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1 Introduction

Farmers and agricultural scientists are facing a major challenge to ensure food security for the rapidly growing world population through sustainable crop production practices. Both the challenges of demographic pressure and environmental ecology require innovative and smart solutions to counteract further negative consequences in the future, despite the current difficulties in reconciling these goals (Gaffney et al., 2019).

Weed management is the most representative example of this apparent discrepancy, since the use of chemical herbicides is a cheap and practical solution that has guaranteed farmers weed-free plots for the past 50–70 years. However, the continued use of herbicides is a debatable issue, given their detrimental impacts on the environment and the potential consequences on animal and human health. Today, social and political pressures are mounting to either withdraw them from the market or restrict their use (Barzman and Dachbrodt-Saaydeh, 2011). For example, the Swiss population voted in June 2021 in two popular initiatives aiming at limiting and even banning the use of synthetic pesticides in agriculture: the initiative for clean drinking water and the

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initiative for a synthetic pesticide-free Switzerland (Schmidt et al., 2019). The alternative means of weed control, as part of integrated weed management (IWM) strategies, is a key objective. The phenomenon of allelopathy is a promising avenue in this regard.

The term 'allelopathy' can be defined as the inhibitory or stimulatory effect of one plant on another via the production of chemical compounds (called allelochemicals) and their release into the environment (Rice, 1984). In general, there are two plant partners: the donor plant, which produces and releases the allelochemicals, and the receiver plant, which is the plant 'responding' to the released compounds. It appears that all plants release compounds into the environment, but the responses of the receiver plants to the release of allelochemicals are difficult to characterise, especially while categorising them in terms of 'negative' or 'positive' to fit the common definition of allelopathy. Some plants release compounds into the environment with variations caused by various parameters such as diffusion distance, quantity, chemical composition, and organ localisation. Indeed, the adaptation to neighbouring plants requires a high level of plasticity in wild plants, and to define the contribution of allelopathy in terms of the expression of plastic trait responses is challenging (Callaway et al., 2003; Uesugi et al., 2019).

The precise definition of allelopathy has been the subject of controversy with many opinions depending on a scientific background, an idea that holds true for the authors of this paper (plant molecular biologist, plant ecophysiologist, plant biotechnologist and agronomist). The challenge is indeed to reconcile different scientific approaches in a multidisciplinary future model on how allelopathy could contribute to IWM with effective and long-lasting solutions for a farm that should operate as a profitable economic entity. From the perspective of a biologist interested in chemical ecology, there is a need to understand plant–plant interactions, especially between crops and weeds, to promote interactions that are neither positive nor negative but may result in environmental adaptation such as niche differentiation. In addition, it is essential to identify new allelochemicals that show significant efficacies on weeds as alternatives for chemical herbicides. Moreover, from an agronomical perspective, it is important to focus on the underlying principles of the allelopathic crop–weed interactions that could contribute to future weed control in the field. It is also important to remind the reader to consider all factors carefully when selecting crops with the allelopathic potential to manage the likely high expectations from farmers and even agricultural advisors for high-yielding weed-suppressive crops.

In line with these priorities, the chapter covers two topics. In Section 2, we discuss allelopathy in crop–weed interactions while the second part focuses on the practical aspects of allelopathy with reference to IWM. Section 3 includes a detailed discussion on the research findings on buckwheat (*Fagopyrum*

esculentum), as our research group has studied its potential allelopathic properties during the past ten years.

2 Understanding allelopathy in crop–weed interactions

2.1 Allelochemical classes and plant defence

Considering allelochemicals from an evolutionary viewpoint shows that allelopathic compounds have high structural diversity with a wide degree of multi-functionality. Most allelopathic compounds are secondary metabolites, and as by-products of primary metabolism, they are not directly involved in plant development. The production of secondary metabolites requires an expenditure of energy and resources with functions in signal transduction and defence that contribute to the adaptation of plants to their environment (Bourgaud et al., 2001; Wink, 2003).

Wink (2003) stated that the production of allelochemicals by plants should be understood as the optimisation of plant resources to control a wide range of potential enemies. For example, gramine is an alkaloid produced by barley (*Hordeum vulgare*), and its efficacy and toxicity have been demonstrated on fungi (Wippich and Wink, 1985; Matsuo et al., 2001), bacteria (Sepulveda and Corcuera, 1990), mammals (Gallagher et al., 1964; Goelz et al., 1980), insects (Corcuera, 1984) and plants (Liu and Lovett, 1993; Kremer and Ben-Hammouda, 2009).

The example of rice (*Oryza sativa*) illustrates the complexity of allelochemical induction and the possible functions of allelochemicals (Fig. 1). The diterpenoids momilactone A and B were first identified in rice husk and were subsequently found to be secreted from the roots of various rive cultivars (Kato-Noguchi and Ino, 2003; Kato-Noguchi, 2008; Kong et al., 2004; Kato et al., 1973). Momilactone synthesis is induced by various external stimuli such as the phytohormone jasmonic acid (JA) (Yoshida et al., 2017), UV light (Kato-Noguchi et al., 2007a), root exudates (Zhang et al., 2018a), drought and salinity (Xuan et al., 2016), soil microorganisms (Xie et al., 2017) and elicitors from insects and fungi (Wari et al., 2019; Schmelz et al., 2014), suggesting that they might be critical compounds in stress tolerance. The induction of momilactones is associated with plant responses in two categories: physiology and defence. They probably protect plant leaves against UV light (not demonstrated) and preserve seed dormancy in rice husks (Kato et al., 1973). Moreover, they are implicated in the growth inhibition of neighbouring plants (Kato-Noguchi and Peters, 2013). Momilactone A is accumulated at higher concentrations upon fungal infections. Various mutant rice lines that over-accumulate momilactone A showed increased resistance to pathogenic fungi *Magnaporthe grisea*, *Rhizoctonia solani*, *Blumeria graminearum* and *Fusarium oxysporium* and pathogenic microbes *Xanthomonas oryzae* (Sawada et al., 2004; Mori

Stimulus

Hormonal
- Jasmonic acid

Abiotic
- UV light
- Root exudates of barnyard grass
- Drought and salinity

Biotic
- Soil microorganisms
- Elicitors from insects and fungi

Momilactone
A and B
production

Plant responses

Physiological
- Protection against UV light
- Seed dormancy in rice husk

Defense
- Growth inhibition in neighboring plants
- Against pathogenic fungi
 (*Magnaporthe grisea*, *Rhizoctonia solani*,
 Blumeria graminearum,
 Fusaria oxysporum)
- Against pathogenic microbes
 (*Xanthomonas oryzae*)

?

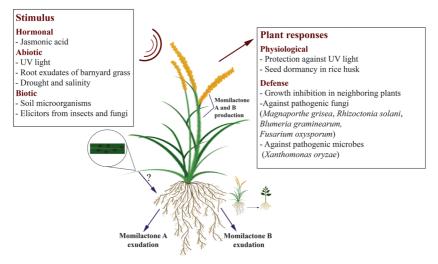Momilactone A
exudation

Momilactone B
exudation

Figure 1 The induction of momilactone production and subsequent plant responses in rice.

et al., 2007; Hasegawa et al., 2010; Kurusu et al., 2010; Gu et al., 2019) While momilactone B has a higher allelopathic activity, momilactone A has a higher activity against fungal pathogens (Kato-Noguchi and Peters, 2013).

In terms of the structural diversity of allelochemicals, many chemical classes can be identified, from alkaloids (Liu and Lovett, 1993) to terpenoids (Kato-Noguchi and Peters, 2013), phenolics (Li et al., 2010), quinones (Dayan et al., 2010) and flavonoids (Weston and Mathesius, 2013; Huang et al., 2015). A wide range of modes-of-action belong to these chemical classes, and the authors would like to refer to other references for an overview of the exhaustive list of mechanisms and targets of the different allelochemicals (Reigosa et al., 2006; Dayan and Duke, 2014).

2.2 Production of allelochemicals

Plants are sessile organisms coping with changing environmental conditions that affect their growth and survival, but with the ability to integrate signals and adapt to changes in resource supply. Plants collect information from their belowground and aboveground environments with regard to nutrient availability and light and can detect chemical cues such as volatile compounds, leachates and root exudates (Wang et al., 2021).

The production of allelochemicals in living plants is an inducible process, except for the release of allelochemicals during residue degradation (decaying plant material). It is influenced by various biotic factors such as the neighbouring

plants (Hazrati et al., 2020; Hazrati et al., 2021) and their microbial underground partners, and abiotic factors from the environment such as temperature (Hess et al., 1992) and light (Dayan, 2006), while the developmental stage (Liu and Lovett, 1993) of the donor plant is also a factor of interference.

The inducible production of allelopathic compounds in a neighbouring plant is a topic that has received considerable scientific interest during the past years (Section 2.4). Molecular communication between plants is an essential component to study plant–plant interactions. Specific messenger molecules that are a part of signal transduction contribute to an integrated response at the plant level in the neighbouring plant (van Dam and Bouwmeester, 2016).

When two plants grow next to each other, the primary mechanism for the recognition of plant neighbours is through changes in light quality. For example, changes in red to far-red light ratios and the blue light caused by the neighbours can induce changes in stem and/or petiole growth as well as redirect leaf growth (Smith et al., 1990). It was also suggested to potentially affect the production of secondary molecules with allelopathic potential (Kegge et al., 2015). In sorghum (*Sorghum bicolor*), changing the wavelength of light caused variations in the levels of sorgoleone synthesised (Dayan, 2006), whereas exposure to low-intensity light can increase the level of hordenine production in barley (Lovett et al., 1994).

Plants can also produce a blend of unique volatile organic compounds (VOCs) that contribute to communication via air (aboveground compartment) and can trigger a response in receiver plants at the level of growth, reproduction and defence, with the overall result of improved resilience (Novoplansky, 2009). When barley plants were exposed to VOCs emitted by another barley cultivar, more biomass was allocated to the root (Ninkovic, 2003). In tobacco (*Nicotiana tabacum*), the perception of the volatile phytohormone ethylene is necessary to promote shade avoidance (Pierik et al., 2003).

One important route for allelopathic communication between plants is the root exudation of a wide variety of chemical compounds, including VOCs, into the rhizosphere (belowground soil compartment). In petri dish experiments, root VOCs from the bitou bush (*Chrysanthemoides monilifera* spp. *Rotundata*) negatively affected seed germination and seedling growth of different native plants from Australia (Ens et al., 2009; Jassbi et al., 2010), but the role of root VOCs as mediators of plant–plant interactions under field conditions still remains to be further investigated (Delory et al., 2016).

2.3 Rhizosphere model for belowground microbial interactions in allelopathy

In general, rhizosphere research is still very much an unknown science, which is partly due to the complexity of studying the hidden and heterogeneous

soil environment (Shelef et al., 2019). Many questions are still unanswered in terms of the mechanistic understanding and functionality of allelochemicals in the rhizosphere, such as the perception of belowground root exudates by neighbouring plants, signal transmission pathways, the effects of other rhizosphere microorganisms in signal transmission and the plants' response to various stimuli. The communication between the roots and the rhizosphere community is based on chemical compounds (van Dam and Bouwmeester, 2016; Wang et al., 2021) which are protected from degradation by oxygen and light, making belowground chemical signals more stable and possibly more reliable than those above ground (Karlovsky, 2008). However, plants produce and secrete root exudates consisting of secondary metabolites which can signal to and interfere with the other soil organisms (Venturi and Keel, 2016). Root exudates provide nutrients for the microbial community, and there is a known relationship between root exudation and enhanced microbial activity and diversity in the rhizosphere. Since root exudates are rich in organic carbon, they serve as substrate and attract microorganisms, thereby altering the chemical composition of the rhizosphere (Karlovsky, 2008; Bakker et al., 2013).

Allelopathy is a sophisticated process with various factors to consider in terms of understanding the activity of allelochemicals in the soil. Upon release into the environment, rhizospheric microorganisms affect the allelopathic interactions of root-exuded compounds through degradation mechanisms that could either improve the allelopathic interactions, by resulting in the accumulation of phytotoxic products, or render them inactive. For instance, the benzoxazinoid (BX) allelochemicals found in crops such as wheat (*Titricum sp.*), rye (*Secale cereale*) and maize (*Zea mays*) are subjected to microbial degradation in the soil. Bacterial enzymes convert DIBOA (2,4-dihydroxy-1,4-benzoxazin-3-one) to BOA (2-benzoxazolinone) and DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) to MBOA (6-methoxybenzoxazolin-2-one) through heterocyclic ring contraction, making the compounds more stable, which allows them to remain in the soil for a longer period of time. However, they are less active than their precursors (Macías et al., 2005a; Macías et al., 2005b; Schütz et al., 2019). DIBOA indirectly promotes plant fitness by attracting *Pseudomonas putida* upon pathogen attack, and this might lead to systemic defence priming in maize plants (Neal et al., 2012; Schandry and Becker, 2020).

BOA and MBOA further degrade to the aminophenoxazines APO (2-Aminophenoxazin3-one) and AMPO (2-amino-7-methoxyphenoxazin-3-one) and can also degrade to their *N*-acetyl derivatives AAPO (2-acetamido-phenoxazin-3-one) and AAMPO (2-acetamido-7-methoxyphenoxazin-3-one) through the action of non-pathogenic organisms. While AMPO was shown to have no phytotoxic effects, APO has higher phytotoxicity than BOA and DIBOA (Macías et al., 2005a). Additionally, AZOB (2,2`-oxo-l,l`-azobenzene), another

derivative of BOA, has a higher inhibiting effect on barnyard grass and garden cress than its precursor BOA (Inderjit, 2005; Chase et al., 1991; Nair et al., 1990). Soil microorganisms degrade rice flavone glycosides and the resulting products have adverse effects on microorganisms and fungi (Macías et al., 2019). Sorghum root hairs exude the weed-inhibiting allelochemical sorgoleone throughout the crop's growing season, but it undergoes mineralisation, a process that involves complete microbial degradation into inorganic compounds (Gimsing et al., 2009). The phenolic compounds such as *p*-coumaric, ferulic, *p*-hydroxybenzoic and *trans*-cinnamic acids are degraded by microorganisms that utilise the root exudates as an energy source hence influences the dynamics of plant–plant interactions.

The previous studies suggest that various compounds from different plant species either degrade at slower rates or in negligible amounts in sterile soil (Gimsing et al., 2009; Macías et al., 2005b), suggesting not only the action of root exudates but also that the microorganisms in the soil might be involved in these complex underground interactions.

In the next paragraph, a rhizosphere model shows in more detail the two-way communication involving root exudates between plant partners for various crop–weed interactions.

2.4 Allelochemical interactions in wheat, rice, buckwheat and sorghum

In this section, we illustrate how four different pairs of heterospecific neighbouring plant species perceive each other via root exudates: wheat/ different species, rice/barnyard grass (*Echinochloa crus-galli*), buckwheat/ redroot pigweed (*Amaranthus retroflexus*) and sorghum/velvetleaf (*Abutilon theophrasti*).

The possibility of wheat allelopathy was suggested a very long time ago (Schreiner and Reed, 1907) and it was reported that the roots of wheat (and other crop plants) could exude compounds that inhibit their own seedlings. It could be shown that the production of DIMBOA was induced by root exudates released from neighbouring plants (Li et al., 2016; Zhang et al., 2016) (Fig. 2). By using a mesh to avoid direct root contact between wheat and the different weed species, the allelopathic effect changed, suggesting that root contact plays a role in wheat allelopathy and might be restricted to a given weed species (Zhang et al., 2016). In addition, Kong et al. (2018) reported that wheat could respond to at least 100 plant species by producing DIMBOA and as loliolide and JA were present in root exudates from different species, it was suggested that these molecules are involved in the belowground signaling events. Wheat plants can detect, early in their development, conspecific (of their own species) and heterospecific (from different species) neighbours by these
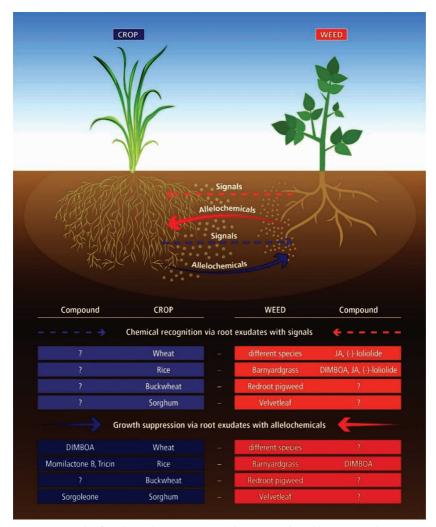
Figure 2 Examples for plant–plant interactions that are mediated by root exudates. Crops (wheat, rice, buckwheat and sorghum) can recognise chemical signals in weed (different species, barnyard grass, redroot pigweed and velvet leaf) root exudates (red broken arrow), but no information is available on crop recognition by weeds (blue broken arrow). Furthermore, crops can exudate allelochemicals to suppress weed growth (blue full arrow) and weeds might also release allelochemicals into the rhizosphere (red full arrow). The question mark (?) indicates that no compounds have been identified yet. The small dots around the roots represent soil microorganisms that might modify allelochemicals and their signals (Section 2.3).

ubiquitous signaling chemicals and subsequently increase the production of the allelochemical DIMBOA. However, in wheat, DIMBOA levels appear not to correlate well with weed inhibition, suggesting that weed suppression is caused by multiple factors.

Dilday et al. (1998) first reported the possibility of weed-inhibitory effects in the rice rhizosphere, and today a wide variety of rice allelochemicals such as momilactone A and B, phenolic acids, phenylalkanoic acids, hydroxamic acids, fatty acids, terpenes and indoles are known (Kato-Noguchi, 2008; Kato-Noguchi, 2011b), as mentioned previously in Section 2.1. It is easier to characterise rice–weed interactions since rice is grown in paddy soils, a liquid environment that helps with the collection of root exudates. Rice has the further benefit of including both allelopathic and non-allelopathic varieties, helping with the design of experimental set-ups to discriminate between allelopathic effects (see Section 3.3.2). The best-characterised example of induction strategies and plant response in rice is the rice–barnyard grass interaction. Allelopathic rice varieties can detect barnyard grass and will increase their production of allelochemicals (Kong et al., 2006; Zhao et al., 2005; Kato-Noguchi, 2011a) (Fig. 2). Barnyard grass root exudates can induce the production of rice allelochemicals (Kong et al., 2006; Yang and Kong, 2017), suggesting that signaling chemicals are present in the barnyard grass root exudates. It has been shown that DIMBOA is a signaling chemical emitted into the soil by barnyard grass (Guo et al., 2017), and the neighbouring rice will subsequently induce its own allelopathic response by increasing the secretion of the allelochemical momilactone B (Zhang et al., 2018; Kato-Noguchi, 2011a). Studies of the production of the rice allelochemicals momilactone B and tricin in the presence of different biotypes of barnyard grass have also confirmed the hypothesis that allelopathic rice detects the presence of barnyard grass through the presence of loliolide and JA in barnyard grass as signaling compounds (Li et al., 2019).

Our research efforts showed that buckwheat modifies its root exudation when co-cultivated with redroot pigweed, with a growth-repressive effect on redroot pigweed seedlings. Some of the unidentified compounds in the root exudates were only present when the two species were co-cultivated, suggesting some level of recognition between species, while the induction in buckwheat appears to be mediated by the presence of redroot pigweed (Fig. 2) (Gfeller et al., 2018b). However, the authors have not investigated the identity of the signaling compound(s) and the mechanism of the growth repression in redroot pigweed up to now. In another study where buckwheat was grown in culture solution for ten days with lettuce, a dose–response suppressive activity on root and hypocotyl elongation of lettuce seedlings was found (Kato-Noguchi et al., 2007b). Tin et al. (2009) identified caprolactam (azepan-2-one) as a candidate allelopathic molecule responsible for this type of elongation inhibition. Water extracts from buckwheat-grown soil showed significant

repressive activity on root elongation of barnyard grass and common purslane (*Portulaca oleracea*), whereas hairy galinsoga (*Galinsoga quadriradiata*), livid amaranth (*Amaranthus blitum*) and lettuce (*Lactuca sativa*) did not respond (Kalinova et al., 2005; Tominaga and Uezu, 1995). Kalinova et al. (2007) showed that soil from a buckwheat stand had significant suppressive activity against lettuce radicle elongation after three days of growth. Methanol and boiling water extracts of the same soil revealed the presence of several phytotoxic molecules that include a gallic acid derivative, palmitic acid methyl ester, vanillic acid, rutin and a 4-hydroxyacetophenone derivative, but it was not clear whether these compounds originated from root exudates, leachates or the necrotic parts of buckwheat. The authors addressed this result further by analysing the agar medium on which buckwheat was grown for 12 days, and the identified compounds included a quercetin derivative, palmitic acid, squalene, epicatechin, vitexin and very interestingly, the same gallic acid derivative that was originally present in the soil extract.

The main allelochemical of sorghum is sorgoleone, which is specific for the Sorghum genus and is synthesised by the tips of root hairs (Weston et al., 2013). Environmental factors influence sorgoleone production (Hess et al., 1992) and plant hormones like auxin can also stimulate sorgoleone synthesis (Uddin et al., 2010). A more indirect way is also through methyl-jasmonate and JA that act as plant hormones responsible for root growth and hair formation (Uddin et al., 2013). Moreover, it was suggested that sorghum seedlings can secrete sorgoleone after germination and can also respond to the presence of the neighbouring plant (velvetleaf) by releasing more sorgoleone (Dayan, 2006) (Fig. 2).

2.5 Experimental methodology and allelopathic trait selection

Most studies on allelochemicals are being conducted under laboratory conditions. To identify/quantify chemical compounds in exudates/leachates, the ideal situation is to extract these compounds under optimal and sterile conditions with minimal interference for further chemical characterisation such as mass spectrometric analyses.

The most common approaches to study allelopathy have been compared by Zhang et al. (2021). The basic idea is to identify an allelochemical or a cocktail of allelochemicals under laboratory conditions in a first step, and secondly, to design protocols for chemical detection and activity characterisation, such as persistence, under field conditions. Since a major area of agronomic interest is the discovery of weed-suppressive crops/cultivars as part of an IWM strategy, it is a prerequisite to confirm a high level of persistence and activity for a potential allelochemical under field conditions. In this regard, testing a plant extract from donor plants on different receiver plant species under controlled laboratory

conditions is the general approach in order to reach a conclusion on growth-suppressive effects. However, the demonstration of the efficacy of allelopathy is hard to confirm in the field, which is a complex ecosystem with a multitude of interactions.

One aspect to consider in the interpretation of research intended to characterise allelopathic potential is that effects due to resource competition are an integral part of allelopathy. It is almost impossible to completely separate competition from allelopathy, either under laboratory or under field conditions. Enhanced weed suppression can result from competitive advantages of the crop, such as plant height, leaf shape, leaf angle, absorption of water and nutrients, and/or growth-repressive allelochemicals that are released into the environment. Specific competitive traits like plant height or leaf angle can be determined quite easily, but monitoring water and nutrient uptake is more difficult. It is further helpful to consider allelopathy not as a measurable plant trait *per se* but a concept to illustrate the mechanisms implicated in the regulation, production, release and action of chemical compounds that affect the surrounding environment of a plant. The validation of suitable and measurable traits that reflect allelopathic potential under field conditions requires careful investigations. The traits studied for the receiver plant (ideally a weed) include features such as weed occurrence, size, biomass, seed set, different physiological traits such as chlorophyll fluorescence while for the allelopathic crop neighbour, the trait characteristics include allelochemical content in the crop and other phenotypic traits (Weidenhamer et al., 2014). In rice, the specific leaf area is correlated with rice allelopathic potential (Gaofeng et al., 2018). A fact worth mentioning is that for the farmer, the question of whether allelopathy is implicated in weed suppression is of secondary importance, as long as the desired result is achieved. However, to integrate allelopathy successfully into the weed control programmes of the future, it is essential to understand the underlying mechanisms.

2.6 Swiss case study: buckwheat

Our research group began to study the weed-suppressive effect of buckwheat almost a decade ago, after field observations in 2009 and 2010 in Switzerland showed that buckwheat field stands were basically weed free. This prompted us to follow up with a series of studies to understand the growth-suppressive properties of buckwheat on various other plants.

Our first approach tested the effects of the soil in which buckwheat had been grown (in the field and in pots) on lettuce and redroot pigweed growth, in petri dish experiments, but no growth-suppressive effects were found. In parallel, we tested the effect of water extracts from the same soil samples on lettuce growth, and this study did not identify growth-suppressive effects either. We draw the

following three conclusions: Firstly, there are either no allelopathic molecules in the soil solution (not soluble in water), or they are rapidly degraded; secondly, the growth-inhibiting effect is due to a long-term and constant exposure of small quantities of allelochemicals and; thirdly, the root must be in direct contact to mediate allelopathic effects (Gfeller and Wirth, 2015).

Further efforts were focused on dissecting the effects of resource competition from allelopathy as suggested in the literature (Falquet et al., 2015). In field trials with two shading levels, redroot pigweed biomass was similar, demonstrating that light interception by buckwheat was not the primary mechanism responsible for redroot pigweed growth suppression (Gfeller et al., 2018b).

We also developed a method to separate resource competition for water, nutrients and light from allelopathic root interactions in pot trials (Fig. 3). In these investigations, water and nutrient supply were kept constant and in sufficient amounts while the effect of shading was evaluated by the presence or absence of vertical nets, and impenetrable plastic barriers separated the rhizospheres of the weed (redroot pigweed) and the crop (buckwheat) to prevent the roots of the different plants from interacting. We found that, in the absence of shading, redroot pigweed growth was repressed by at least 65% by direct root interactions of a potentially allelopathic nature (Falquet et al., 2014). In the next step, the experimental setup was improved to study the effects of chemical diffusion. The roots of buckwheat and redroot pigweed were separated with a permeable mesh. The growth of redroot pigweed was evaluated in the presence and absence of buckwheat. The results showed that buckwheat suppressed the growth of redroot pigweed by 41% (Gfeller et al., 2018a) and 68% (Gfeller et al., 2018b) when roots were directly interacting, whereas buckwheat suppressed redroot pigweed growth by 53% (Gfeller et al., 2018a) and 46% (Gfeller et al., 2018a) without physical root interactions, probably through the diffusion of allelopathic compounds. The originality of
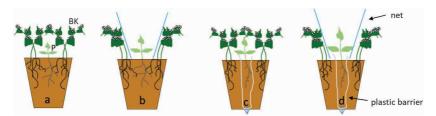

Figure 3 Experimental design of pot trials with buckwheat (BK) and redroot pigweed (P) plants. BK plants were grown on the outer sides of the pots while P was sown in the center of the pots in different conditions: without any barrier separating them (a), nets separating the aerial parts to prevent shading (b), impermeable plastic bags separating the roots of P from BK to prevent root interactions (c), both nets separating the aerial parts and plastic bags separating the roots (d). Adapted from Falquet et al. (2014).

our approach was to test the buckwheat–redroot pigweed interactions with plants and not with seedlings; and the pot trial was performed for 28 days while we followed redroot pigweed growth for 55 days in the field.

In parallel, studies to cultivate buckwheat in glass sand (Fig. 4) were performed to obtain 'clean' root exudates after extraction with methanol and further analysis by high-resolution mass spectrometry, a step that is inevitable for chemical characterisation.

We found that the BK-P root exudates inhibited redroot pigweed root growth by 49% (Fig. 5a). Moreover, the characterisation of root exudates by UHPLC-HRMS and principal component analysis (PCA) showed that BK and BK-P had different metabolic profiles (Fig. 5b). We concluded that buckwheat

Figure 4 Experimental setup of buckwheat and redroot pigweed glass sand cultures for root exudate collection. From right to left: plastic culture box filled with glass sand without any plants for control (C), containing redroot pigweed only (P), buckwheat only (BK) and buckwheat and redroot pigweed growing together (BK–P). Adapted from Gfeller et al. (2018a).
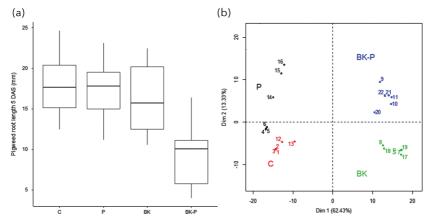

Figure 5 Results from experiments with sand cultures of buckwheat and redroot pigweed. (a) Redroot pigweed root length five days after sowing (DAS) when treated with different root exudates obtained from glass sand cultures; Tukey's HSD, *P*-value <.05, *n* = 9. (b) Principal component analysis (PCA) score plots of dimensions (Dim) 1 and 2. PCA on markers obtained from the different root exudates from sand culture and separated by UHPLC-HRMS. The root exudates were obtained from 11-day-old sand cultures of boxes shown above, *n* = 6. Adapted from Gfeller et al. (2018a).

changes its root exudation in the presence of redroot pigweed, which indicates heterospecific recognition (Gfeller et al., 2018a).

However, we could not isolate the compounds responsible for the growth-repressive effects and it was difficult to separate the outcome from the potential effects attributable to competition for resources (Gfeller et al., 2018a). To select interesting allelochemical candidates in future experiments, we will concentrate on the differences between allelochemical production by a buckwheat plant grown with redroot pigweed and one grown without the weed plant. No recent studies on buckwheat–weed interactions are available and the latest works have focused on residue degradation of buckwheat roots (Szwed et al., 2020; Szwed et al., 2019), a topic that is further addressed in the following section.

3 Allelopathy: a future component of IWM

The concept presented so far in this chapter has focused on the growth-suppressive properties of some plants (a crop or a weed plant) on a neighbouring plant. The next logical step will be to apply this knowledge advantageously at the farmer's level, and/or in an agricultural setting for improved efficiency in terms of weed control, such as in crop rotations or as a complementary management tool. Different possibilities exist to exploit growth-suppressive effects, such as the development of new (bio)herbicides based on allelochemicals and the use of allelopathic crops.

Since the 1950s, farmers have been using chemical herbicides (with high efficacy of over 95%), which are cheap, easy-to-use and guarantee weed-free fields, and therefore the natural compounds with lower efficiency were not likely to be used by farmers. However, pressure is rising from various actors along the food chain for more sustainable agriculture, more biodiversity and pesticide-free food/products. In the future, IWM will be based on the combination of different weed management tools.

3.1 Development of new herbicides based on allelochemical templates

Allelochemical compounds constitute an incredible reservoir of new molecules whose modes of action have been shaped by evolutionary processes, with the advantage that they differ from the modes of action known for traditional synthetic herbicides (De Souza Barros et al., 2020). The idea of an unexplored reserve of future new modes of action is strengthened by an analysis of registration data for plant protection products in the United States. For the period 1997–2010, about 30% of insecticides and fungicides registered were for natural products or derivatives of natural products, while the proportion for herbicides was only 8% (Cantrell et al., 2012). This avenue of detecting new

herbicides is also particularly interesting in view of the alarming trend where weeds are developing resistance to traditional herbicides. The other advantages might include benefits with regard to improved soil biodegradability of molecules of natural origin compared to synthetic compounds (Dayan et al., 2009). The current research focuses on strategies where partial weed control is no longer a knock-out criterion in the search for new herbicidal compounds (Ciriminna et al., 2019; Duke et al., 2014).

3.1.1 New chemical herbicides

To develop a new chemical herbicide based on the structure of a natural molecule, it is essential to establish a structure–activity relationship for the given molecule of interest to design more effective molecular analogues (Dayan and Duke, 2014). This possibility is particularly interesting if the starting molecule acts according to a novel mode of action but potentially involves the loss of the superior biodegradability attributed to natural compounds, depending on the chemical modifications made.

An excellent example of herbicides developed from an allelochemical compound is the triketones (e.g. the maize herbicide mesotrione) based on the molecule leptospermone, which is produced by both the bottlebrush plant (*Callistemon citrinus*) and the Manuka tree (*Leptospermum scoparium*) (Lee et al., 1997; Dayan et al., 2011). Triketones are bleaching herbicides that inhibit hydroxyphenylpyruvate dioxygenase (HPPD), an enzyme that plays a crucial role in plastoquinone and tocopherol biosynthesis in plants (Beaudegnies et al., 2009). Triketones are the latest herbicide site-of-action introduced on the market (Dayan and Duke, 2020). Many molecular target sites of natural phytotoxins used for the development of new herbicides are known (Dayan and Duke, 2014), but so far, commercial herbicides with a new herbicide site-of-action have not been developed yet (Dayan and Duke, 2020). An allelochemical-based benzothiazine derivate, originating from the rice allelochemical tricin, was developed and applied to paddy fields and resulted in effective weed control of the dominant weeds (Zhao et al., 2019).

3.1.2 New bioherbicides

In addition to the focus on new allelochemicals with growth-suppressive characteristics based on precursors with structural similarities, another approach is to identify plant extracts with allelochemical properties. Bioherbicides are defined as products of natural origin for weed control and include phytotoxic plant-based secondary metabolites (Cordeau et al., 2016). However, most of the current bioherbicides on the market are based on fungal or bacterial microorganisms and only very few contain natural plant extracts. One example

of the latter is a product that contains the active ingredient pelargonic acid and other saturated fatty acids (Cordeau et al., 2016). However, pelargonic acid is not an allelochemical, but an acid that occurs naturally in different vegetables and fruits and partially controls broadleaf and grass weeds (Ciriminna et al., 2019). An example of a bioherbicide based on an allelochemical is sorgaab, a water extract of the green parts of mature sorghum plants that inhibits weeds in wheat (Cheema and Khaliq, 2000; Cheema et al., 2008; Głąb et al., 2017). Moreover, in 2005, a patent (https://patents.google.com/patent/KR200600837 74A/en) was registered in South Korea for the rice momilactones A and B, and the respective products are under commercial development (Zhao et al., 2018).

3.2 Allelopathic crops

The use of allelopathic crops in IWM relies on the cultivation of plants with high allelopathic potential of economic interest (Wu et al., 1999). From a biological point of view, allelopathy can be an active and plant-regulated process related to the chemical response of a living organism to its environment or a passive process related to the presence of a plant decaying in the environment of another plant. In agricultural systems, within the same field, both processes may happen simultaneously, mediated by the same allelopathic crop.

3.2.1 Release of allelochemicals

The release of allelochemical compounds into the environment includes processes such as the leaching of aerial parts, volatilisation, decomposition of plant residues and root exudation (Fig. 6). Although not all of these
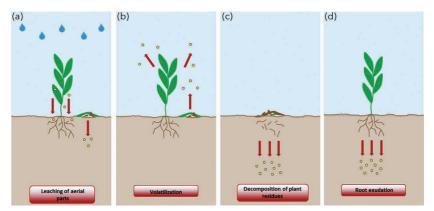

Figure 6 Representation of the different kinds of allelochemical release. Leaching of aerial parts (a), volatilization (b), decomposition of plant residues (c) and root exudation (d).

mechanisms are achievable targets in terms of IWM, we will discuss all the possible mechanisms in the following sections.

Organic and inorganic metabolites may be released from plants by rain, dew and mist in a process referred to as *leaching* (Tukey, 1966) (Fig. 6a), and a classical example is the fern species, *Pteridium aquilinum*, whose fronds release phytotoxic compounds into the environment after rainfall (García-Jorgensen et al., 2020). The water that runs off the trunks and foliage of various eucalyptus species has also been reported to be particularly phytotoxic (May and Ash, 1990; Song et al., 2019). However, to our knowledge, no allelopathic leachates from arable crops for weed control have been reported.

Volatilisation (Fig. 6b) appears to be the preferable route for the environmental spread of monoterpenes produced by the two Mediterranean plants, sage (*Salvia leucophylla* Greene) (Muller and Muller, 1964) and pine (*Pinus halepensis*) (Santonja et al., 2019), a process favoured by the climate of the Mediterranean region (Reigosa et al., 2006). The colloidal matter present in the soil causes their fixation by adsorption from where they can exert their toxic effect on the surrounding plants (Muller and del Moral, 1966). Just like the case of leachates, allelopathic volatiles have not been utilised for weed control in arable crops. A recent review presented an understanding of the role of plant volatiles as mediators of plant interaction (Ninkovic et al., 2021).

The use of plant residues can be an effective tool for weed management, since decaying plant residues can negatively affect plant growth and performance through various release mechanisms (Fig. 6c) (Zhang et al., 2021). Examples include the monocotyledons rye (Barnes and Putnam, 1983; Flood and Entz, 2018) rice (Chou and Lin, 1976) and dicotyledons such as sunflower (*Helianthus annuus*) (Leather, 1983; Alsaadawi et al., 2012), hairy vetch (*Vicia villosa*) (Teasdale and Mohler, 1993; Campiglia et al., 2010), buckwheat (Szwed et al., 2020) and red clover (*Trifolium pratense*) (Ohno et al., 2000; Marcinkevičienė et al., 2013).

In Sections 2.3 and 2.4, the role of root exudates (Fig. 6d) have been described for crop–weed interactions in wheat, rice, buckwheat and sorghum, but allelochemicals have also been identified in root exudates of various other plant species and agricultural crops (Wang et al., 2021). Furthermore, the BXs exuded by rye to the rhizosphere are taken up by the neighbour hairy vetch and subsequently detected in hairy vetch shoots (Hazrati et al., 2020).

3.2.2 Current agricultural and farming practices based on the principles of allelopathy

In agriculture, the three farmer practices that implement the principles of allelopathy in the field include intercropping, the use of cover crops and the use of plant residues.

Intercropping involves growing two or more compatible crops simultaneously on the same field with the intention of improving yield by enhancing resource utilisation; and secondly, it could be a practice where one crop (the intercrop) is used as soil cover to control weeds in the field without having a negative effect on the main crop. One example of how to implement this practice was seen in the tall interrow crops like cotton, maize or soybean. Intercropping of cotton with sorghum and sunflower strongly suppressed weeds and had a positive effect on cotton yield (Kandhro et al., 2014); sunn hemp (*Crotalaria juncea*) with its high contents of phenolics and terpenoids also suppressed weeds in cotton (Blaise et al., 2020). Sorghum intercropping in maize controlled purple nutsedge (*Cyperus rotundus*) (Mahmood et al., 2013a); and the forage legume silver leaf desmodium (*Desmodium uncinatum*) used as an intercrop reduced *Striga hermonthica* infestation in maize (*Z. mays*) (Hooper et al., 2010). In soybean cultivation, buckwheat grown in the interrow provided good weed control (Biszczak et al., 2020). Moreover, fenugreek (*Trigonella foenum-graecum*) was reported to produce flavonol glycosides which showed allelopathic activity (Omezzine et al., 2014) and provided excellent weed control when grown as an intercrop in coriander (*Coriandrum sativum*) (Pouryousef et al., 2015).

In the case of cover crops (CC), the idea is to plant the CC in between two main crops to cover the soil and not to harvest the CC. In this way, the CC provides multiple ecosystem services. Weeds can be suppressed by 70% to 95% through direct competition for resources, by allelochemicals in living field stands (Gerhards and Schappert, 2020; Blanco-Canqui et al., 2015) and by CC residue degradation. The threshold value to apply in this case is that above 3 t/ha of CC biomass, weed suppression occurs for all CC (Gebhard et al., 2013; Gfeller et al., 2018b), but below this threshold, only some CCs like Brassicaceae and black oat (*Avena strigosa*) successfully suppressed weeds, which might be due to growth-suppressive root exudates from the CC (Gfeller et al., 2018b). In field trials, it is almost impossible to separate the competitive and allelopathic effects of CCs on weed growth. Our experiments (also discussed in Section 2.7) showed that light interception by the CC was not the primary mechanism responsible for redroot pigweed growth suppression (Gfeller et al., 2018b).

Kunz et al. (2016) also investigated the question of how to separate the effects due to resource competition from allelochemical effects in field studies. It was reported that the aboveground dry biomass and canopy cover of mustard (*Sinapis alba*), fodder radish (*Raphanus sativus* var. niger) and spring vetch (*Vicia sativa*) did not correlate with the density of the predominant weeds goosefoot (*Chenopodium album)*, chamomile (*Matricaria chamomilla)* and chickweed (*Stellaria media*). Although CC suppressed weeds by 60%, the competition for the light seemed to play a minor role in total weed-suppressive ability. By correlating the results of two experiments at two different scales, a field trial

that evaluated weed density in different CC systems and a Petri dish assay on the germination capacity of several weeds treated with aqueous extracts of the CCs grown in the field trial, the authors concluded that 50% of the variation in weed density could be explained by allelopathy (Kunz et al., 2016).

The physical and biochemical characteristics of plant residues may alter weed germination and growth, but the specific mechanisms involved are difficult to study. Several field studies have reported the weed-suppressive effects of crop residues or mulch and the allelopathic effects were confirmed under controlled conditions in experiments but not in field settings. Studies that focused on the effects of plant residues from different crops or cover crops on the germination and growth of several weeds under field and laboratory conditions have shown that the weed species appear to have varying sensitivity towards allelopathic cover crop residues (Sturm et al., 2018). Biochemical effects on weed suppression in the field across various treatments and locations indicating the importance of studying environmental factors in well-designed set-ups (Swanton et al., 2015). Although it is known that certain plant residues release allelochemicals that inhibit seed germination and growth (Jabran et al., 2015; Kelton et al., 2012; Nichols et al., 2015), a very interesting finding is that phytotoxic crop residue effects are stronger on small-seeded weeds than on large-seeded crops (Kruidhof et al., 2010; Petersen et al., 2001). This result is promising, considering future IWM strategies.

The allelopathic effects of crop residues will be described for different crops in the next section. The *Brassica* species produce a large number of allelochemicals including glucosinolates, brassinosteroids and isothiocyanates with weed-suppressive potential in several cropping systems (Rehman et al., 2019). Even if some Brassica species showed inhibition of wheat germination and seedling growth (Bialy et al., 1990), it could be a sustainable tool for IWM. Some successful examples are: brassica residue incorporation at 6 t/ha in mung bean reduced weed dry weight and density by 61% and 52%, respectively (Ullah et al., 2020); and turnip (*Brassica rapa*) mulches released inhibitory isothiocyanates that were part of the observed weed suppression in the field (Petersen et al., 2001).

Buckwheat residues in the soil can suppress various weeds, and the two most important classes of compounds identified are flavonoids and phenolic acids (Falquet et al., 2015). Based on the hypothesis that phytotoxic compounds from buckwheat tissues are released during plant decomposition, several studies focused on assessing the inhibitive effect of buckwheat extracts under laboratory conditions. Leaf extracts showed the greatest inhibition (followed by shoot and inflorescence extracts) on the root elongation of lettuce and several weeds (Golisz et al., 2007; Hayashi, 1998; Ohsawa and Nakatani, 2005). In pot bioassays, the incorporation of root residues showed no inhibitory effect on the growth of Powell's amaranth (*Amaranthus powellii*) (Kumar et al., 2009). In

contrast, Szwed et al. (2019) stated that buckwheat root residues had a much stronger allelopathic effect on several weed species than residues of the aerial buckwheat parts. No studies were found examining the effects of buckwheat residues incorporated in field trials.

Field studies on the incorporation of sunflower (*Helianthus annuus*) residues significantly inhibited weed growth (Alsaadawi et al., 2012; Leather, 1983). Furthermore, a genotype-dependent effect was reported for eight different sunflower genotypes while chemical analysis revealed higher concentrations of phenolic compounds in the most suppressive genotypes, compared with the least-suppressive genotypes.

Monocotyledonous crop residues like rice, black oat, maize, wheat and rye appear to release similar allelochemicals (BX and phenolic acids) and also with similar effects on weed growth. Cereal rye (*Secale cereale*) is one of the most studied allelopathic crops (Jabran et al., 2015). It produces a persistent ground cover, its mulch decomposes slowly and it efficiently controls summer annual weeds (Mirsky et al., 2013). In addition to BX exuded by rye roots (Belz and Hurle, 2005), phenolics appear to be a rye decomposition product (Otte et al., 2020). Interestingly, the timing of allelochemical release plays an important role in potentially maximising allelopathic effects, as shown for coumaric and vanillic acids (phenolic compounds), which were exuded at higher rates during the first week after field termination of rye (Otte et al., 2020). However, the phenolic acid concentrations measured in rye were three-fold lower than the toxicity thresholds previously reported for coumaric, vanillic and ferulic acids in horticultural and field crops (Otte et al., 2020; Chou and Patrick, 1976). Furthermore, it appears that the allelopathic effects of wheat, particularly on ryegrass *(Lolium perenne L.*) and field forget-me-not *(Myosotis arvensis L.)* cannot be attributed to the synergistic effects of otherwise weakly active allelopathic compounds (Jia et al., 2006). Finally, there is no conclusion on whether tillage influences phenolic acid release from rye. Otte et al. (2020) observed no big differences between tillage and no-tillage systems, whereas Kruidhof et al. (2014) observed a maximised allelopathic effect of tillage two weeks after rye termination.

Rice straw may produce and release allelochemicals into the paddy, which suppress the growth of plants germinating later (Chung et al., 2001; Inderjit et al., 2004), but no difference exists between the allelopathic and non-allelopathic varieties. Kong et al. (2006) observed that rice residues released growth-repressive momilactone B and lignin-related phenolic acids into the soil during decomposition.

To conclude this section, the authors would like to re-emphasize the issue regarding the design and selection of new allelochemical molecules for the purpose of growth inhibition in crops of interest (Section 3.1.1). It is important to characterise the biodegradability of allelochemicals and to investigate their environmental persistence and their potential impact on present and future

crops. Residue management, for example, could not only have an immediate negative effect on the development of weeds but also a prolonged negative effect on the succeeding crop.

3.3 Breeding for allelopathic traits in crops

3.3.1 Genetic variation in plants with allelopathic potential

It is evident from previous discussions (Section 2.3 on allelopathic and non-allelopathic rice varieties) that potential exists amongst several crop varieties such as alfalfa, oat, wheat and rapeseed (Zubair et al., 2017; Fernández-Aparicio and Rubiales, 2019; Shamaya et al., 2018; Raman et al., 2018). The genetic control of allelopathic properties was studied intensively in rice (Subrahmaniam et al., 2018; Jensen et al., 2001). The focus of the research efforts was to understand the biochemical pathways of the momilactone allelochemicals, and specifically momilactone B (Kato-Noguchi and Ino, 2003; Kato-Noguchi and Peters, 2013; Shimura et al., 2007). Moreover, it was possible to identify the underlying genetic basis for the production of momilactone B and the inactivation of two selected genes (copalyl diphosphate synthase 4 and kaurene synthase-like 4) that decreased the allelopathic potential of three mutants compared to the wild type (Xu et al., 2012). Rice germplasm was also screened for allelopathic genetic potential (Pheng et al., 2009), but a drawback is that studies to understand natural variation are not designed to accommodate the possibility that allelopathy is also an inducible process mediated by the presence of weeds. The exogenous application of the signaling hormones methyl jasmonate and methyl salicylate lead to differential induction of the allelopathic potential in two rice cultivars, and interestingly, the cultivar with the higher allelopathic potential responded more strongly than the cultivar with the lower potential (Mahmood et al., 2013b), showing that plant hormones can also affect genetic potential.

Gramine biosynthesis starts from tryptophan and then it is further converted into two intermediates (Gross et al., 1974). In the barley cultivar Proctor, the first known stable intermediate from tryptophan could not be identified, a finding that might explain the lack of allelopathy in this cultivar (Hanson et al., 1983). Indeed, the amount of gramine produced by barley varies greatly depending on the cultivar (Hanson et al., 1983; Liu and Lovett, 1993) and this was used as a selection criterion in a study of 127 landraces and cultivars covering the gene pool from Nordic countries (collected over 100 years) in a screen for allelopathic activity against ryegrass. Interestingly, the level of gramine was lower in the new cultivars (Bertholdsson, 2004). Similar results were observed in a study with Tunisian barley landraces and modern accessions (Bouhaouel et al., 2018; Bouhaouel et al., 2020). Both research groups suggested that the old

landraces were more allelopathic and that modern selection methodologies favour other traits and might even counter-select for allelopathic traits. A recent study screened 18 accessions of barley from the Middle East, one accession from Tibet and a modern cultivar for their gramine and hordenine content in different plant parts, and this study also demonstrated the impact of domestication on the production and distribution of the two allelochemicals in barley (Maver et al., 2020). Similar conclusions were drawn Tibugari et al. (2019) for sorgoleone in 353 different African sorghum accessions where new sorghum accessions had very little sorgoleone compared to some landraces and wild sorghum.

3.3.2 Breeding programmes and allelopathic rice varieties

Breeding for improved weed suppressiveness is a function of weed-competitive ability that is the outcome of the interaction of several traits, e.g. plant height, leaf area (Dimaano et al., 2017) and allelopathic activity. The identification of quantitative trait loci (QTLs) for allelopathic functions represents a strategy to enhance allelopathic activity in crops by using marker-assisted selection (Schulz et al., 2013). However, not many allelopathic crop cultivars have been developed, although breeding programmes exist in crops like wheat and rice (Bertholdsson et al., 2012).

Huagan-3 was the first allelopathic rice cultivar to be developed based on the identification of a QTL linked to an increased allelopathic effect of rice (Kong et al., 2011). It was released by the administration of Guangdong province (China) in 2009 and by the Ministry of Agriculture of China in 2015. Another three allelopathic rice cultivars (N-liangyou-201, Hualiangyou-78 and Huagan-2205) were released by the local administrations of Guangdong province, Guangxi province and Anhui province between 2017 and 2019. Currently, farmers cultivate these allelopathic rice cultivars on at least 50 000 ha in the provinces of Anhui, Guandong, Guangxi and Hainan in South China (Kong CH, 2020, pers. comm.).

Breeding for rice allelopathy in Asia is an enduring process, and one such breeding programme was stopped after several years of research and development due to problems with autotoxicity and other problems associated with weed susceptibility, since Asian rice fields are infested with mixtures of weed species. Another problem is that rice breeders mainly focus on high-yielding cultivars and breeding for allelopathic cultivars may not be their priority. Moreover, hand weeding is still affordable in some Asian countries, which means that investments in crop allelopathy for use in IWM are not attractive (Bhagirath SC, pers. comm.).

One discrepancy for modern-day breeders is to breed crops that are both high-yielding and have strong allelopathic potential. This dilemma exists also

for disease-resistant crops as they are lower-yielding, and the quality of the harvested product is also considered to be lower (Brown and Rant, 2013). In organic farming, the use of disease-resistant plants is also associated with yield loss, but compensation comes from higher product prices.

An interesting possibility could be to focus on studies to increase the allelopathic potential of cover crops, since they do not have the constraint of high quality and high yield. However, the authors are not aware of any breeding programmes with this objective.

4 Conclusion

The performance of crops in agricultural systems with low herbicide input is dependent on a detailed understanding of weed biology, weed population dynamics and crop–weed interactions. Furthermore, each agrosystem is specific, dynamic and influenced by numerous crop–weed interactions with varying biotic and abiotic environmental factors. In this complex environment, only a few examples of crop allelopathy have been documented (Fig. 2). In the first part of this chapter, we discussed the challenges of studying allelopathy in terms of experimental methodology and allelopathic trait selection. The biggest challenge remains to identify and characterise compounds involved in rhizosphere interactions and signaling, which further affect the root growth and performance of neighbouring plants.

We also presented a case study based on ten years of research and expertise in understanding the allelopathic interactions of buckwheat. During the past years, we studied the belowground interactions between buckwheat and redroot pigweed, but have expanded the research efforts recently to other *cover crops* and *weeds* based on observations of growth suppression in other plant–plant interactions in both the field and under controlled conditions (Gfeller et al., 2018a,b). In particular, we are interested in the root growth effects between plants in different crop–weed set-ups (monocot/monocot, monocot/dicot and dicot/dicot).

Some current research objectives that require scientific expertise across various disciplines are:

- Patterns of root exudation as a consequence of direct crop–weed root interactions,
- Selection of potential candidate chemical compounds in root exudates induced by plant neighbours,
- Root morphological traits induced by neighbouring plants and candidate allelochemicals,
- Potential gene candidates in weed model plants (transcriptional level), and
- Understanding the soil behaviour of candidate chemical compounds.

Once it becomes possible to characterise the promising allelochemicals in the cover crop which are induced by the presence of the neighbouring weed plants, further applications in IWM can be developed, and it will be possible to meet consumer expectations for more sustainable food production.

5 Where to look for further information

Recently, the journal Plant, Cell and Environment published a special Issue on plant-plant interactions covering the communication among plants and their mechanisms in an ecological context including light and volatile signaling, and underground communication networks.

Plant, Cell and Environment, Special Issue: Plant-Plant interactions, Volume44, Issue 8, August 2021.

We would like to endorse the special issue in Trends in Plant Science: Unraveling the Secrets of the Rhizosphere focusing on the interactions of plants with rhizosphere microorganisms. It also covers the mechanisms behind the belowground interactions and gives insights on root-root interactions and methodological aspects to study belowground interactions.

Trends in Plant Science, Special Issue: Unravelling the Secrets of the Rhizosphere, Volume 21, Issue 3, 169-278, March 2016.

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