Kin discrimination in allelopathy and consequences for agriculture

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Abstract

Recent research has shown that plants can distinguish genetically-related individuals from strangers (kin recognition) and exhibit more cooperative behaviours towards these more related individuals (kin discrimination). The first evidence for this was found when Cakile edentula plants growing with half-sibs allocated relatively less biomass to roots than plants growing with unrelated individuals, indicating that kin recognition can reduce the intensity of competition (Dudley & File, 2007). Since then, kin discrimination has been shown to result in reduced competition for soil resources (Semchenko, Saar, & Lepik, 2014), light (Crepy & Casal, 2015) and pollinators (Torices, Gómez, & Pannell, 2018). On the other hand, allelopathy, plants producing chemical compounds that negatively affect performance of neighbour plants, has also been widely documented (Inderjit & Duke, 2003) and shown to profoundly affect local species coexistence and plant community structure (Meiners, Kong, Ladwig, Pisula, & Lang, 2012). In crops allelopathy can also be beneficial in suppressing weeds (Macías, Mejías, & Molinillo, 2019). In the current issue, Xu, Cheng, Kong, and Meiners (2021) published the first study to show that kin discrimination can also affect the balance between direct competition for resources and allelopathy, and this together may lead to improved weed suppression in rice.

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Recent research has shown that plants can distinguish genetically-related individuals from strangers (kin recognition) and exhibit more cooperative behaviours towards these more related individuals (kin discrimination). The first evidence for this was found when *Cakile edentula* plants growing with half-sibs allocated relatively less biomass to roots than plants growing with unrelated individuals, indicating that kin recognition can reduce the intensity of competition (Dudley & File, 2007). Since then, kin discrimination has been shown to result in reduced competition for soil resources (Semchenko, Saar, & Lepik, 2014), light (Crepy & Casal, 2015) and pollinators (Torices, Gómez, & Pannell, 2018). On the other hand, allelopathy, plants producing chemical compounds that negatively affect performance of neighbour plants, has also been widely documented (Inderjit & Duke, 2003) and shown to profoundly affect local species coexistence and plant community structure (Meiners, Kong, Ladwig, Pisula, & Lang, 2012). In crops allelopathy can also be beneficial in suppressing weeds (Macías, Mejías, & Molinillo, 2019). In the current issue, Xu, Cheng, Kong, and Meiners (2021) published the first study to show that kin discrimination can also affect the balance between direct competition for resources and allelopathy, and this together may lead to improved weed suppression in rice.

Xu et al. grew target plants of two rice cultivars known to be both allelopathic and capable of kin recognition, with four different neighbour-plant treatments in order of decreasing relatedness: neighbours being of the same cultivar, a genetically closely-related cultivar, a genetically more distant cultivar but of the same ecotype ('indica') or of a different type ('japonica'). They explored: root allocation, allelopathy, weed suppression and biomass production of target plants in these treatments. They found that plants grown with neighbouring rice plants of the same cultivar or a closely-related cultivar allocated their roots less towards neighbouring rice plants but more towards weeds, with a consequence of greater suppression of the weeds. This showed that kin interaction could lead to reduced intraspecific and more effective interspecific competition, consistent with results from wild plants Semchenko et al. (2014). However, results for allelopathy were less clear. Rice plants produced less allelochemicals when growing with neighbours of a closely-related cultivar than when growing with less related ones, but produced the highest level when growing with neighbours of the same cultivar. This indicates that the pattern through which kin recognition may affect allopathy is still unclear. Moreover, despite of the differences in root allocation, allelochemical production and weed suppression among treatments, there was no clear pattern in grain production of rice plants across treatments. This could imply that weed suppression did not contribute to yields. It could also be that more related individuals being phenotypically more similar competed more intensively for e.g. light, a phenomenon known as kin competition (Platt & Bever, 2009), so that positive kin cooperative effects and negative kin competitive effects compensated each other in their effects on yield (Anten & Chen, 2021).

Implications for ecological weed control in agricultural crops

Farmers generally aim to maximize performance (e.g. yields or resource-use efficiency) at the crop stand (hence, plant population) level. This may be in conflict with the fact that in dense vegetation natural selection favours the most competitive plants rather than those maximizing group performance (see Anten & Vermeulen 2016; Denison, 2011). As kin selection can lead to more cooperative traits in plants and greater group performance, its potential use in crop breeding could be considered (Anten & Chen, 2021; Murphy, Van Acker, Rajcan, & Swanton, 2017). The results of Xu et al. are particularly interesting in this regard. Among all biotic stress types (i.e. pathogens, pests and weeds), weeds have the largest potential for yield reduction (larger than the other two stress types combined) (Oerke, 2006). Chemical control of weeds is coming under increasing pressure due to concerns about their health- and environmental impacts and increasing herbicide resistance of weeds. This in turn, has led to an increased interest in ecological weed control, of which development of weed-suppressive crops can be an important part (Bastiaans, Paolini, & Baumann, 2008). Thus, if kin discrimination can reduce intraspecific competition among crop plants in favour of interspecific competition with weeds as shown by Xu et al., this could be part of a strategy for ecological weed control.

The question however is whether kin selection is the most effective means of obtaining cooperative crop types. Conceptually, kin discriminating plants can be considered as facultative co-operators, that is, they exhibit cooperative behaviours only in the presence of kin and not in the presence of non-kin. In a crop variety mixture such a facultative co-operator may do worse than an obligate co-operator, i.e., a crop type that expresses cooperative behaviours irrespective of whether it interacts with kin or non-kin (Anten & Chen, 2021). Thus, the question arises whether preferential root placement towards the roots of weeds rather than towards con-specific crop plants could also be selected as a constitutive trait.

Quantifying benefits of kinship dependent variation in allelopathy

Plants produce a wide variety of allelopathic compounds which can have negative effects on con-specific plants or negative effects on hetero-specific plants, the former also being called autotoxicity. Autotoxicity has been documented in a wide variety of plants and is thought as a mechanism to avoid local intraspecific competition and thus ensure a greater spatial and temporal seed dispersal (Singh, Batish, & Kohli, 1999). It is also well documented in several crops including rice (Singh et al., 1999) and is believed as an important cause of yield reductions in continuous mono-cropping (i.e., growing the same crop on a field year after year, Chi et al., 2013). Xu et al.'s finding of reduced allelopathic activities in rice plants only interacting with closely-related-cultivar neighbours may suggest this reduction to reflect a kinship-selected cooperative strategy avoiding auto-toxic effects on kin. However, this raises the question why the highest allelopathic

activities were found in plants interacting with neighbours of the same cultivar (i.e., the treatment with the greatest degree of neighbour relatedness).Recent research has shown for wheat that plants may produce allelochemicals in response to exudates produced by neighbours, particularly loliolide and jasmonic acid (Kong et al., 2018). It is possible that such signalling also occurs in rice and that it differs between cultivars, independently of relatedness, and that the two focal cultivars in Xu et al. (2021) may have happened to be active producers of such signalling compounds. Clearly, more research is needed to better understand the possible connection between kin recognition and allopathy.

Towards a quantitative approach to research on kin recognition

Since the first documentation if kin recognition in plants (Dudley & File, 2007), and despite of mounting interest on this topic, there is still no consensus on how to define the distinction between 'kin' and 'non-kin'. Many studies, especially those on wild species, reserve the word 'kin' for plants sharing the same mother, being either sibs or half-sibs (e.g. Lepik, Abakumova, Zobel, & Semchenko, 2012; Semchenko et al., 2014; Torices et al., 2018). But several studies with crop species also categorise kin and non-kin at the cultivar or variety level (e.g. Pezzola, Pandolfi, & Mancuso, 2020), while studies using the model species *Arabidopsis thaliana* separate kin and non-kin at the accession level (e.g, Biedrzycki, Jilany, Dudley, & Bais, 2010; Palmer et al., 2016). This variation in definition makes it difficult to compare results across studies, and could explain some of the discrepancies between different studies. Moreover, most studies on kin discrimination simply compare trait values and performance between discrete kin- and non-kin groups, often without actually quantifying the level of genetic relatedness (but see Karban, Shiojiri, Ishizaki, Wetzel, & Evans, 2013 and Xu et al., 2021 as notable exception). As kinship describes the extent of genetic similarity between individuals, it is rather arbitrary to categorise this relationship. We therefore propose that kinship should be expressed as a continuous quantitative measure in terms of genetic relatedness.

Furthermore, the level of replication at the genotypic is often insufficient (rarely more than 10 genotypes) to determine robust correlations of trait expression at different levels of relatedness. To our opinion addressing questions about kin discrimination and its consequences for agricultural or fitness entails firstly quantifying genetic variation in kin discrimination within a sufficiently large population of plants, and secondly, determining whether this variation correlates positively with performance in kin groups. We thus urge for a broader quantitative genetic approach to the research on the selection effects of kin recognition.

Keywords : allelopathy, Darwinian agriculture, ecological weed control, interference competition, kin recognition, rice

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Data availability

The paper did not use data.

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