COMMENTARY

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Kin discrimination in allelopathy and consequences for agricultural weed control

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Among all biotic stress types (i.e., pathogens, pests and weeds), weeds have the largest potential for yield reduction (larger than the other two combined) (Oerke, 2006). Chemical control of weeds is under increasing pressure due to concerns about its health- and environmental impacts, and increasing herbicide resistance of weeds. As a consequence, there is an increased interest in ecological weed control, of which the development of weed-suppressive crops can be an important part (Bastiaans, Paolini, & Baumann, 2008). In the current issue, Xu, Cheng, Kong, and Meiners (2021) for the first time, show that kin recognition (the ability of plants to distinguish genetically related individuals from strangers) can make rice plants more competitive against weeds potentially being a new strategy in ecological weed control.

Recent research has shown that plants are capable of kin recognition and may hence exhibit more cooperative behaviours towards genetically more related individuals (positive kin discrimination). The first evidence for this was found when *Cakile edentula* plants growing with half-siblings 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 the 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).

Xu et al., for the first time, showed that kin recognition can also affect the balance between direct competition for resources and allelopathy, and this together may lead to improved weed suppression in rice (Figure 1). They grew target plants of two rice cultivars, known to be both allelopathic and capable of kin recognition, with four different neighbour-plant treatments in the order of decreasing relatedness, neighbours being: 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 four distinct traits: 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 these neighbours but more towards weeds, with a consequence of greater suppression of the weeds. This directional root growth showed that kin interaction could lead to reduced intraspecific competition and more effective interspecific competition, consistent with results from wild plants (Semchenko et al., 2014). However, the results for allelopathy were ambiguous. 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 disparity indicates that the pattern through which kin recognition affects allopathy is still unclear. Moreover, despite the differences in root allocation, allelochemical production and weed suppression among treatments, there was no clear pattern in grain production of rice plants across all treatments implying

Neighbour rice plant   Focal rice plant   Weed

(a) from the same cultivar

(b) from a closely related cultivar

(c) from a more distant cultivar

The allelopathic activity of focal plants as indicated by the shades of grey
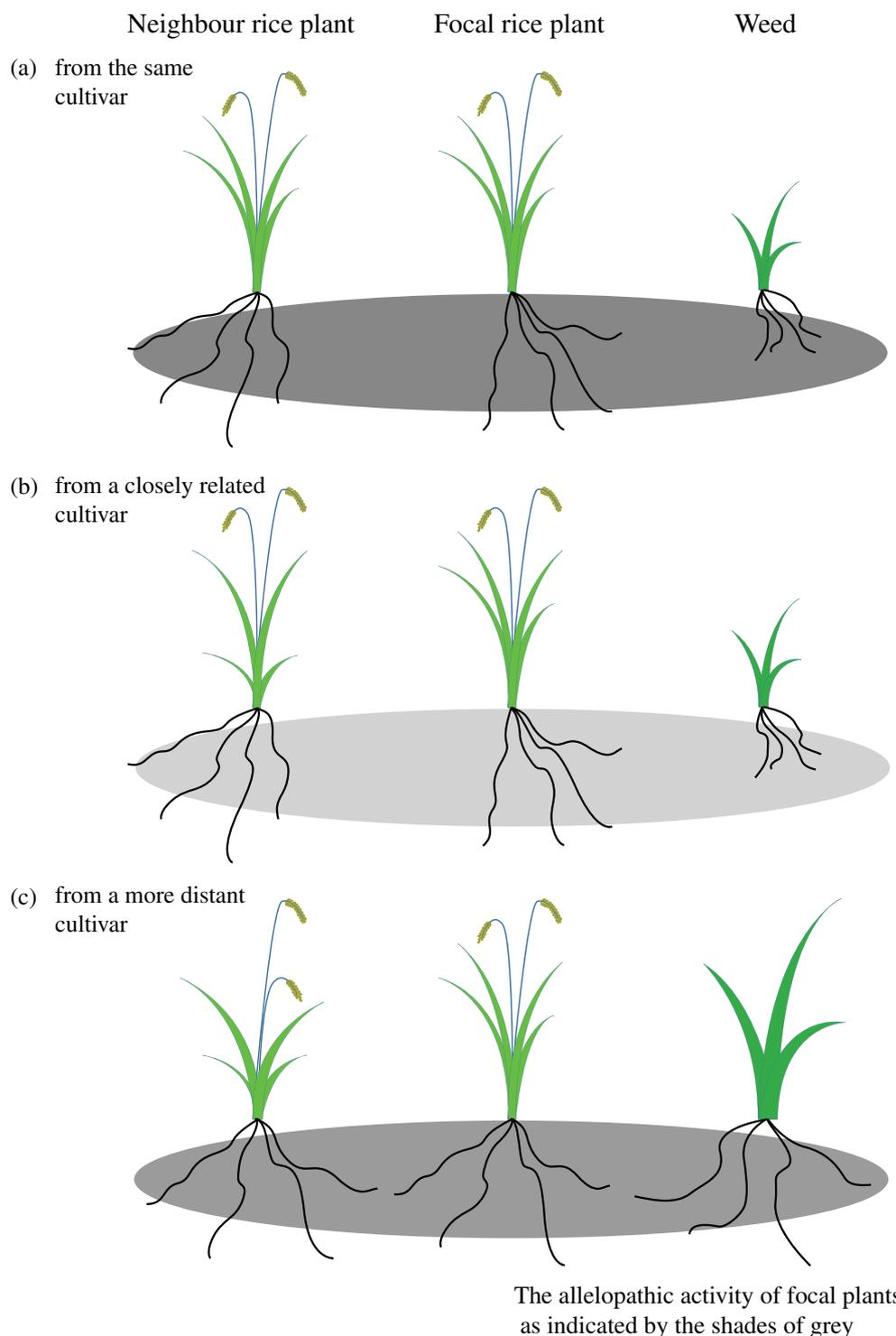
FIGURE 1   The directional root growth towards weeds and allelopathic activity (or allelochemical productivity) of rice plants grown with neighbouring rice plants of (a) the same cultivar, (b) a closely related cultivar and (c) a more distant cultivar, and the consequences of suppression effect on weed growth. The shades of grey ellipses in the root zones indicate the allelopathic activity of focal plants [Colour figure can be viewed at wileyonlinelibrary.com]

that weed suppression did not contribute to yields. Alternatively, the more related individuals, being phenotypically more similar, probably competed more intensively for example for light, a phenomenon known as kin competition (Platt & Bever, 2009). In effect, the positive kin cooperative outcomes and the negative kin competitive outcomes may have compensated each other for their impacts on yield (Anten & Chen, 2021).

1 | IMPLICATIONS FOR ECOLOGICAL WEED CONTROL IN CROPS

Farmers generally aim to maximize performance (e.g., yields or resource-use efficiency) at the crop stand (hence, plant population) level. This strategy 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). Most research on the role of kin recognition in increasing crop yields focussed on reducing intra-specific competition and more allocation to harvestable plant parts. Xu et al. showed that in addition kin recognition may also contribute to weed suppression.

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, that is, 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.

2 | VARIATION IN ALLELOPATHY DETERMINES THE BENEFITS OF KINSHIP

Plants produce a wide variety of allelopathic compounds that 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 of as a mechanism to avoid local intraspecific competition to ensure a greater spatial and temporal seed dispersal (Singh, Batish, & Kohli, 1999). It is well documented in several crops including rice (Singh et al., 1999) and is considered to be 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 grown next to closely related-cultivar neighbours may suggest a kinship-selected cooperative strategy to avoid auto-toxic effects on kin. However, this behaviour raises the question of why the strongest 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 that wheat 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. More research is needed to better understand the possible connection between kin recognition and allelopathy.

3 | TOWARDS A QUANTITATIVE APPROACH TO INVESTIGATE KIN RECOGNITION

Since the first documentation of 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 siblings or half-siblings (e.g., Lepik, Abakumova, Zobel, & Semchenko, 2012; Semchenko et al., 2014; Torices et al., 2018). But several studies with crop species also categorize kin and non-kin at the cultivar or variety level (e.g., Pezzola, Pandolfi, & Mancuso, 2020; Yang, Li, Xu, & Kong, 2018), while studies using the model species *Arabidopsis thaliana* separate kin and non-kin often 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 it 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 a notable exception). As kinship describes the extent of genetic similarity between individuals, it is rather arbitrary to categorize this relationship. We therefore propose that kinship should be expressed as a continuous quantitative measure in terms of genetic relatedness.

Furthermore, the degree of replication at the genotypic level 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 (a) quantifying genetic variation in kin discrimination within a sufficiently large population of plants, and (b) determining whether this variation correlates positively with performance in kin groups. We thus urge for a broader quantitative genetic approach to investigate the selection effects of kin recognition.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
This paper did not use any data.

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