organisms. In an interesting work, Broz et al. (2010) showed that *Centaura stoebe*, an exotic invasive weed, may modulate its defensive strategy in response to different plant neighbours. In conspecific cultures, *C. stoebe*, grown with other *C. stoebe*, plants up-regulated their defence response as compared to cultures with heterospecific neighbours (Fig. 1). These results suggest that an individual *C. stoebe* plant can change its defensive strategy based on the identity of plant neighbours. This strategy is likely to have important consequences for individual and community success. These recent studies allow us to speculate that plants grown in a conspecific community may be more resistant to pathogen attack compared with when grown in a heterospecific environment. Although the conspecific cultures of *C. stoebe* were not reared as siblings, it would be interesting to determine if the defence and biochemical strategy of plants may shift in a kin versus conspecific environment. The results from all of these studies suggest that invasive plant species have clearly evolved mechanisms to control its plant neighbours in an effort to monopolize the territory and available nutrients.

Yet another study reveals and validates that plants are capable of integrating information related to nutrients and neighbours. Cahill et al. (2010) showed that an annual plant, *Abutilon theophrasti*, shows a differential response towards the presence of a competitor and heterogeneous resource distributions (Fig. 1). Plants sensing neighbours and grown in uniform soil nutrient distributions exhibited reductions in rooting. By contrast, plants with competitors and heterogeneous soil nutrient distributions reduced their root growth only modestly (Cahill et al., 2010). These data, although conflicting with the data from Broz et al. (2010), indicate that plant responses to its neighbours are heavily governed by the availability of the nutrient resources in soil.

From the many examples of plant–plant communications, it is clear that plants actively participate in the shaping of their communities. These communications can be harmful to one, or beneficial to both plants and, given the diversity of these interactions, is it hard to consider that plants may be interacting specifically with their kin? One can speculate that it would be very beneficial for plants to be able to recognize their kin versus non-kin for situations such as to alert relatives of herbivore or pathogen attack, prevent competition for resources between kin or to recruit beneficial bacteria or fungi.

**Kin recognition in plants**

Before kin recognition studies came to light, self/non-self recognition in plants was examined. Mahall and Callaway examined the response of desert shrub roots (*Ambrosia dumosa*) to roots from the same plant, roots from a different plant from the same population, and roots from a clone. It was found that desert shrub root growth was inhibited if it came across a root from a different individual or from a clone but not when it came across roots from the same plant (Mahall and Callaway, 1991, 1992, 1996). In further experiments, it was found that the desert shrub does not recognize shrub roots from a different genotype (different population) therefore, the self/non-self recognition only occurs with closely related plants (Mahall and Callaway, 1992, 1996). One self/non-self recognition study in peas determined that root behaviour between two separate plants differed from that when in contact with detached clones and, further, that behaviour towards attached non-clones was intermediate of the previous behaviours suggesting that self/non-self and kin/non-kin recognition may exist (Falik et al., 2003).

As previously mentioned, Dudley and File (2007), examined the root growth of sea rocket (*Cakile edentula*). When grown in pots, sea rocket increased root allocation in the presence of strangers versus when in the presence of kin.
Inspired by this study, Biedrzycki et al. (2010) examined kin recognition in Arabidopsis thaliana (Fig. 1). Here, A. thaliana plants were grown in individual wells of tissue-culture plates in liquid growth media. Plants were kept in their own well or switched into a well that had previously contained a kin or stranger plant every day for 7 d (Biedrzycki et al., 2010). The results supported the findings of Dudley and File (2007), in that A. thaliana plants exposed to stranger secretions produced more lateral roots than those exposed to kin secretions (Biedrzycki et al., 2010). This change in root growth in response to relatedness of neighbours supports the theory that, at least some plants, are indeed able to identify other plants of the same species based on their relatedness. The results from Biedrzycki et al. (2010) also indicated that self/non-self recognition may be through a different mechanism as plants exposed only to their own secretions had a longer primary root length than plants exposed to kin or stranger secretions. Further, Biedrzycki et al. (2010) added sodium orthovanadate (Na$_3$VO$_4$), a root secretion inhibitor, to plants grown exposed to their own kin or stranger secretions. Addition of this root secretion inhibitor abolished the change in root growth between plants exposed to strangers indicating that root secretions (secondary metabolite compounds released by plant roots into the soil) are at least partially responsible for kin recognition in A. thaliana.

In another study, Murphy and Dudley (2009) examined kin recognition in Impatiens pallida (Murphy and Dudley, 2009). In contrast to the previous studies which showed that below-ground neighbours responded to kin or strangers by altering the growth of underground traits, this experiment illustrated that below-ground kin or stranger neighbours may also influence above-ground traits. I. pallida increased allocation in stems and leaves rather than to roots by increasing plant height and number of branches when grown in the presence of strangers versus being grown in the presence of kin (Murphy and Dudley, 2009). This difference in competitive traits and how species respond
differently to kin and strangers mirrors the differences in mechanisms and responses found in animals species kin recognition.

Although the above studies illustrate kin recognition patterns in plants, results indicating a clear evolutionary trade-off have been difficult to pinpoint. However, Karban and Shiojiri (2009) have demonstrated that sagebrush (Artemisia tridentata) emits VOC cues to surrounding neighbours as a result of wounding or herbivory (Masclaux et al., 2010). Interestingly, sagebrush plants that received the VOC cues from self-cuttings were damaged less than plants that were signalled by non-self cuttings (Karban and Shiojiri, 2009). This study is the first to demonstrate clearly a tangible benefit for plants interacting with kin versus with non-kin plants.

As mentioned previously, kin recognition mechanisms and motivations in animal and bacterial species are highly diverse and may or may not be present in a species. Further, this kin recognition may not lead to any kin bias or discrimination or may only lead to kin bias under favourable conditions. Other recent studies by Masclaux et al. (2009) and Milla et al. (2009) have refuted the possibility of kin recognition in plants because they did not find sufficient evidence of changes in plant growth or reproductive fitness in their studies. However, one can hypothesize that, since diversity in kin recognition is present among animal species and in given environments, this diversity also exists in plant species.

**Future directions**

Further research into the field of plant kin recognition will aid in better understanding of plant–plant communications and of plant evolution, in general. Identification of additional plant species with the ability to recognize kin, especially among crop species, tree varieties or perennial species would prove very exciting. Investigation of the mechanisms and signalling components involved in kin recognition, including root secretions and volatile emissions, will be crucial and may also have implications on plant interactions on a larger multitrophic scale. Continued studies and explorations are needed to help bring this growing field out of the fog.

**References**


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