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Ecological Chemistry of Pest Control in Push-Pull Intercropping Systems: What We Know, and Where to Go?

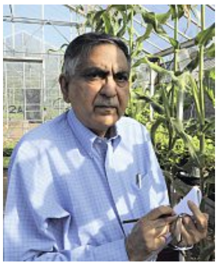
Jakob Lang[a], Frank Chidawanyika[bc], Zeyaur R. Khan[b], and Meredith C. Schuman*[a]

Abstract: Push-pull technology (PPT) employs mixed cropping for sustainable intensification: an intercrop repels or suppresses pests of the focal crop (push), while a trap crop attracts pests out of the field (pull), where they may be targeted for control. Underlying chemical-ecological mechanisms have been demonstrated in controlled settings, primarily for some of the best-established cereal PPT systems developed in east Africa. Yet, many questions remain regarding mechanisms, and strategies to adapt PPT for different crops and locations. We conducted a systematic review of scientific literature on PPT and related practices for biological control of pests of food and fodder. Of 3335 results, we identified 45 reporting on chemistry of trap- or intercropping systems for pest control, of which 30 focused on cereals or African pests. Seven of these reported primary chemical data: measurements from glasshouse and laboratory studies (5), or of field-collected samples (2). From these 30, we provide a database of compounds, discussing degrees of evidence for their mediation of push-pull. We depict hypothesized spatial distributions of selected compounds in PPT fields from physical properties and emission/exudation rates, and design of the east African cereal PPT system, and discuss influences on activity in field settings likely to affect success.

Keywords: Chemical ecology · *Desmodium* spp. (tick clover) · Pest management · Sustainable agricultural intensification · *Zea mays* (maize)

Jakob Lang obtained his MSc degree in chemistry with a focus on analytical chemistry at the University of Zurich, Switzerland, in 2021. He is currently a PhD candidate at the University of Zurich Department of Chemistry, funded by the EU project UPSCALE (H2020 SFS-35-2019-2020). His research focuses on applications of mass spectrometry-based metabolomics in plant ecology, and method development for the efficient preservation and analysis of spatially and botanically attributed, field-collected samples of soluble and volatile plant metabolites. He was granted a 2022 Chemistry Travel Award from the SCS and SCNAT to support his work with ICIPE in push-pull systems.

Frank Chidawanyika obtained his MSc in entomology at Stellenbosch University, South Africa (SA), in 2010 and a PhD in chemical ecology from University of the Witwatersrand, SA, in 2015. He is a scientist at the International Center of Insect Physiology in Kenya (ICIPE), and research associate at University of the Free State (UFS), SA. Previously, he was a Senior Lecturer at UFS. His research addresses applied and theoretical questions in insect climate stress resistance, chemical ecology and pest management in sustainably intensified agroecological systems. He has received several awards, including the DAAD-ARPPIS scholarship and Carnergie Corporation of New York Fellowship.



Zeyaur R. Khan obtained his MSc in 1977 and his PhD in 1980, in entomology, from the Indian Agricultural Research Institute, New Delhi. Since 1993, he is Principal Scientist and Leader of the Habitat Management Programme with the International Center of Insect Physiology in Kenya (ICIPE). He is also Visiting Professor at Cornell University, Ithaca, NY, USA (since 2009), member of the African Academy of Sciences (since 2012), and a PI on UPSCALE. He has received many awards for creative and solution-oriented contributions in entomology and integrated pest management, particularly his leadership of the development and implementation of push-pull technology.

Meredith C. Schuman obtained her PhD in chemical ecology in 2012 from the Friedrich Schiller University, Jena, Germany, for research conducted at the Max Planck Institute for Chemical Ecology (MPICE), following a Fulbright postbaccalaureate fellowship at MPICE. Her PhD research was awarded the Otto Hahn Medal of the Max Planck Society for demonstrating indirect defensive functions of herbivory-induced plant volatiles. She is Assistant Professor of Spatial Genetics at the Departments of Chemistry and Geography at the University of Zurich, Switzerland, and a PI on UPSCALE. Her group investigates patterns, and

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**Correspondence:* Prof. M. C. Schuman[a], E-Mail: meredithchristine.schuman@uzh.ch

[a]Departments of Geography and Chemistry, University of Zurich, Switzerland; [b]International Centre of Insect Physiology and Ecology, Kenya; [c]Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa

consequences for ecosystems, of plant genetic and biochemical variation.

1. Introduction

Push-pull agricultural technology (PPT) is gaining increasing interest as a method for pest control and sustainable intensification of cereal and vegetable cropping systems. The technology uses on-farm crop diversification for management of pests through their chemically and physically mediated interactions with nonhost plants, together with their natural enemies. The first PPT system was reported by Pyke and colleagues in 1987 as a form of integrated pest management for cotton in Australia,[1,2] and the approach was formalized by Miller and Cowles in 1990 as 'stimulo-deterrent diversion' reported for an onion system in the United States.[3] Thereafter, in 1997, Khan and colleagues[4,5] described a PPT system for maize in Kenya, using molasses grass (*Melinis minutiflora*) as an intercrop (push) to repel stemborer moths and increase their parasitization, and Sudan grass (*Sorghum vulgare sudanensis*) as a bordering trap crop (pull). Over the years, further assays evaluating increased attraction of stemborers to several grasses (all Poaceae) compared to maize resulted in the selection of Napier grass (*Pennisetum purpureum*) as the main trap crop.[6] Additional evaluations for repellent plants resulted in molasses grass being replaced as an intercrop by the leguminous tick clovers (silverleaf desmodium, *Desmodium uncinatum* and greenleaf desmodium, *D. intortum*), largely owing to their nonweediness and propensity for nitrogen fixation, despite molasses grass being marginally more effective at repelling pests and recruiting parasitoids.[6]

Further empirical investigations, inspired by farmers' anecdotal reports, also demonstrated that the desmodium plants suppress development of the witchweed *Striga hermonthica* (Orobanchaceae), presumably *via* stimulation of witchweed germination and interference with the development of haustoria.[6] An updated cropping system employs greenleaf desmodium paired with the border grass *Brachiaria* cv Mulato II, which form a more drought-tolerant version of the cereal PPT system termed 'climate-smart' push-pull.[7] The mixture of volatiles emitted by maize and *Desmodium* spp. (silverleaf or greenleaf desmodium) was furthermore found to be less attractive to fall armyworm (*Spodoptera frugiperda*) moths in wind tunnel assays, and to reduce oviposition by moths under laboratory conditions, compared to maize volatiles alone; while parasitoid wasps (*Cotesia icipe* and *Coccygidium luteum*) were attracted to volatiles from green and silverleaf desmodium, and *Brachiaria* cv Mulato II, in laboratory olfactometer assays.[8] Recently, field tests of a 'third-generation' push-pull system were reported, using the creeping beggarweed *D. incanum* as a desmodium intercrop, which benefits from more reliable seed production in Kenya and good drought tolerance; and *Brachiaria* cv Xaraes as the trap crop, which was rated highly by farmers for drought tolerance as well as biomass yield, and resistance to spider mites.[9]

Given its substantial success in east Africa and recent introductions in other African regions, the cereal system described above is one of the best-studied PPT systems. Central to the studies and development of the cereal PPT system in east Africa is the participatory rural appraisal approach, which allows for co-creation and validation of technologies with farmers. This has enabled incorporation of combinations of crops which are accepted by farmers and have desirable traits supporting sustainable use, critical pest control, livestock fodder, and farmers' nutritional and financial well-being. These urgent concerns, important for utility and for promoting adoption, have taken precedence over a detailed mechanistic understanding of how PPT systems work; rather, designs have built on existing knowledge in chemical ecology, and laboratory tests of bioactive chemistry for specific companion plants have followed extensive testing of pest damage reduction and yield improvements.[2] The demonstrated potential of these systems has raised interest in expanding PPT to other crops, and other geographical locations, bringing with them different challenges and requirements. As the potential applications multiply, advances in the mechanistic understanding of PPT systems may support their continued development, as well as efficient PPT expansion into different scenarios.[10]

Here, our goal is to provide an overview of molecules linked to pest management success in the maize-desmodium PPT system, as well as related intercropping systems, by conducting a systematic literature review. The approach was designed to obtain a database of the available literature about intercropping systems targeting pest control, which was filtered to obtain a list of publications studying the chemical ecology and molecular features of systems developed for cereal crops or for pests threatening food security in Africa. We highlight molecules that have been isolated from plants used in PPT systems, specifying where there is general evidence of bioactivity, or more specific evidence of activity supporting push-pull. We quantify and discuss efforts to demonstrate the chemical mechanisms of PPT under field conditions, which differ from laboratory conditions in several ways which may be relevant for activity.[11] Finally, we depict expected spatial distributions of bioactive plant chemicals in PPT systems, and important considerations for understanding these distributions. We hope that this work provides steps towards a deeper or more general mechanistic understanding of the chemical ecology of PPT agroecosystems, to support their further development and expansion.

2. Materials and Methods

2.1 *Overview of the Systematic Review*

The collection of publications was performed using R (versions 4.0.4. and 4.1.2) with the package litsearchR version 0.4.0.[12] A basic search query (see Supplementary Information) was used to obtain an initial selection of 492 references from Scopus and Web of Science, which were evaluated with litsearchR to obtain a list of 396 potential search terms. The search terms were grouped into six categories – agriculture, pests, plants, farming techniques, functionality and goals or dangers – while keywords that did not match any of the categories were discarded. Of the keywords, 118 were used in the search query (Supplementary Information), which mandates the presence of at least one keyword of each category in the publication. This query was run against the Scopus and Web of Science databases on March 08th, 2021, and returned a total of 3,335 publications (after removal of duplicates), which were screened and categorized (Fig. 1, Supplementary Table SI1).

Screening was performed based on abstracts, which were exported from the databases. In cases where abstracts were not included in the database export, an attempt was made to find the full-text publication and if that was not successful, the publication was evaluated based on its title.

The screening stage comprised four filters based on the content of the titles and abstracts: (1) publications studying a trap- or intercropping system were retained and those from the fields of social sciences or economics were removed; (2) publications that did not mention pest management, which can refer to either insect or weed management, were removed; (3) publications investigating a cereal crop or focusing on African pests were retained; (4) publications that did not contain a study of molecules or mechanisms involved in pest management were removed. We note that publications passing filters (1) and (2), but not (3), were also initially assessed for filter (4).

2.2 *Catalogue of Push-Pull Chemistry*

Publications reporting on the chemistry of inter- and trap cropping systems relevant to cereal crops or to east Africa were used to generate a list of molecules with potential mechanistic

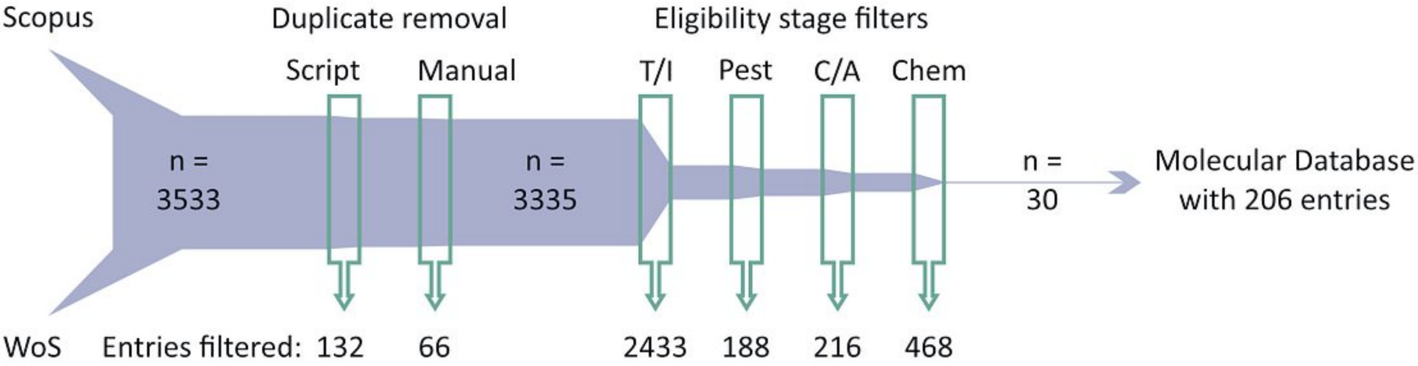


Fig. 1. Diagram of the filter process and the number of publications passing the filter stages (n) or excluded by the filter ('Entries filtered'). The filter T/I refers to trap- or intercropping systems and C/A refers to cereal crops or studies performed in Africa.

relevance. The publications were individually screened, and all listed molecules were added to the catalogue. Duplicate entries, as well as alternative names for the same molecule, were then removed manually. Additionally, entries were classified into plant volatiles and exudates, and grouped into molecular classes such as terpenoids or glycosides (Supplementary Information Table SI2).

2.3 *Spatial Distribution of Push-Pull Chemical Factors*

To estimate the possible spatial distributions of known or potentially active molecules in PPT fields, physical properties were retrieved from ChemSpider (Royal Society of Chemistry, http://www.chemspider.com/). A simple model of diffusion was used to estimate order-of-magnitude changes in concentration with distance,[13] treating emission as a series of 'puffs' at a constant rate over 1 min from 1 g tissue in a 1 cm^2 source, and based on diffusion volume increments or volumes for different atoms and molecular structures in the gas phase;[14] diffusion equations were built from Chapter 2 from Cushman[15] (see Supplementary Information for a Python notebook containing the model code and details). For exudates, we refer to evidence from Turlings and colleagues that small, nonpolar molecules diffuse most rapidly in the gas phase belowground,[16] and assume that diffusion in soil can, under some circumstances, be approximated as diffusion rates in air. We furthermore note expected degradation rates, where known, for compounds or compound classes in the environment[17] (see considerations in the Results and Discussion). Estimated concentrations were found in literature[18–20] for the plant volatiles (*Z*)-3-hexenyl acetate and (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) (emission rates published in maize); the maize root exudate component 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA), and the desmodium root exudate component 6-C-arabinosyl-8-C-galactosylapigenin (isoschaftoside), respectively.

3. Results

3.1 *Overview of Publications on Push-Pull and Related Systems*

Of the 3,335 publications which were assessed for eligibility (Supplementary Material Table SI1), the vast majority (2,433 publications) did not include a trap- or intercropping system of the type used in PPT. One reason is that the word 'intercropping' refers to both a spatial intercropping, where multiple crops are grown simultaneously on the same plot; as well as a temporal intercropping, where alternative crops are grown in-between cropping seasons. Temporal intercropping was retrieved by the search queries and filtered out manually in the screening procedure (Fig. 1).

The pest management filter removed another 188 publications, and the remaining 714 publications were grouped into either original research papers in natural sciences, or reviews, book chapters, and various other dissemination publications. Filtering for work on cereal crops or African cropping systems removed 216 publications. Of the remaining 498 publications, 468 did not contain any mention of chemistry or molecules, and only 30 publications passed the entire screening stage. All publication numbers as well as percentage of publications functioning to review or disseminate, rather than reporting relevant primary data, are shown in Table 1. We also identified 15 publications among those passing filters Stages 1 and 2 which passed Stage 4 (Chemistry), but not Stage 3 (Cereals/Africa) (see Supplementary Information Table SI1). These studies were not used for the molecular database and thus not evaluated in more detail..

3.2 *The Ecological Chemistry of Push-Pull Systems*

Different aspects of plant-pest interactions were studied in the thirty publications mentioning chemistry in the context of PPT in African or in cereal systems. Root exudates were a focus in studies of weed management, while plant volatiles were a focus

Table 1. Summary of the publication count passing each filter stage, see Supplementary Table SI1 for the full database. Note that the 'review' category may include primary literature which did not investigate the given topic, but reported on it only in the form of a literature review in the introduction or discussion section.

Filter Stage	Stage 1: Trap- / Intercropping	Stage 2: Pest Management	Stage 3: Cereals / Africa	Stage 4: Chemistry
Publications Passed	903	714	498	30
Of which Review or Dissemination	n/a	152	101	23
Percentage Review or Dissemination	n/a	21.3%	20.3%	76.7%

in studies of plant-insect interactions. In the molecular database (Supplementary Information Table SI2), we provide a set of 206 compounds extracted from these references, including compound names, SMILES codes, molecular masses, sum formulae and an estimation of type (exudate or volatile), and classification like flavonoids or terpenoids. The catalogue thus contains a variety of compound classes with a wide range of chemical properties and biosynthetic origins, from the enormous group of terpenoids and fatty acid-derived green leaf volatiles, to other common groups of specialized metabolites like flavonoids and glycosides.

Some molecules were detected in intercropping systems, but not directly linked to biological activity. Others, like (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT, Fig. 2), were found in PPT systems and are known from other studies to negatively affect insect larvae directly (*e.g.* through disruption of gut membranes[21]) or to be associated with indirect defense of maize plants, in which volatile blends attract parasitoids of herbivore eggs and larvae.[22] Many of the other volatiles in the catalogue, like green leaf volatiles (GLVs) and volatile terpenoids, have been reported to influence insect behavior as part of plant defense against herbivores in maize and many other plant systems.[13] However, it was not yet clearly shown how, or whether, these specific molecules are responsible for push or pull effects in the intercropping system, alone or in blends.

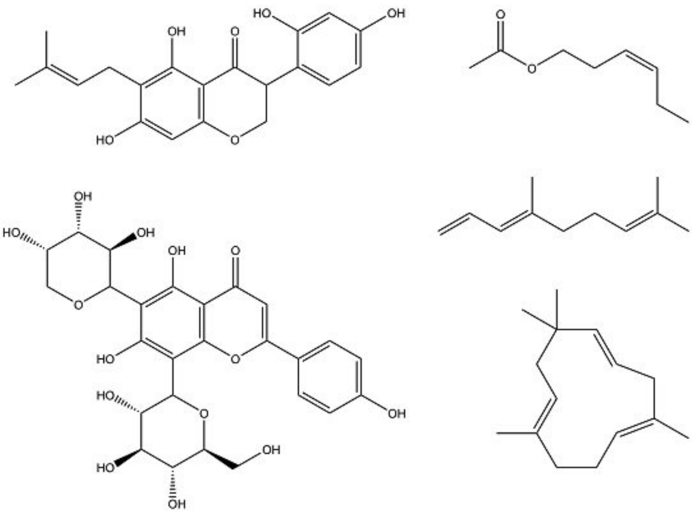


Fig. 2. Exemplary molecules from the created catalogue (Table SI2). The main compound groups are root exudates like uncinanone A (left top) and isoschaftoside (left bottom) and plant volatiles like the green leaf volatile ester (*Z*)-3-hexenyl acetate, the homoterpene (3*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), and the sesquiterpene α-humulene (right, top to bottom).

The best-studied of the PPT molecular mechanisms is the suppression of *Striga* weeds through root exudation. It was shown that some of the flavonoids exuded by *Desmodium* spp. inhibit the germination of the parasitic weed *Striga hermonthica*, and the active compounds were isolated and identified. Three isoflavanones (uncinanone A, B and C) and a glycosylflavonoid (isoschaftoside) were isolated from silverleaf desmodium (*D. uncinatum*) root exudates, identified by NMR, and shown to inhibit *S. hermonthica* growth.[18,23] The presence of isoschaftoside was verified in root exudates of field-grown *D. unicatum* plants.[18] The only other publication reporting results from field-grown plants identified volatile organic compounds thermally desorbed from leaf tissue, heated up to 100 °C, from three intercrop species used with eggplant: coriander, marigold and mint.[24] Although growing plants under field conditions is a step towards analyzing chemicals from agroecosystems in their usual setting, it is unclear how to connect chemicals emitted from harvested plant tissue heated far above ambient temperatures in a lab, to emission profiles of plants in the field. No study in the scope of this literature search attempted to collect volatiles or exudates under field conditions.

3.3 *Spatial Distributions*

Based on our simple model of diffusion, we estimate that relevant exudates and volatiles from maize, desmodium, and border grasses in the push-pull system can be found in concentrations of ng–µg per m^{-3} (pg-ng L^{-1}) at distances greater than 10 cm from the emitting plant within one minute of emission or exudation. For the maize-desmodium push-pull system, it is recommended to plant border crops 1 m from the intercropped field, and to plant the maize crop in between rows of the intercrop spaced at 75 cm apart (75 cm between desmodium rows, with maize planted between these), as depicted in Fig. 3.[25]

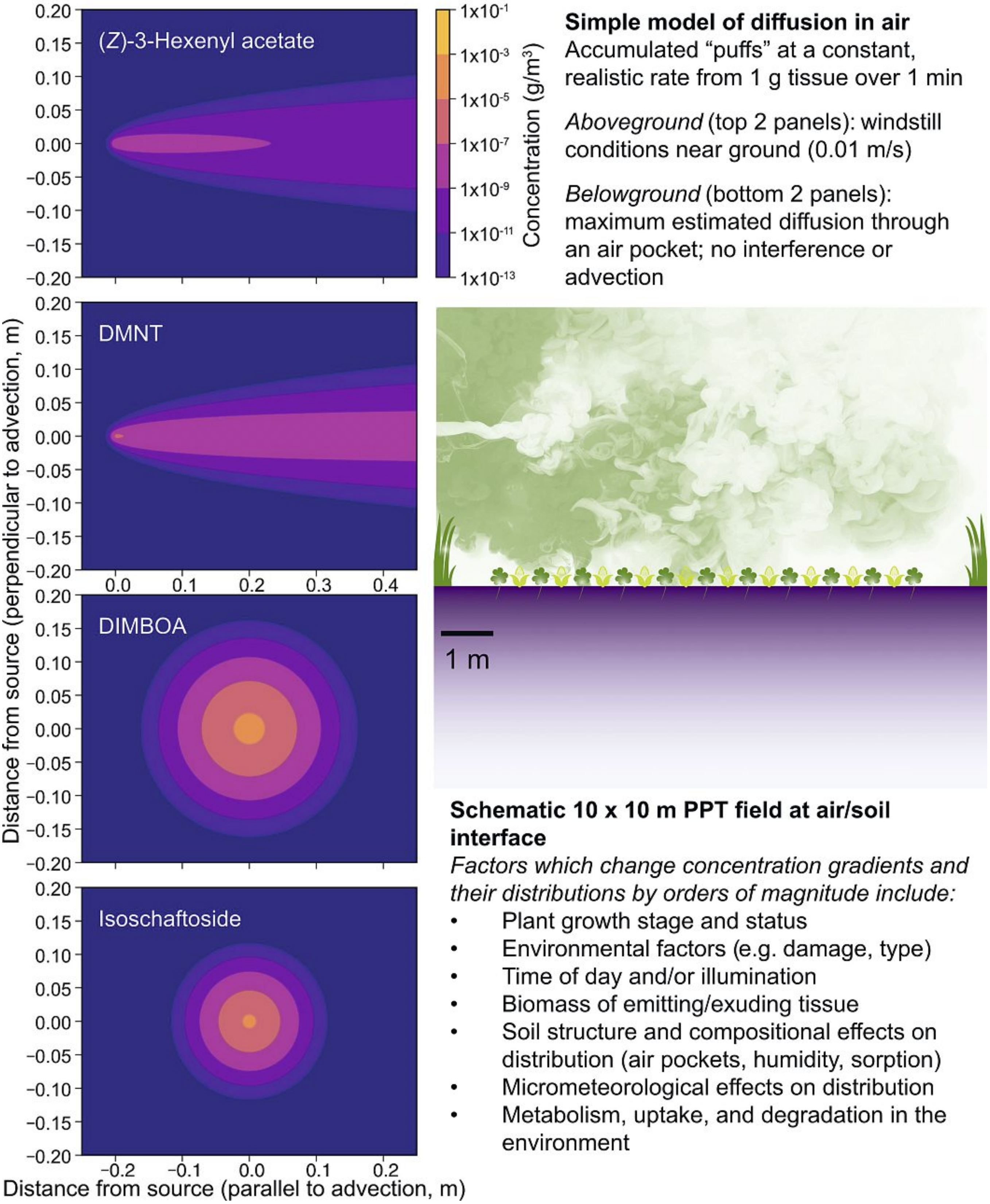
For exudates in soil, actual concentration gradients are likely to be very inhomogeneous as a result of structure, composition, and humidity, as well as biological activity in the belowground matrix;[16] the distribution depicted in Fig. 3 treats the soil as one large air pocket (see also Turlings and colleagues[16] and citations therein) and so indicates maximum spread by diffusion over the one-minute period. The Python notebook (Supplementary Information) includes a very approximate simulation of diffusion through solids, using a rule of thumb estimate that diffusion coefficients in solids are on the order of 10^{-12} m^{-2} s^{-1}, versus *ca.* 10^{-5} m^{-2} s^{-1} or 10^{-6} m^{-2} s^{-1} in the gas phase;[26] this results in a correspondingly smaller radius of diffusion, with comparable concentrations reaching only µm rather than cm from the source within one minute.

Over time, processes more rapid than diffusion, such as advection (wind) and eddies due to micrometeorological effects,[27] will dominate distributions aboveground. Any active transport by advection due to temperature differences or other means will also modify belowground distributions. Uptake, breakdown, and modification of compounds, both biotic and abiotic, further modify both aboveground and belowground distributions; terpenoids are generally more susceptible to degradation and oxidation due to atmospheric pollutants than are GLVs.[17] Ongoing emission and exudation generally do not enrich the gradient, but rather continue to provide a source, so that the gradient or plume may expand and persist. Last but not least, plant volatile emission (and likely exudation) may be strongly influenced by environmental factors, including details like the larval stage of feeding herbivores, plant growth stage and condition, and time of day (see Schuman[13] and citations therein). These factors and considerations are listed and depicted in Fig. 3, and the Python notebook and environment (Supplementary Information) allows the interested reader to try different parameters for the simple diffusion model.

4. Discussion

4.1 *Summary Analysis of the Systematic Review*

Intercropping systems are used for crop protection in many different systems like eggplant,[24] rice,[28] cotton[29] or maize.[7] The systems are tested and evaluated in field trials and are then adapted by farmers if they provide sufficient levels of crop protection, and if these benefits outweigh costs of implementation.[30] The study of the protection mechanisms, however, is often lacking or non-existent. Out of the 714 screened publications on pest management through intercropping, only seven reported on the analysis and identification of molecules that drive the crop protection effects, and those publications were then referred to in reviews and other publications focused on dissemination of knowledge.



Simple model of diffusion in air
Accumulated "puffs" at a constant, realistic rate from 1 g tissue over 1 min

Aboveground (top 2 panels): windstill conditions near ground (0.01 m/s)

Belowground (bottom 2 panels): maximum estimated diffusion through an air pocket; no interference or advection

Schematic 10 x 10 m PPT field at air/soil interface

Factors which change concentration gradients and their distributions by orders of magnitude include:

- Plant growth stage and status
- Environmental factors (e.g. damage, type)
- Time of day and/or illumination
- Biomass of emitting/exuding tissue
- Soil structure and compositional effects on distribution (air pockets, humidity, sorption)
- Micrometeorological effects on distribution
- Metabolism, uptake, and degradation in the environment

Fig. 3. Spatial considerations for chemical mediators in PPT fields.

4.2 *How Field Measurements of Chemistry Could Contribute to Push-Pull Success*

Since the database exports in 2021, two additional papers were published about the volatile emissions of desmodium plants (silverleaf desmodium, *D. uncinatum* and greenleaf desmodium, *D. intortum*) in PPT systems. While one of these confirmed the presence of volatiles such as β-ocimene, β-caryophyllene and α-pinene in glasshouse measurements,[8] the other (still a preprint at the time of writing) found very low release rates of volatiles from the desmodium intercrop in both glasshouse and field collections.[31] Notably, the first of these publications reports on multiple volatiles which previously had not been linked to push-pull systems (see Supplementary Information Table SI2): (*S*)-linalool, 1-octen-3-ol, 3-octanone, (*E*, *E*)-allo-ocimene and α-copaene were identified through injection of authentic standards. Additionally, the following compounds were identified through spectral library and retention index databases: cumene, methyl benzoate, linalool oxide, (+)-cyclosativene, β-elemene, *trans*-α-bergamotene, β-selinene and α-muurolene. The second publication, which found very low levels of volatile emission from desmodium plants, still confirmed that intercropping desmodium had a beneficial effect on crop protection, but linked this to physical trapping of insects rather than repellence.[31] Both publications used seeds sourced from Kenyan seed companies, but it is impossible to know whether these originated from the same biological source. PPT establishment in East Africa began with systems using molasses grass (*Melinis minutiflora*) as an intercrop, and this species has been shown – under laboratory or glasshouse conditions – to release volatiles repellent to stemborer moths and attractive to parasitoid wasps.[5] The switch to desmodium was motivated by its ability to control witchweed (*Striga* spp.), while compromising somewhat on stemborer control in comparison to molasses grass.[6] Desmodium intercrops clearly support pest control in east African cereal PPT systems,[32] but the mechanisms remain controversial.

Further studies of plant volatiles and extrudates under field conditions could help to improve the understanding of PPT and intercropping systems in several ways: by filling gaps in data on the chemistry of these systems; serving as a 'reality check' of measurements under more refined conditions; resolving conflicting reports; improving understanding of the relationship between field spatial layout and size and crop protection; or providing chemical indicators of specific plant states or interactions. Ideally, such studies would capture data with both spatial and temporal resolution, to monitor changes within a field and allow association with ecological phenomena. Advances such as those in mobile mass spectrometry instrumentation, the design of polymer- and metal-based sensors, and scalable approaches to *in situ* sampling can enable such measurements.[33] An array of such approaches, especially for the analysis of plant volatiles (not necessarily in field contexts), has been recently reviewed,[33–35] and we summarize some key considerations here.

The real-time or near-real-time monitoring of volatiles by direct injection mass spectrometers, such as proton transfer mass spectrometers (PTR-MS), is well established for fluxes, detected in trace amounts (down to parts per trillion, ppt), of atmospherically abundant plant volatiles like isoprene in the air around fields and forests, or for real-time monitoring of volatile profiles from partially or completely enclosed samples, even from a large number of samples in parallel.[33,34,36] PTR-MS instruments are large and are therefore usually installed on fixed, or motorized mobile systems. Direct-injection MS monitoring comes at the cost of greatly reduced information on compound identity as a result of eliminating chromatographic separation; PTR-MS, though employing a near-quantitative (*i.e.,* highly sensitive) ionization technique, also produces very sim,ple fragmentation patterns of one or a few fragments, so that in practice, signals are most often assigned to a structural class rather than to a specific compound even when coupled with high mass resolution; and additional solutions (tandem ionization) generally require bulkier and more complex instrumentation.[35]

Alternatives are generally smaller, more scalable, and provide more chemical information about samples, at the cost of reduced temporal resolution. Miniaturized MS and gas chromatograph (GC)-MS solutions (≤15 kg), including rapid GC separation, are actively developed for high-sensitivity portable diagnostics in medical, military and police applications, and have also been employed for the field measurements of plant volatiles.[33,34] These have limited chromatographic resolution and mass precision. A different approach uses arrays of metal- or polymer-based sensors which produce low-dimensional read-outs in the form of electrical (E-nose) or optical signals: different signal compositions can be associated with different compositions of volatile organic compounds in contact with the sensor.[33,34] These sensors are usually less sensitive than MS-based detectors and cannot be used to identify unknown compounds.[33] All sensors may furthermore be sensitive to fluctuating environmental conditions, *e.g.* in temperature and humidity. Thus, it is still a favorable option to employ scalable sampling procedures, such as equilibrium-based techniques using polymers to absorb non-polar and low-polarity small molecules from the atmosphere or soil; to take direct headspace samples, or to pump air through filters.[33,37] The equilibrium-based approaches are generally least costly, and easiest to scale as well as to employ above- and belowground, whereas headspace or filter sampling is better for quantitation, and concentration of samples onto filters is most sensitive.[33,37] Samples can be taken at defined locations across a field at documented times, as well as from multiple fields in parallel, and subsequently analyzed in high throughput and at full chemical resolution on laboratory GC-MS systems. All of the approaches discussed here will benefit from further advances in the analysis and interpretation of spatiotemporally resolved, potentially high dimensional data, and coupling with ecological and physiological data and observations for interpretation.[34,35,38]

4.3 *Spatial Relationships in Push-Pull Systems*

In Fig. 3, we depict a schematic indicating how different processes can influence spatial distributions of important chemical volatiles and exudates in push-pull fields, in relation to recommended spatial scales of planting. The primary aim of this figure, and the accompanying results text, is to support investigations of these spatial relationships and to consider the distribution of chemical mediators as one factor affecting the outcomes of different spatial arrangements. It is of primary concern to avoid competition among the different plants in the push-pull system, and rather to permit facilitation mediated by chemical attractants and repellents of pests (and other mechanisms of pest suppression), as well as by soil modification, including nitrogen fixation. It is challenging both to model, and to accurately measure, such spatial distributions, due to many influences which are spatially heterogenous components of macro- and micro-environments, and which affect the outcomes by several orders of magnitude – in addition to the common challenges of conducting chemical measurements and sampling in the field as discussed in the previous section. A spatially explicit, individual-based modeling framework has been proposed to predict favorable spatial arrangements in mixed cropping systems for integrated pest management.[39]

At a broader spatial scale, that of geographic regions, we can consider whether molecules which may help to effect push-pull in sub-Saharan east Africa are likely to support sustainable intensification in other locations. The small molecules implicated in push-pull effects have physical properties which generally allow for volatility or transport in air or soil under a broad range of conditions on the Earth's surface; thus, although differences in soil composition and humidity are still likely to impact typical belowground distributions, geographic differences in the effects of small molecules may often be driven by gradients of pollution (causing degradation) and distribution ranges of target species (pests and beneficials).[13,17] Many of the most problematic agricultural pests are broadly distributed along with the crops they feed on. The fall armyworm *Spodoptera frugiperda* may cause severe damage to maize fields in Mexico (where it is native), as well as in Kenya or Uganda,[40,41] and has spread across the African continent from north to south, and east to west;[42] as has the Asian spotted stemborer *Chilo partellus*.[43] *Cotesia sesamiae* wasps, which parasitize several stemborer species, are reported to have similarly wide distributions as their hosts across sub-Saharan Africa.[44] In comparison, witchweeds, which cause large losses and crop failures in much of sub-Saharan Africa, have a narrower distribution associated with rain-fed agriculture and poor and disturbed soils.[45]

4.4 *Limitations and Outlook*

We present an overview of publications studying molecular features that have been indicated to drive beneficial effects of intercropping systems. While the chosen approach drew on a data-based, extensive list of search terms, and two commonly used, large databases of scientific literature, it is inevitable that some publications were not caught by the search query or were not in either of the two searched databases. Furthermore, our search query was designed to return publications that report on intercropping systems for pest management in cereal, or of pests problematic in Africa, and none of the search keywords referred to the chemical analysis of intercropping systems. Therefore, some publications related to mechanisms of PPT were not returned (like the structural elucidation of root exudates[23]) because they did not fulfil other criteria. We preferred this strategy, because we wanted to determine to what extent the literature focused on developing and testing such intercropping systems included an accounting of molecular mechanisms as assessed during the systematic review procedure. We were specifically *not* looking for literature reporting on chemistry of potentially relevant molecules, without a direct connection to these agricultural systems. Readers can draw on the assembled catalogue of 206 compounds in Table S1 to selectively search for other literature suggesting or supporting activity in PPT systems (as we did for the case of desmodium root exudates and other cases presented in this review).

PPT continues to draw attention as a promising approach for sustainable intensification. Adoption depends more on the demonstration of witchweed (*Striga* spp.) suppression and maintenance of soil health, nutritional and economic benefits, and the dissemination of required agronomic knowledge, than it does on knowledge of the underlying molecular mechanisms. Therefore, while it remains a priority to demonstrate the scientific basis of PPT,[2] the focus has been more on dissemination and agronomic demonstrations than on chemistry in the literature reporting on developments of these systems. A growing molecular understanding of PPT effects, however, is likely to prove useful both for implementing adjustments to currently established systems, as well as expanding push-pull approaches to new systems.[10] Here, it is important to be aware of the environmental sensitivity of these mechanisms: how well do they operate under relevant field conditions?[11]

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Author Contributions

Conceptualization: JL, MCS, Data curation: JL, MCS, Formal analysis: JL, MCS, Funding acquisition: MCS, ZRK, Investigation: JL, MCS, Methodology: JL, MCS, Project administration: MCS, Resources: MCS, Software: JL, MCS, Supervision: FC, MCS, ZRK, Visualization: JL, MCS, Writing – original draft: JL, FC, MCS, Writing – review & editing: JL, FC, MCS

Supplementary Information

Supplementary Information for this publication is available on https://chimia.ch/chimia/article/view/2022_906

SI1_Table-PublicationList: Complete publication list after removal of duplicates including the pass / fail of the four filter stages.

SI2_Table-Database_nonCD: Catalogue of molecules and their chemical groups reported in agricultural intercropping systems.

SI_SearchQueries: Search queries for the initial selection and the final retrieval of the publication list.

SI_R-script: Source code for the litsearcheR keyword generation.

SI_Notebook: Python notebook with simple diffusion model and documentation.

SI_environment: Python environment file.

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