

Cropping system redesign for allelopathy: A vision for the 'post-herbicide era'

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Abstract

Arable weed management faces an uncertain future. A climate of tightening regulations and widespread herbicide resistance has led to suggestions that we are entering the 'post herbicide era', but successful weed management with no, or fewer, herbicides will require a diversification and de-intensification of management strategies. One underappreciated strategy is to utilise the natural chemical interactions between plants, both antagonistic (allelopathy), and benign (allelobiosis). The prevailing, reductionist approach to allelopathy is as a substitution for synthetic herbicides, which has had the effect of limiting our ecological understanding of these plant-plant interactions. I posit here that allelopathy and allelobiosis will only be effective in regulating arable weeds through ecological redesign, inspired by the ecosystems outside of agricultural land in which these interactions affect plant growth. Increased integration of concepts from studies of these ecosystems should therefore be prioritised in allelopathic weed management. Research should, for instance, consider recognition interactions, the stimuli which can induce allelopathic responses, and the effects of plant community diversity on these interactions. In short, researchers should consider the desired outcome of allelopathic weed management and the context in which it would be required to operate. As such, management of agricultural land should prioritise reductions in disturbance and especially tillage, to foster the development of a benign, self-regulatory weed community based on low-level competition and allelopathic inhibition, which does not require intensive management efforts.

KEYWORDS

agroecology, Allelobiosis, Ecological Weed Management, holistic

1 | INTRODUCTION

Weed management has long been reliant on extensive use of synthetic herbicides, but this approach is clearly not sustainable. This is a reality indicated by myriad human and environmental health concerns, tightening regulations, and the rampant proliferation of herbicide resistance (Haywood et al., 2021; Kudsk & Mathiassen, 2020). Weed interference with crops also appears to be more complicated than the

simplistic race for resources traditionally perceived (Storkey & Neve, 2018), leading one to question the extent of our hostility towards weeds.

Weed detriment seems to be at least partially modulated by chemical interactions between species, and their alteration by extraneous factors (Horvath et al., 2023). Indeed, competition can be affected by these interactions, both detrimentally as allelopathy (Weston & Duke, 2003), and in more benign signalling interactions as

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allelobiosis (Ninkovic et al., 2006). As we venture into the ‘post-herbicide era’ of reduced inputs (Merfield, 2022) and increasingly vocal calls for cropping system redesign informed by ecological principles (Bommarco, 2024), there is an opportunity for these phenomena to become more influential in sustainable agroecosystem management. In realising this, however, it is necessary to build on recommendations for more holistic approaches to apply allelopathy to agricultural weed management in contemporary agricultural systems (Hickman et al., 2023), by considering if these systems can adequately support allelopathy as a weed management strategy, and what could be done at the system level to improve this capacity. I argue here that our current approach to allelopathy, as scientists, reinforces its marginalisation in cropping system design, while exacerbating its abstraction and isolation from other disciplines like insect pest and pathogen resistance. Future research should therefore look beyond the current role of allelopathy and allelobiosis in agricultural weed management and include broader knowledge of these ecological phenomena to inform cropping system redesign.

2 | ALLELOPATHY AND WEEDS: TWO CONTEXTS, TWO APPROACHES

Research on plant–plant chemical interactions is primarily within two to areas of weed ecology, which I distinguish here as the ‘agricultural’ and ‘invasion’ contexts. The reconciliation of these two contexts, and the integration of ecological perspectives into agricultural allelopathy research, have long been advocated for (Cheng & Cheng, 2015; Hierro & Callaway, 2021; Inderjit et al., 2011; Meiners et al., 2012; Reigosa et al., 1999), and have led to some progress in our understanding (da Silva et al., 2017; Weidenhamer et al., 2023). Crucially, though, they have not yet translated to advancement in understanding or applying allelopathy or allelobiosis in the ‘agricultural’ context (Cordeau et al., 2016; Hickman et al., 2023).

Research in ‘agricultural’ crop–weed allelopathy focuses on how these interactions either benefit or disfavour the crop; scientific interest lies in augmenting the former and minimising the latter. There is thus a wealth of literature investigating the efficacy of a particular plant species, through living tissues, mulches, or extracts, and sometimes identifying the active compounds present and their concentrations. It is typical for these studies to focus on an individual crop and weed species, or even an individual constituent compound. Current progress, and potential future perspectives on application to contemporary agricultural systems, are extensively reviewed by Hickman et al. (2023), so additional detail will not be provided here. The existing body of literature on agricultural allelopathy thus chiefly constitutes case studies, rather than insights into its effects as a general ecological phenomenon (Meiners et al., 2012; Weidenhamer et al., 2023). This case-study-centred approach may relate to the predominant intended application of allelopathy, as an alternative to herbicide application where other strategies are suboptimal, sometimes even as a direct substitution in the form of a bioherbicide (Weidenhamer et al., 2023). These applications are, however, hindered

by the context-dependency of the interactions at play. Different target species (Jensen & Ehlers, 2010), and even populations of a single species (Hickman et al., unpublished data), can respond differently to individual allelochemicals, while different crop varieties, or even individuals of the same variety or population, can vary in allelopathic potential (Hickman, Withall, et al., 2025; Lankau, 2011; Quader et al., 2001; Uesugi et al., 2019; Weidenhamer et al., 2023). In both examples, context-dependency is likely to relate to natural variability of constituent compounds in crude extracts or exudates, both in concentration (Cheng & Cheng, 2015), and in identity (Hickman, Withall, et al., 2025; Köllner et al., 2008). I argue that the abundance of case studies, and lack of ecological context are, to some extent, symptoms of the reductionist focus on individual interactions (Bärberi, 2002). This is a common occurrence in arable weed management (Radosevich & Ghersa, 1992; Ward et al., 2014), probably relating to its distance from ecological theory (Blank & Mesgaran, 2024). Such reductionism is necessary to gain understanding of the mechanisms at work, but it also obscures trends which could lead to generalisation and wider application (Levins & Lewontin, 1980).

Ecological interactions are more effectively considered in the second, ‘invasion’ context for plant–plant interactions in weed science, where dynamics concerning the dominance of invasive plant species entering an unfamiliar environment are explored (Callaway & Ridenour, 2004). Therein, the rapid expansion of an invader is rationalised by its deployment of compounds inhibitory to the development of surrounding species which have not encountered them before, and have therefore not developed tolerance of their effects. Key here is that this research places more emphasis on relative success on a community, rather than pairwise level (Wardle et al., 1998).

3 | IS ALLELOPATHIC WEED MANAGEMENT REALISTIC IN CONTEMPORARY CROPPING SYSTEMS?

The distinction between the agricultural and invasion contexts for allelopathy echoes more broadly in weed science (Rasmussen, 2024; Ward et al., 2014), and indicates their different approaches to chemical ecology (and weeds). While this disparity echoes the distinction between agronomy and ecology, it is becoming apparent that the processes, if not the scale, are consistent between invasion and agricultural studies—they both involve plants emigrating to environments where their presence is detrimental (Metcalf et al., 2019). This disconnect highlights a fundamental disparity between the environments in which allelopathy is influential to plant growth, and the environment in which agricultural weed scientists expect it to be influential. Allelopathy in less managed systems is subtle, and can be difficult to elucidate in real-world conditions with complex webs of co-existing flora (Williamson, 1990). It seems to be highly sensitive, and predominantly regulatory to floral biodiversity (Chou, 1999), for example, maintaining co-existence between familiar species (Ehlers et al., 2016), and their associated microbial communities in grasslands (Semchenko et al., 2019). Exceptions, where one plant can

significantly suppress another, seem to occur exclusively in more heavily disturbed environments, for instance where species like *Lupinus polyphyllus* or *Fallopia japonica* utilise novel allelochemicals to become dominant in an invaded ecosystem (Kalske et al., 2020; Murrell et al., 2011). Another example, of greater relevance to agriculture, is the use of selectively bred allelopathic rice lines for weed suppression, which has required intensive research (around 35 years) to achieve a specific solution to a specific weed problem (namely barnyard-grass, *Echinochloa crus-galli*) (Worthington & Reberg-Horton, 2013). This example shows that allelopathy can be applied in current cropping systems, but this development time is impractical in light of the pressing weed problems we face, even considering recent technological advances. Solutions of this nature are furthermore vulnerable to circumvention by the development of tolerance in the single target weed, or the emergence of another similarly dominant species (Hickman et al., 2021). In all, then, application of an allelopathic crop for weed management is currently rare, hard won, and inadequate for widespread benefit in contemporary cropping systems (Hickman et al., 2023).

It is therefore necessary to interrogate our expectations of how allelopathy can act as a tool for arable weed management. No allelochemical has yet been identified which acts with the efficacy and broad-spectrum consistency of a commercial herbicide. One could furthermore question the ecological rationale for such a compound existing, given the floral diversity of most unmanaged ecosystems, and the benefits that it provides for ecosystem function as a whole (Isbell et al., 2011). This is a reality exemplified by the paucity of plant-derived bioherbicides developed to date (Cordeau et al., 2016), and is emphasised by the relative effectiveness of living plants or decomposing tissues for weed management, rather than their isolated bioactive molecules (Hickman, Withall, et al., 2025; Hierro & Callaway, 2021). Put simply, we cannot, and should not, expect an allelochemical to be a straightforward substitution for a synthetic formulation.

Plant-plant allelopathy is analogous to plant defence against other organisms (Dahlin & Ninkovic, 2013; Hickman et al., 2021), and even physiological responses to abiotic stress (Reigosa et al., 1999; Tang et al., 1994). It may therefore be a general stress response, but if so, this also creates a paradox: A stressed plant may have greater allelopathic potential, but it will, by definition, not develop or yield effectively. A stressful environment is not ideal for crop production either; in fact, it is also unlikely to support weeds with a large number of competitive traits, and would instead favour those adapted to tolerate disturbance and stress (Hickman, MacLaren, & Menegat, 2025; MacLaren et al., 2020). In this way, allelopathy would provide limited benefit to a stressed agroecosystem along the lines in which we often intend to apply it at present. A stressful environment is also antithetical to modern conventional agriculture, which is highly dependent on nutrient inputs to create favourable conditions for a crop (and, coincidentally, the problematic weeds it competes with (Berquer et al., 2023)), so that resources committed to yield are maximised. Considering the inducibility of allelopathy, it is possible that its benefits would only be realised in the presence of an existing weed community, which may not be a satisfactory compromise for many farmers in existing systems.

4 | ECOLOGICAL CROPPING SYSTEM REDESIGN CAN FACILITATE ALLELOPATHY

If widespread allelopathic weed management is incompatible with contemporary cropping systems, it is logical to consider how system redesign can benefit these interactions. Redesign has potential to drive less intensive ('ecological') weed management, facilitated by targeted practices focusing specifically on minimising the effects of highly detrimental species, and maximising the value of ecological interactions (including allelopathy and allelobiosis), to foster a self-regulating and benevolent plant community (Hickman, MacLaren, & Menegat, 2025; MacLaren et al., 2020). In this regard, the role that allelopathy could play in shaping the transformation of sustainable agricultural systems has received little consideration to date.

4.1 | Adapting management for weed diversity: The allelopathy perspective

The more diverse weed communities and crop rotations created by ecological weed management would provide an ecosystem where allelopathy and allelobiosis can provide balance and regulation to the floral community, as we see in non-arable environments (Ehlers et al., 2014; Semchenko et al., 2019). In the process, this approach would drive further integration of concepts and knowledge from invasion allelopathy into an agricultural context, a necessity for more widespread application. The regulatory role of allelopathy in unmanaged systems is made possible by the relatively limited disturbance regime, allowing species to adapt to each other, co-evolving in favour of an equilibrium where diversity is supported (Hierro & Callaway, 2021; Huang et al., 2018). Thus, to create a cropping system which favours these dynamics, disturbance intensity and frequency would need to be reduced. This would obviously include reductions in herbicide application, but also in soil disturbance. Reduced ploughing intensity has also been correlated with smaller weed species with lower nutrient requirements (Armengot et al., 2016), which would theoretically be less competitive towards the crop (Hickman, MacLaren, & Menegat, 2025). By extension, there is evidence of a trade-off between allelopathic potential and physical competitive ability (Meiners et al., 2012), effectively a contextualisation of the growth-defence trade-off which maintains plant fitness (Herms & Mattson, 1992; Huot et al., 2014). Interestingly, recent work indicates that crops do not conform to this trade-off (Giolai & Laine, 2024), indicating that simultaneously allelopathic and physically competitive material can be used in cropping systems, as is the case in the previously described example of weed-suppressive rice. Allelopathy and physical resource competition are not commonly explicitly examined together, although exceptions exist (Fernandez et al., 2016; Reiss et al., 2018). This hinders our understanding of how these two interactions can be combined to benefit plant fitness. Because of the complex relationships between allelopathy and resource competition, I suggest that research should first focus on producing effective interactions in the field, prioritising their connection with the real-world

conditions where they would be applied (Stowe, 1979). The underlying mechanisms can then be examined to determine the relative contributions of allelopathy and resource competition.

4.2 | From species to ecosystems

A more stable management regime would enable research efforts probing deeper into the dynamics influencing allelopathy in communities of varying complexity, containing different plant families, of different levels of phenotypic similarity, with different ecological roles. All of these factors are likely to influence the strength and outcome of allelopathic and competitive interactions (Byun et al., 2013; Hussain et al., 2022; Singh & Daehler, 2023), but in ways which are currently largely unknown, or at least not sufficiently consistently observed to attribute to a generalisable trend. More diverse weed communities would offer an opportunity to probe into the factors influencing the strength of allelopathic and competitive interactions, in keeping with the perspective of Mahaut et al. (2020) that weed communities represent underutilised, semi-natural model systems which can be used to examine short-term evolutionary and ecological dynamics. I suggest that future work in allelopathy and plant–plant interactions should make increased effort to move beyond the single ‘donor’/‘recipient’ model of typical allelopathy studies (aimed at controlling a single problematic weed species), and into exploring trends between a wider range of different, agroecologically relevant biotypes. Such approaches have previously been used in studies of resource competition (Goldberg, 1996), and also of invasion allelopathy, particularly in comparing community-level effects of invaders. As an example of this latter application, Murrell et al. (2011) examined allelopathic effects of *Fallopia japonica* invasion on native plant communities in pot experiments containing six other species, finding that the invader was specifically inhibitory to forbs while grasses were apparently unaffected. At the least, a similar experiment in an agricultural context would facilitate application by expediting the screening process, while also indicating the species which are relatively sensitive and insensitive to a specific allelopathic agent.

4.3 | Beyond allelopathy, beyond weeds

There are a diversity of actors in an agroecosystem beyond the weed community and the crop, with consequences for their interactions (Hickman et al., 2021). For instance, the soil microbial community interacts particularly closely with allelochemicals (Cipollini et al., 2012), so its influence is a necessity to consider when redesigning a system for more effective application of allelopathy. Although allelochemical persistence is a common limitation for allelopathic crops, examination of how this may affect weed management is rare (Hickman, Withall, et al., 2025). This is again more common in invasion allelopathy; Del Fabbro and Prati (2015) looked into allelochemical persistence in a number of invasive plant species and found that this was greater when these species were under competitive pressure,

thereby providing insight into the ultimate consequences of allelopathic induction. There is also complementary evidence indicating that weeds contribute significantly to the formation of a healthy rhizosphere in agricultural soils (Hu et al., 2023), further emphasising the interlinkages between these concepts. A wider focus on the place of allelopathy in an agroecosystem would therefore be a more substantial knowledge base of complex interactions between the diverse organisms that operate within an agroecosystem and the benefits that they can have for agricultural sustainability.

5 | CONCLUSION

As weed science was long tantamount to ‘herbicide science’ (Ward et al., 2014), so too has agricultural allelopathy often been ‘plant-derived bioherbicide science’. In that regard, it is difficult to argue that it has realised its potential. From our understanding of plant–plant interactions as ecological phenomena, there appears to be a remarkable propensity for individuals to detect and react to each other and the world around them, which should be preserved for the good of agriculture, food production, and society. In doing so, it is vital that we look to broader investigations of the trends underpinning allelopathic responses, beyond agricultural fields. This will allow us to develop cropping systems informed by naturally-occurring plant–plant interactions, where allelopathy can realistically contribute to the management and regulation of a stable and relatively benign weed community.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

No original data have been used in the production of this insight piece.

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