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DOI 10.1007/s13593-020-00631-6
ISSN 1774-0746
ESSN 1773-0155

Publisher: Springer Verlag (Germany)

Agronomy for Sustainable Development (2020) 40:24
https://doi.org/10.1007/s13593-020-00631-6

REVIEW ARTICLE

An ecological future for weed science to sustain crop production and the environment. A review

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Accepted: 26 June 2020

Abstract

Sustainable strategies for managing weeds are critical to meeting agriculture's potential to feed the world's population while conserving the ecosystems and biodiversity on which we depend. The dominant paradigm of weed management in developed countries is currently founded on the two principal tools of herbicides and tillage to remove weeds. However, evidence of negative environmental impacts from both tools is growing, and herbicide resistance is increasingly prevalent. These challenges emerge from a lack of attention to how weeds interact with and are regulated by the agroecosystem as a whole. Novel technological tools proposed for weed control, such as new herbicides, gene editing, and seed destructors, do not address these systemic challenges and thus are unlikely to provide truly sustainable solutions. Combining multiple tools and techniques in an Integrated Weed Management strategy is a step forward, but many integrated strategies still remain overly reliant on too few tools. In contrast, advances in weed ecology are revealing a wealth of options to manage weeds *at the agroecosystem level* that, rather than aiming to eradicate weeds, act to regulate populations to limit their negative impacts while conserving diversity. Here, we review the current state of knowledge in weed ecology and identify how this can be translated into practical weed management. The major points are the following: (1) the diversity and type of crops, management actions and limiting resources can be manipulated to limit weed competitiveness while promoting weed diversity; (2) in contrast to technological tools, ecological approaches to weed management tend to be synergistic with other agroecosystem functions; and (3) there are many existing practices compatible with this approach that could be integrated into current systems, alongside new options to explore. Overall, this review demonstrates that integrating systems-level ecological thinking into agronomic decision-making offers the best route to achieving sustainable weed management.

Keywords Ecological weed management · Sustainability · Agroecosystems · Weed diversity · Weed community · Weed-crop competition

Contents

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Published online: 08 July 2020

1 Introduction

Agriculture faces the dual challenge of feeding the world's growing population while sustaining the ecosystems and biodiversity that support humanity. Weeds and their management are critical to achieving agriculture's potential in both these roles. Uncontrolled, weeds could reduce global yields of major crops by around 34% (Oerke 2006), yet when too many weeds are removed from farmed landscapes, major declines in other wildlife follow (Marshall et al. 2003; Bretagnolle and Gaba 2015; Smith et al. 2020). Current agricultural systems, particularly in the developed world, are dominated by a paradigm of large-scale, intensive, mechanised farming of a few major crops supported by inputs of mineral fertilisers and chemical crop protection products (Stoate et al. 2001). These systems rely on the intensive long-term use of herbicides and/or tillage to control weeds which can have negative impacts on both the environment and long-term farm productivity. Over-reliance on herbicides can lead to environmental pollution (DeLorenzo et al. 2001; Relyea 2005), non-target damage to crops, loss of natural vegetation and soil biodiversity (Marshall 2001; Druille et al. 2013; Rose et al. 2016) and can have negative effects on the health of farmworkers (Waggoner et al. 2013; Mamane et al. 2015) and the public (Landrigan and Benbrook 2015; Myers et al. 2016; Almberg et al. 2018). The main non-chemical approach to weed control, tillage, can increase soil erosion rates to orders of magnitude above rates of soil creation (Montgomery 2007; Hobbs et al. 2008; Verheijen et al. 2009), compromise soil function and contribute to climate change through the use of fossil fuels and release of greenhouse gases from the soil (Lal 2004a; Huang et al. 2018). This is not to say that the judicious use of either tillage or herbicides is always problematic (tillage in particular may contribute to soil aeration and nitrous oxide reduction in some cases; Huang et al. 2018), but decoupling mainstream weed management from an over reliance on these two tools would give farmers greater freedom to use them only if and when they contribute to overall agroecosystem sustainability. This would inevitably lead to a reduction in the intensity and frequency of their use and the associated negative environmental impacts, for example, deep inversion tillage could be replaced with less invasive practices such as strip tillage or inter-row hoeing

The dominance of chemical and mechanical control in weed management also raises concerns that weeds are adapting to these types of control and that few proven alternatives are available where their effects diminish. For example, weeds are more likely to evolve resistance to herbicides where herbicide use is more intense (Mortensen et al. 2012; Hicks et al. 2018). Weed community shifts toward species more tolerant of control can also occur, such as an increase in 'wandering perennials' (weeds with vegetative propagules) in response to regular tillage (Mohler 2001) or highly ruderal species in response to more frequent and intense disturbance events (Fried et al. 2012; Gaba et al. 2017; Bourgeois et al. 2019). As a result, agricultural landscapes now tend to be dominated by a few weed species that are difficult to control (Neve et al. 2009; Garnier and Navas 2012) and that provide a poor resource for other farmland biodiversity (Marshall et al. 2003; Hawes et al. 2009).

These long-term costs and unsustainability of current weed management are becoming increasingly apparent to farmers, to the public and to policymakers. This is evidenced by increasing demand for organic produce and recent discussions around banning widely used herbicides such as glyphosate (Reganold and Wachter 2016). At the time of writing, bans on glyphosate use or import were in place in several countries around the world, with further public referendums or parliamentary votes awaited in Austria, Germany and Switzerland. Further environmental pressures, such as the need to improve soil health, have also led to a shift in farming practices to reduced tillage in many regions around the world. In these systems, ploughing is minimised or excluded from farm management and soil disturbance reduced, with the aim of promoting soil organic matter sequestration, reducing soil erosion and conserving soil moisture (Hobbs et al. 2008). The impacts of herbicides and tillage highlight an urgent need to reassess the current approach to weed management and adopt new approaches that can sustain productive agriculture while conserving biodiversity and natural ecosystems.

The dominant current paradigm in weed science and management is the use of specific tools of techniques to remove weeds at the level of an individual field, often with a short-term single-species focus. While delivering immediate benefits to the farmer, this agronomic approach does not sufficiently account for ecological and evolutionary processes that lead, for example, to weed removal actions simply creating opportunities for new weeds to establish (Smith 2015) or to a ‘co-evolutionary arms race’ between weeds and weed control (Neve et al. 2009). This arms race is seen most clearly in respect to herbicides, where the selection pressure imposed by the successive introduction of different herbicides has promoted the successive evolution of resistance to each herbicide and eventually to multiple herbicide resistance within weed species (Bourguet et al. 2013; Délye et al. 2013; Comont et al. 2020). The focus on weed removal also overlooks the need to assess whether short-term measures taken to control weeds have higher costs in the long term, in terms of reduced farm productivity, environmental degradation and human health. We argue in this article, therefore, for the integration of ‘ecological thinking’ (at larger temporal and spatial scales than a single field in a single growing season) into agronomic decision-making.

Previous articles have highlighted the risks inherent to weed control strategies that are over-reliant on herbicides and have called for alternative approaches to be developed and implemented (Mortensen et al. 2012; Harker 2013; Harker and O’Donovan 2013; Shaner and Beckie 2013; Ward et al. 2014; Bagavathiannan and Davis 2018). To achieve sustainable weed management, there is a need to explicitly consider the interactions between weeds, management actions and the surrounding ecosystem, both in the short and long terms, in order to sustain productive yet biodiverse farming systems (Bàrberi 2002; Fernandez-Quintanilla et al. 2008; Ward et al. 2014; Neve et al. 2018). Despite these numerous previous calls to action, many recent reviews seeking to guide future weed science and management continue to be dominated by chemical and mechanical technologies (see reviews by Gianessi 2013; Shaner and Beckie 2013; Bajwa et al. 2015; Westwood et al. 2018).

Fig. 1 A focus on indiscriminate weed removal can lead to a low diversity of resistant and competitive species **a** that can be more problematic for crop production and biodiversity than **b** a diverse community of weeds that provide multiple services. These photos were taken on vineyards with contrasting management approaches; **a** used only herbicides to try to remove all weeds from vine rows, while **b** employed a mixture of grazing, mowing, and shallow cultivation to manage a short ‘lawn’ of diverse weeds

In this article, we offer an alternative, ecological vision for the future of weed science. Central to this vision is shifting the focus away from weed removal, and toward an understanding of which characteristics of agroecosystems confer resilience to problematic weed outbreaks yet foster a diverse weed community to sustain ecosystem services (Fig. 1). We begin with a discussion of why this ecological approach focused on regulating weed communities, rather than a technological approach focused on removing weeds, holds greater potential to achieve sustainable agriculture (Section 2). We then review established and emerging ecological theories with relevance to weeds (Section 3), and use these theories to infer which farm and landscape-scale practices could be promising components of sustainable weed management systems (Section 4). Our aim is to provide an overview of the current scientific landscape to enable weed researchers and agronomists to more readily identify practical management actions that will contribute to sustaining crop production as well as biodiversity and ecosystem function. While we present examples of these practices, their implementation will be determined by context specific combinations of cropping systems and landscapes. We do not, therefore, aim to offer prescriptive advice but rather provide a knowledge base and framework for designing sustainable weed management strategies. We hope this article will inspire further research that adds to and refines this framework to develop robust, locally relevant weed management strategies for the variety of agroecosystems around the world.

2 An ecological vs. technological focus for weed science and management

In this section, we argue that a technological focus for weed science, consisting primarily of further refinements to chemical and mechanical technology, will not address the fundamental limitations of weed management focused on weed removal via standalone tools and techniques. Current weed science suffers from an overabundance of 'techno-fixes' that may solve specific problems in the short term, but when 'taking a wider and longer view they tend to delay, transform and relocate problems, as well as creating new ones' (Scott 2011). Research focused on techno-fixes can identify ways to very effectively remove weeds in the short term, but cannot address the fundamental vulnerability of agricultural systems that are dependent on just a few tools, nor identify sufficient feasible alternatives in the face of herbicide-resistant weeds, environmental impacts and public health concerns (Mortensen et al. 2012; Altieri et al. 2017; Bagavathiannan and Davis 2018; Storkey and Neve 2018).

Herbicides are an example of a techno-fix. Worldwide, herbicide resistance has been recorded in 262 weed species and to 23 out of the 26 known modes of action (Heap 2020), limiting the use of currently available chemicals. The discovery of new herbicide modes of action has stagnated, with none developed since the early 1990s. Westwood et al. (2018) predict that another four modes of action could be discovered by 2050, but this may be optimistic given that none has been discovered in the last 25 years. Legislative hurdles for registration of new compounds and re-registration of old compounds are also becoming higher in the European Union and elsewhere (Kudsk and Streibig 2003). Furthermore, pursuing new chemicals is of dubious benefit if herbicides continue to be treated as standalone solutions, given that weeds can evolve resistance to new control measures within mere years of their introduction (Palumbi 2001; Ashworth et al. 2015) and that many weeds can tolerate or resist multiple herbicides through either morphological or metabolic adaptations (i.e. cross resistance; Mortensen et al. 2012; Délye et al. 2013; Comont et al. 2020). Varah et al. (2020) estimate that complete herbicide resistance in blackgrass (*Alopecurus myosuroides*) in the UK alone would cost £1 billion and 3.4 million tons of wheat yield and cite evidence indicating the over-use of herbicides as the key driver of resistance (Sandermann 2006; Hicks et al. 2018). It is also increasingly credible that public concerns around herbicide toxicity and the scale at which herbicides are used will result in widespread bans, under which weeds could be expected to limit agricultural productivity by around one-third if alternatives are not in place (Oerke 2006).

Many other technological tools for weed management proposed in recent weed reviews (e.g. Westwood et al. 2018; Shaner and Beckie 2013) have the potential to pose similar risks as herbicides. Genetic engineering for herbicide resistance, or gene drives to eradicate weeds, for example, runs the risk of altering ecosystems in unforeseen ways by creating novel organisms that may respond to their environment in unpredictable ways (Palumbi 2001; Steinbrecher and Paul 2017). While this risk does not necessarily outweigh the other potential contributions of genetically modified organisms to sustainability, it does emphasise that the interactions of such tools with both agroecosystems and natural ecosystems need to be considered extremely thoroughly in order to avoid long-term negative impacts (Myers et al. 2016; Altieri et al. 2017). This has been demonstrated by the 'Roundup Ready' crops, which were released with the promise of reducing overall herbicide use, but within two decades have led to an overall increase in herbicide use (Bonny 2016). In addition, herbicide-resistant genes from transgenic crops have been observed in volunteer crops (Knispel et al. 2008), feral crops (Bagavathiannan and Van Acker 2008) and their weedy relatives (Gressel 2015). There is thus a risk that such technologies could result in resistant weed problems in both agricultural systems and any natural ecosystems also invaded by these weeds (Bagavathiannan and Van Acker 2008; Gressel 2015).

A range of less risky weed control techniques do exist, such as those reviewed by Bajwa et al. (2015). However, it is not clear that any would prove any more sustainable if used at large scales in the long term. An interesting example is the recent introduction of harvest weed seed destructors and collectors, heralded as a new approach to control herbicide-resistant weeds (Walsh et al. 2013). Within a few years however, certain weed species were observed adapting to this technology through shedding seed earlier in the season, thus avoiding seed destruction at harvest (Ashworth et al. 2015). Given the ubiquity, diversity, plasticity and adaptability of weeds around the world, it seems impossible that any single weed control technique, including herbicides, will prove to be a lasting panacea for weed management.

Not all weed science focuses on standalone tools, and indeed, integrated weed management (IWM) explicitly calls for combining an array of chemical, cultural and mechanical control tools and techniques (Shaw 1982; Swanton and Weise 1991). This approach of using 'many little hammers' (Liebman and Gallandt 1997) can prevent weeds from adapting and lead to successful long-term control and may also sustain weed diversity (and its benefits to other taxa) to a greater degree (Storkey and Neve 2018). IWM strategies with crop rotation at their core remain the most successful and sustainable long-term weed management strategies practiced so far (Bàrberi 2002; Chauhan et al. 2012; Mortensen et al. 2012; Harker and O'Donovan 2013). However, the effectiveness of IWM strategies varies depending on their implementation. IWM appears to be most successful where crops and management differ substantially between years but are of limited use when only a small set of similar control methods are used continuously (Smith and Gross 2007; MacLaren et al. 2019b; Weisberger et al. 2019). Harker and O'Donovan (2013) note that when IWM consists of little more than 'integrated herbicide management', it is unlikely to remain effective in the long run, as evidenced by the spread of weeds possessing general herbicide tolerance and/or multiple herbicide resistance (Mortensen et al. 2012; Délye et al. 2013; Comont et al. 2020).

The variation in the success of IWM depending on how it is implemented illustrates two points. The first is that any single weed management tool can be vulnerable to becoming obsolete through weed adaptation if applied to remove weeds without regard to its interactions with the wider agroecosystem, yet the same tool could be used judiciously within an ecological weed management framework to contribute to sustainable weed management. The second point is the importance of understanding the underlying ecological processes regulating weed abundance and diversity in order to integrate different tools and practices to design successful agronomic strategies. Effective IWM is not just the use of multiple control actions, but the combination of tools and techniques in ways that truly varies the type and timing of disturbance, and thus acts against adaptation trade-offs made by weeds. Achieving this requires a long-term, systems-based perspective. Ecology, the science of the interactions between organisms and their biophysical environment, is thus ideally placed to identify sustainable weed management practices. However, a transdisciplinary approach that integrates ecology with agronomy, the social sciences and stakeholders' perspectives will be key to make practical use of ecological knowledge in agriculture (Jordan et al. 2016) and to incorporate important contributions from other relevant biophysical sciences.

Despite the potential for optimising ecological function to support crop production (Landis et al. 2005; Pywell et al. 2015), ecological weed management remains relatively understudied and underutilised. IWM was first introduced by Shaw in 1982, and according to Bàrberi (2019), the concept of 'ecological weed management' was introduced by Liebman et al. in 2001. Considerable time has passed since the advent of these ideas, but uptake of further research into both concepts has been relatively low. Harker and O'Donovan (2013) noted that between 1995 and 2011, there were three times as many publications on 'weed control' than on 'weed management' and ten times more than on 'integrated weed management'. Not much has changed since 2011: most publications continue to focus on weed control, and few address either integrated weed management or ecological weed management (Fig. 2).

We thus intend for this article to facilitate a shift in weed science away from techno-fixes for weed control and toward an ecological foundation that enables the design of productive yet biodiverse farming systems (Fig. 3). The subsequent sections demonstrate that while weed ecology can be complex, it nonetheless gives rise to just a handful of key weed management principles or simple 'rules of thumb' that could be applied to different farming systems in different contexts using different sets of tools and strategies. Our ambition is that agronomists and farmers will begin to integrate these ideas with their existing knowledge of agronomy when thinking about their approach to weeds on their farm.

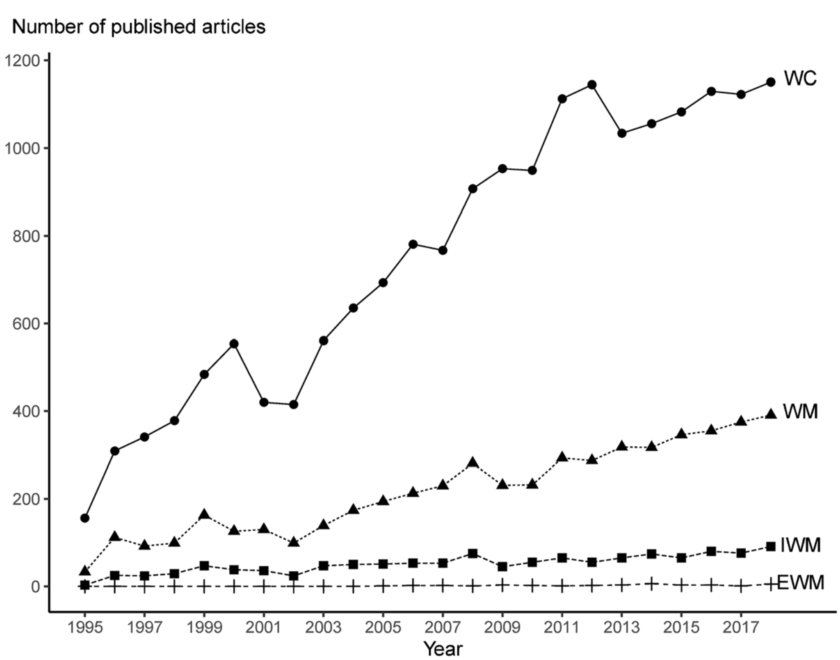

Fig. 2 The number of published articles in each year from 1995 to 2018 from a Scopus query containing either 'weed control' (WC), 'weed management' (WM), 'integrated weed management' (IWM) or 'ecological weed management (EWM) in their title, abstract or keywords. This figure is based on the data acquired using the same methodology as Figure 4 in Harker and O'Donovan (2013)

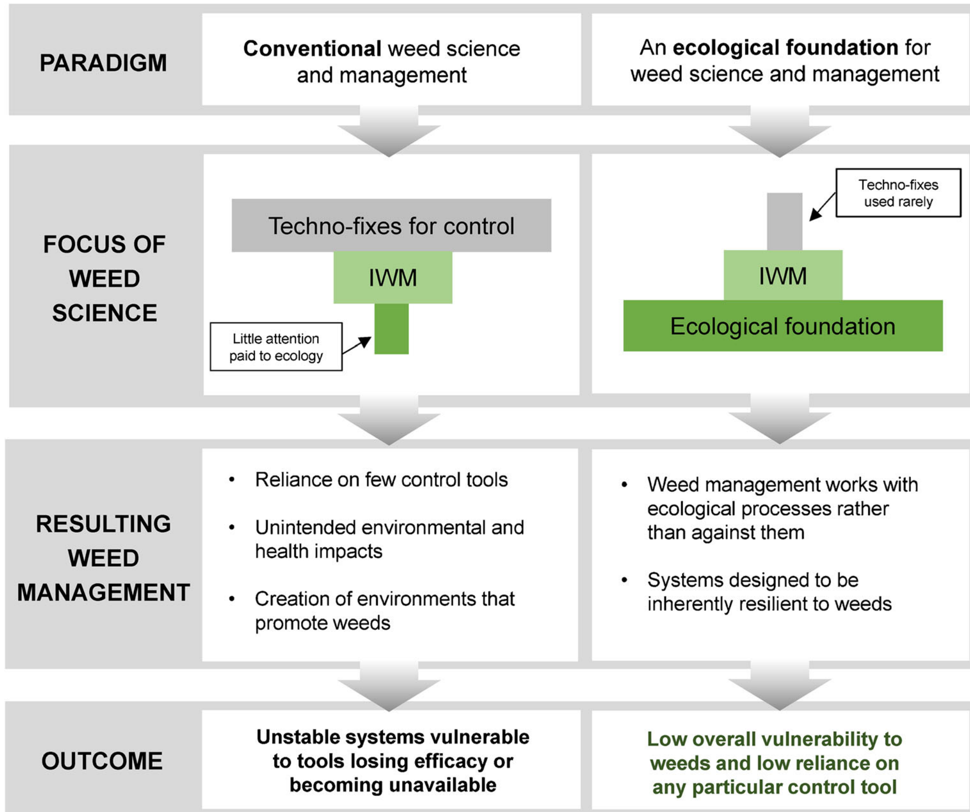

Fig. 3 A conceptual diagram of the relative importance of ecology, integrated weed management and technology in a conventional (left) or ecological (right) paradigm of weed science and management, and the consequences. The size of the shaded rectangles in the 'focus of weed science' panel indicates the relative effort directed toward different disciplines. In both paradigms, IWM is considered relevant, but IWM can build on an ecological foundation or can be dominated by the use of techno-fixes. A strong focus on technology when the ecology is poorly addressed creates an unstable system, resulting from techno-fixes 'tend[ing] to delay, transform and relocate problems, as well as creating new ones' (Scott 2011) when applied to solve specific problems (weed removal) without considering the wider context (processes leading to environmental degradation, health risks and herbicide resistance)

3 The ecological foundation for sustainable weed management

This section presents an up-to-date synthesis of ecological research relevant to weeds, drawing on a range of fields (population ecology, functional ecology, community ecology and invasion ecology) to provide an ecological blueprint for sustainable weed management. It focuses on the properties and processes that govern both the *abundance* of weeds (their total density and biomass) as well as their *diversity and composition* (the number and relative abundance of species in the community). Both aspects affect the magnitude and the balance of negative and positive impacts of weeds on crop production and on sustaining ecosystem health. This distinction between the two components of 'weediness' highlights the contrasting perception of weeds in a techno-fix paradigm compared with an ecological paradigm (Fig. 3). In the former, the emphasis is on reducing overall weed abundance through largely indiscriminate removal, whereas ecological weed management promotes the manipulation of weed communities to balance negative and positive functions (including to regulate the abundance of competitive species).

This emphasis of this review is on weed management in arable crops and temperate climates, reflecting the dominance of these systems in the literature and the authors' experience. Nonetheless, the majority of ecological relationships and processes discussed here would also be relevant to other systems including pasture management, perennial crops and tropical agriculture, but the application of the ecological theory into practice may differ in these contexts. The reader is directed to Bàrberi (2019) for a complementary discussion of ecological weed management in sub-Saharan Africa and to Liebman et al. (2001) for a more in-depth exploration of practical ecological weed management options in a variety of agricultural settings. This paper does not address parasitic weeds, which represent a special case with distinct ecological relationships with the crop and surrounding agroecosystem.

3.1 The ecology of weed abundance

3.1.1 Managing population growth: the weed life cycle and IWM

Restricting the overall incidence of weeds in crops, measured as either total biomass or density, has been the traditional focus of both weed science and weed management (Håkansson 2003; Zimdahl 2013). Crop yield tends to decrease as weed biomass increases, primarily due to competition between weeds and crops (Zimdahl 2007), so it is essential that farmers have tools and approaches available to limit the overall 'weediness' of fields (Oerke 2006). An understanding of the ecological processes that drive weed density and biomass, and how to influence these, is therefore an important element in an ecological weed management framework.

When and how weed populations increase in size can be explained by the interaction of weed seedbank dynamics, seedling establishment, weed growth and seed or propagule production and dispersal to or from the site (Davis 2017). The survival and reproduction of weeds requires their successful transition through a range of life cycle phases that can be influenced by farm management, the local environment and interactions with crops, livestock, other weeds and biodiversity (Mortensen et al. 2000; Chauhan et al. 2012). Population ecology thus underpins IWM based on many little hammers, as a range of control measures aimed at targeting different points of the life cycle should reduce the chances that the population of any one weed species can increase to a level where they become a serious threat to production. IWM is most effective for long-term weed suppression when it maximises the diversity of conditions and disturbances experienced by weeds both within years and between years. Using multiple control tools on a given field within a single season is more likely to eliminate a greater number of weeds in the short term, as the chance of any individual weed being resistant to or tolerant of multiple control methods is lower than for a single control method (Bourguet et al. 2013). Using different combinations of tools and techniques between years however can reduce the selection pressure for tolerance or resistance to any particular set of weed management actions. This is usually achieved via crop rotation, as different crops require different management practices in terms of the timing and types of seedbed preparation, fertilisation and pest control actions. However, these different control techniques must impose truly divergent selection pressures that act on contrasting weed traits in order to effectively limit weed abundance in the long term. For example, MacLaren et al. (2019b) found that high herbicide diversity (several similar 'hammers') in a rotation was less effective for weed suppression than a lower herbicide diversity in combination with grazing by livestock (two distinct 'hammers'), while Mahaut et al. (2019) found that herbicide diversity was less effective than sowing time diversity in crop rotations. Meanwhile, a recent investigation by Comont et al. (2020) suggests that while herbicide diversity can delay the evolution of target-site resistance to individual herbicides in the short-term, it can promote the evolution of metabolic cross-resistance to multiple herbicides in the longer term.

Current mainstream weed management practices do not take full advantage of opportunities to impose divergent selection pressures across weed life cycles (Fig. 4). In natural systems, plant populations are regulated by ecological pressures throughout their life cycle (Fig. 4a). However, current weed control measures tend to capture only some of these aspects of potential control and are generally focused only on interrupting plant growth (Fig. 4b, c). Techno-fix based weed management (Fig. 4c) tends to be even more narrowly focussed than properly applied integrated weed management (Fig. 4b), which limits the potential diversity of selection pressures that these control tools can impose on weeds, creating opportunities for species that can adapt to them to rapidly proliferate.

Given that all techno-fix weed management options (Fig. 4c) rely on a disturbance to induce mortality, any ecological strategy that confers tolerance to this in general may allow weeds to survive any combination of such measures. This can occur through variable seed dormancy and germination times, resprouting from roots or fragments, or sufficiently rapid growth to reproduce between disturbance windows and high fecundity. Fried et al. (2012) describe a shift toward late-germinating weeds as more types of herbicides are used, as this trait allows avoidance of any pre-emergence and early season herbicides. Many of the world's most problematic weed species, such as blackgrass (*Alopecurus myosuroides*) and ryegrass (*Lolium rigidum* and *L. multiflorum*), have ecological strategies to avoid chemical control (Kon et al. 2007; Fried et al. 2012; Bourgeois et al. 2019), as well as some degree of herbicide resistance (Han et al. 2016). To apply a greater range of ecological selection pressures to weeds requires a wider view of the agroecosystem and an exploration of processes mediated by environmental conditions, farm management and other farmed and wild organisms (Fig. 4a). When this wider view is considered, some key vulnerabilities of modern cropping systems to weeds that cannot be addressed by standalone techno-fixes become obvious, such as high resource availability and low biotic resistance to weeds.

3.1.2 Managing agroecosystem vulnerability to weeds: resource availability and biotic resistance

Studies of alien plant invasions in natural ecosystems have revealed that high and fluctuating resource availability ('bottom-up') and low biotic resistance ('top-down') are two key characteristics of ecosystems that determine how easily arriving plants can invade (Richardson and Pyšek 2006; Catford et al. 2009; Jeschke 2014). Both characteristics are typical of agroecosystems. Fluctuating resource levels occur when fertilisers are added and regular disturbance releases resources (light, water and nutrients), creating repeated opportunities for newly arriving species to exploit these resources to establish (Davis et al. 2000). In agroecosystems, regular harvesting and weed control actions release resources from crops and existing weeds, which are then available to new weeds, whether they are already resident in the soil seedbank or part of the transient community arriving via dispersal from elsewhere. As discussed by Smith (2015), such management actions keep annual agroecosystems in a permanent state of early succession, where resources are regularly released and weeds can make use of them to establish. Resource release in

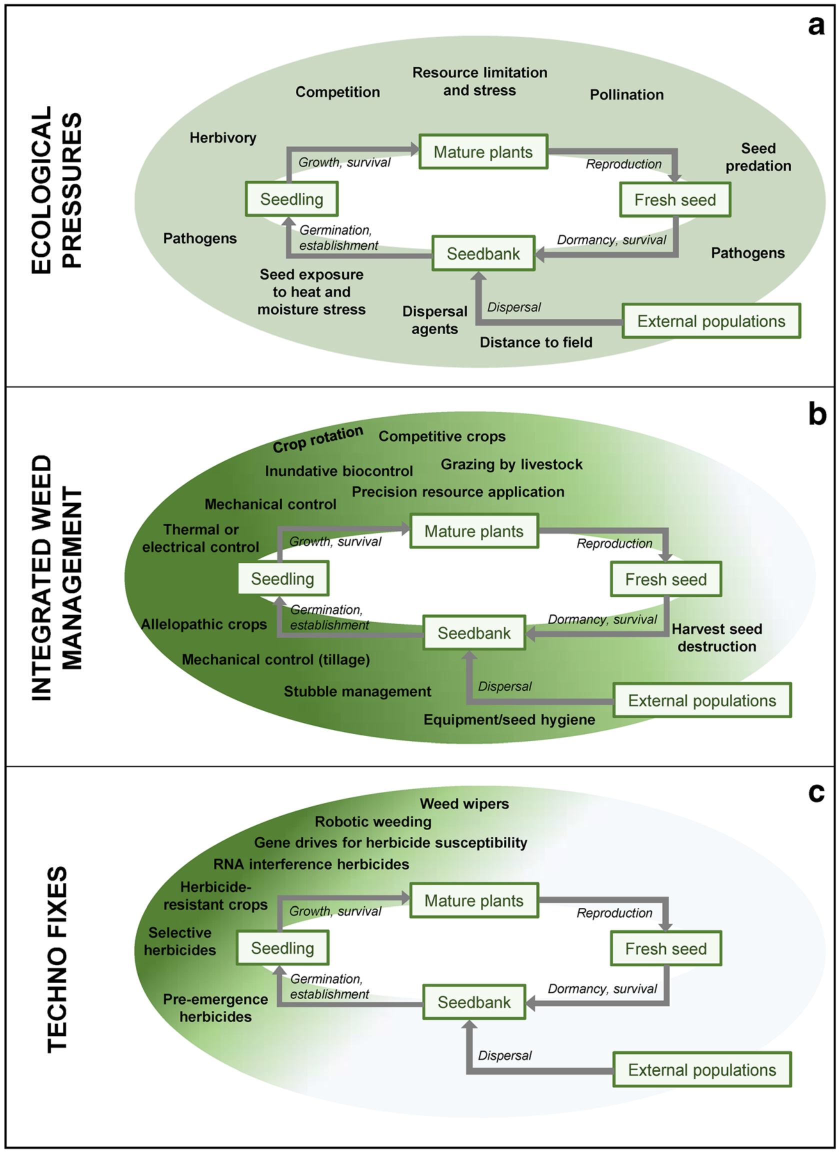

Fig. 4 A simplified weed lifecycle showing the life stages (green text boxes) and the processes that occur as weeds move from one life stage to another (italicised text). Ecological pressures or management tools (bold text) that may regulate or interrupt these transitions indicated roughly at the point of the lifecycle they affect. The shaded green circles indicate how much of the weed life cycle can be targeted by ecological pressures (top panel), integrated weed management tools (middle panel) and techno-fixes for weed control (bottom panel)

agroecosystems is of course necessary to make resources available for crop growth, so the challenge lies in ensuring that crops benefit from these resources while weeds do not. When resources are abundant, there is little initial competition between weeds and crops, but abundant resources allow weeds to produce more biomass, enabling them to become stronger competitors with crops when their canopies and root zones begin to overlap. This is illustrated by a study by Mahajan and Timsina (2011) showing that when weed control is ineffective, increasing resource availability via the addition of nitrogen fertiliser can promote weed growth to the extent that crop yield is much lower than at reduced fertiliser levels. This suggests that nutrient availability in particular influences early weed growth relative to crop growth.

Biotic resistance can be defined as the ability of a resident ecosystem to prevent new species from establishing and spreading via biotic interactions, such as competition, allelopathy or herbivory (Levine and D'Antonio 1999; Richardson and Pyšek 2006). There are few opportunities for this to occur in intensified agroecosystems, where habitat simplification and pesticide use have reduced populations of herbivores and seed predators (Navntoft et al. 2009; Geiger et al. 2010; Davis et al. 2011). Monocultures may also be relatively inefficient at competing for a suite of resources compared with a diverse plant community (Funk et al. 2008; Finn et al. 2013), and modern short-straw cereal cultivars can be less competitive than taller varieties (Andrew et al. 2015). This lack of biotic resistance combined with an abundance of resources leaves weed control actions as the main 'top-down' mechanism to limit weed survival in agroecosystems. This may increase selection pressure for weeds to adapt to control, given that there would be less chance of a fitness cost of such adaptations in resource-rich, herbivore- and competitor-free conditions (Comont et al. 2019).

Key steps toward ecological weed management systems therefore include exploring how resource availability to weeds can be limited and biotic resistance enhanced in agroecosystems, as this will increase their resistance to weed ingression. Potential practices to address resource availability and biotic resistance will be discussed in Section 4. In particular, it may be possible to manage resource availability and biotic resistance to favour crops rather than weeds. However, given that resources do need to be available to crops, and biotic pressures that limit crop growth avoided, there may be limitations on suppressing weed growth via these mechanisms. As such, completely weed-free fields are an unrealistic goal: weeds will always arrive in farm fields through natural dispersal and dormancy processes, and resource availability and incomplete biotic resistance will always permit some weed establishment. This raises the question of whether it is possible to manage the composition and diversity of weed communities to increase their positive contributions to agroecosystem productivity and sustainability relative to their negative effects on crop growth (Storkey and Westbury 2007; Smith et al. 2020).

Under certain conditions and with certain weeds, it may be possible to retain higher weed densities without higher impacts on yield. For example, Adeux et al. (2019b) recently demonstrated from a long-term cropping system experiment that yield loss from weeds is substantially reduced in plots with more diverse weed communities. Ryan et al. (2009) found that organic systems could host four to six times the number of weeds yet produce similar yields to a conventional (non-organic) system, while Swanton et al.'s (2015) review notes that the same number of weeds emerging after the crop are much less competitive than if they emerge with or before the crop. In some cases, exerting extra effort to remove more weeds can be counterproductive, by decreasing the overall energy and cost efficiency of crop production (Clements et al. 1995; Petit et al. 2015) and by reducing weeds' positive functions (Blaix et al. 2018). A full understanding of weeds' interactions with their agroecosystems therefore requires knowledge of the types of weeds present and relative abundance, in addition to total weed density or biomass. These examples and others are discussed below.

3.2 The ecology of weed diversity and composition

3.2.1 'Filters' as determinants of weed community diversity and composition

The composition and diversity of a weed community will determine its abilities to compete with crops, support biodiversity and perform other ecosystem functions. Community composition and diversity are determined by community assembly processes (Keddy 1992; Booth and Swanton 2002), in which the set of traits possessed by each weed species in a regional species pool determines whether it is capable of dispersing to a site and of surviving the local environmental conditions and biotic interactions (Fig. 5). Barriers to dispersal and survival act to filter the species that can persist in a community, by removing those species that lack the requisite traits to pass the barriers (Kraft et al. 2015). Strong filters have the potential to remove more species, and soft filters may allow more to survive. 'Filters' in community ecology are thus comparable with Liebman and Gallandt's (1997) 'hammers' in weed management, and the strength of the filter can be considered equivalent to 'selection pressure'. Filters in an agricultural setting can consist of disturbances (e.g. chemical or mechanical control), physical conditions (e.g. temperature, pH), resource availability and biotic interactions (e.g. competition, predation, facilitation).

Since Booth and Swanton (2002) proposed applying community assembly concepts to weed ecology, numerous studies have investigated how different landscape and field management practices select for different types of weeds and different levels of weed diversity (e.g. José-María et al. 2010, 2011; Ryan et al. 2010; Storkey et al. 2010; Navas 2012; MacLaren et al. 2019a). As in natural plant communities, these studies of weed communities have shown that strong filters reduce community diversity while weaker or softer filters allow more diverse communities (Fig. 5). The widespread use of strong and consistent filters in intensified agriculture, including herbicides, tillage and the cultivation of only a few crop species, has thus led to weed communities becoming dominated by only few species that are well adapted to survive those filters (Storkey et al. 2010; Fried et al. 2012; Garnier and Navas 2012; Bourgeois et al. 2019). Reduced diversity however does not necessarily equate to reduced weed abundance: if a species possesses the traits needed to survive the set of filters applied, there is nothing to limit the population growth of that species. Hence, the proliferation of a few weed species worldwide (such as blackgrass, ryegrass and palmer amaranth), which grow well alongside cereals and can readily develop herbicide resistance.

Varying management actions between years, while avoiding frequent use of any particular action, can promote weed diversity by reducing the chances that any single weed species will continuously encounter an unfavourable environment (Clements et al. 1994; Neve et al. 2009; Mahaut et al. 2019). This is particularly the case for weeds that have a persistent seedbank adapted to take advantage of ephemeral favourable growing conditions. A diverse weed community offers benefits in terms of supporting greater biodiversity at other trophic levels (Marshall et al. 2003; Bàrberi et al. 2010), which may in turn regulate weed abundance (Bohan et al. 2011; Petit et al. 2018) as well as pest populations (Gurr et al. 2003; Landis et al. 2005). Weeds can provide a range of ecosystem services for both crop production and environmental protection (Blaix et al. 2018), and the provision of these is expected to increase with increased diversity (Isbell et al. 2011). This has been demonstrated for pollinators: weed diversity can increase bee health, diversity and their contribution to crop yields (Bretagnolle and Gaba 2015).

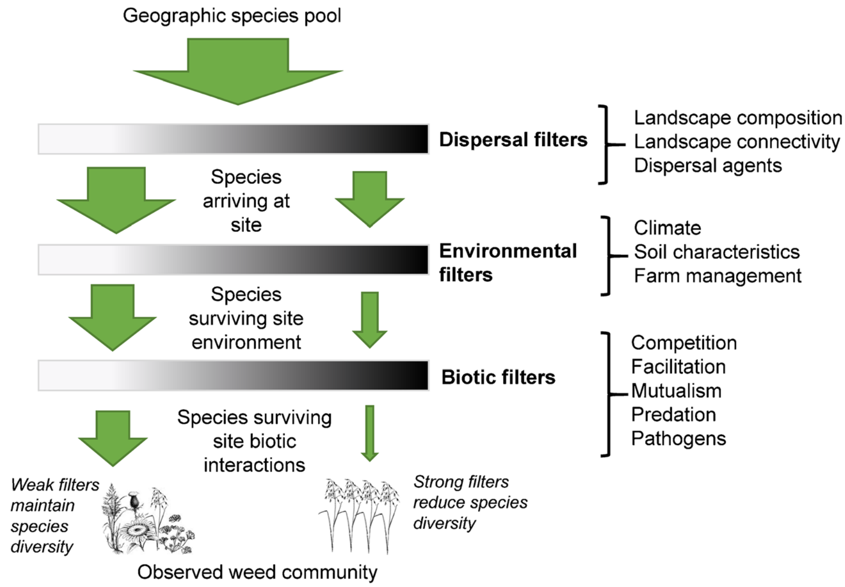

Fig. 5 Community assembly theory applied to weeds (modified from Booth and Swanton 2002). The shading of the bars represents filter strength, and the arrow widths indicate that more species are able to pass through weaker filters

There is also increasing evidence that a more diverse weed community is less competitive with any given crop. For example, Storkey and Neve et al. (2018) observed that an increase in weed species richness from 7 species to 20 species was associated with a decrease in wheat yield loss due to weeds from approximately 60 to 30%. Adeux et al. (2019b) found that more diverse weed communities caused less cereal yield loss and critically that two out of the six weed communities investigated caused *no significant yield loss*. Their study detected that increased yield loss was more strongly associated with reduced weed diversity than with increased weed density. Ferrero et al. (2017) detected a positive association between weed diversity and soybean yields, while Cierjacks et al. (2016) measured greater coconut and banana yields where weed diversity was higher.

There are two potential explanations for this reduced competitiveness of more diverse weed communities. The first is that a range of weed species with different phenologies and resource demands are less likely to overlap with those of the crop, compared with a low diversity of highly crop-mimicking weed species (Adeux et al. 2019b). It is this, rather than direct competition between the weed species, that could explain the reduced competitiveness of more diverse weed communities. Storkey and Neve et al. (2018) point out that when filter strength imposed on weeds is reduced, species with less similar resource demands to the crop can persist. If filter strength can be reduced while populations of competitive weeds are also limited (i.e. through many little hammers, reduced resource availability and enhanced biotic resistance), then it should be possible to maintain a diverse weed community that provides ecosystem services such as soil protection and biodiversity support, yet does not impose substantial competition against the crop.

However, although Adeux et al. (2019b) showed that increased weed diversity better explained reduced yield loss than decreased weed *density*, studies have not yet been able to distinguish the effect of increased weed diversity from decreased weed *biomass*. Of the diverse weed communities studied so far, either biomass has not been recorded or the more diverse communities have tended to have a lower total biomass than less diverse weed communities (Adeux et al. 2019b). It may simply be this reduction in biomass that reduces competition imposed by more diverse communities. However, the next question to ask is why more diverse communities tend to produce less biomass, and whether this can be consistently expected. Intensified agricultural systems do select for fast-growing tall weed species (see next section and Fig. 6), so any action taken to diversify conditions may thus start to favour smaller species. Mohler and Liebman (1987) pose a similar explanation, where any tool or practice that specifically targets the dominant weed in a community will both reduce community biomass (by reducing the dominant weed) and increase community evenness (due to lesser effects on other weeds). Further research is required to clarify the mechanism via which increased weed diversity is associated with reduced crop yield loss. However, from a practical perspective, it may not matter whether weed-crop competition is reduced by the actions that promote weed diversity or reduced by weed diversity itself; the same actions lead to the same result of reducing competition and promoting weed diversity.

Weed diversity can be promoted through 'top-down' management, in terms of varying the management-induced filters and biotic interactions experienced by weeds, through landscape management, the choice of weed control actions and crop rotation (Clements et al. 1994; Storkey and Neve 2018; Alignier et al. 2020). 'Bottom-up' resource management may also increase weed diversity, given that diversifying the nutrient sources available to weeds would facilitate the co-existence of species adapted to different nutrient sources ('the resource pool

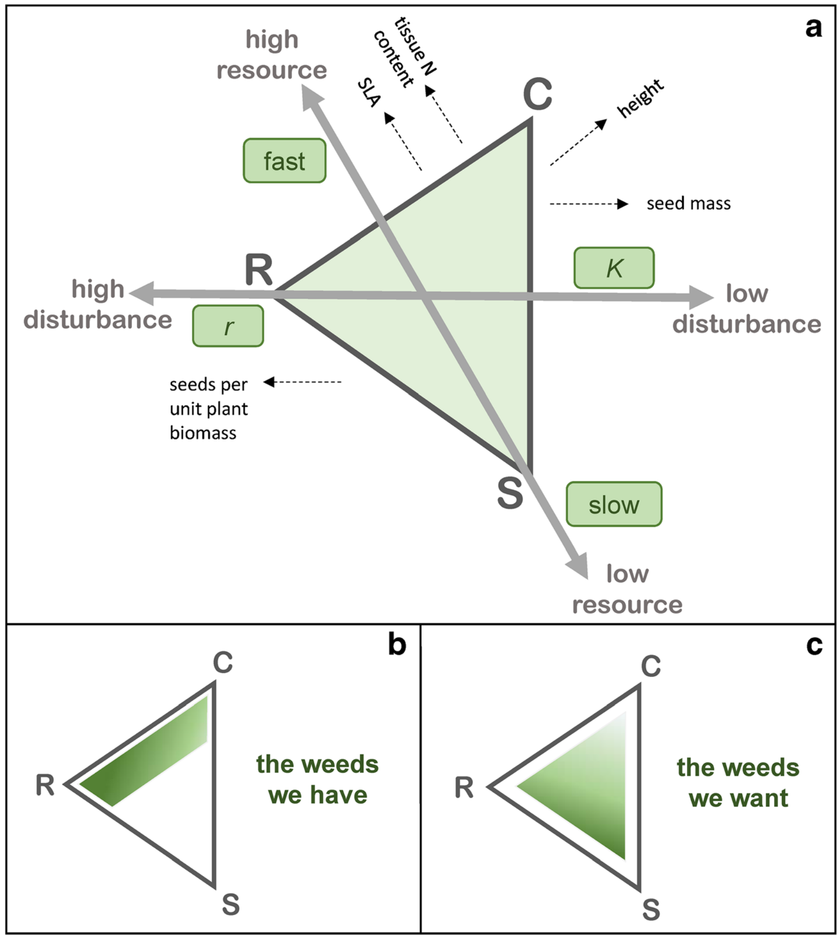

Fig. 6 Schematic showing **a** how different disturbance levels and resource availability are expected to select for weeds with different life history strategies, **b** the distribution in 'CSR' space (Grime 1977) of current common agricultural weeds according to Metcalfe et al. (2019) and Bourgeois et al. (2019) and **c** a more desirable distribution in 'CSR' space implying a functionally diverse community of weeds with a higher representation of species along the R-S axis. Panel **a** is based on several existing theoretical frameworks including Grime's (1977) 'CSR' life history triangle, MacArthur and Levins (1967) r-/K-selection reproduction spectrum and Reich's (2014) 'fast-slow' economic strategy spectrum. Evidence of trait dimensionality presented by Westoby (1998) and Díaz et al. (2016) indicates that synthesising these theoretical frameworks in this way explains much observed variation in global plant life history strategy in response to disturbance and resource availability

diversity hypothesis'; Smith et al. 2010). In particular, different plants can access different chemical forms of nitrogen at different times, and different plants can associate with different microbes in order to obtain these different forms (Smith et al. 2010). A greater diversity of both microbes and forms of nitrogen in organic fertilisers (manures and composts) compared with synthetic nitrogen fertiliser may explain why Ryan et al. (2009) found that organic cropping systems could produce similar yields to a conventional system, despite hosting several times more weeds. Resource diversity is less relevant to light and to moisture, of which different forms do not exist. However, promoting temporal and spatial divergence in these resources between weeds and crops may also be possible; this is discussed in subsequent sections.

3.2.2 Tailoring filters to select for more beneficial weed communities

The conflict between the need to remove weeds to prevent competition with crops and the need to retain weeds for biodiversity and ecosystem function could be mitigated by establishing less competitive weed communities (Storkey 2006; MacLaren et al. 2019a; Smith et al. 2020). This would mean that more weeds could be tolerated without increasing the competition imposed on crops. As described above, increasing weed diversity can reduce yield loss for a given density of weeds. It is also possible that the effect of weeds on yield could be altered through manipulating the particular types of weeds present. The 'response-effect' functional trait framework (Lavorel and Garnier 2002; Suding et al. 2008) can be used to explore this. The framework is based on the hypothesis that the way a plant responds to its environment and management is linked to its ecological function, as certain groups of traits both confer adaptation to a common set of conditions and result in a common set of ecosystem functions. There is evidence for such dimensionality in plant traits (Laughlin 2014; Reich 2014; Díaz et al. 2016), and thus grouping plants into functional types based on their response-effect traits can be used to make generalisations about the effect of agricultural management practices on weeds and their interactions with the agroecosystem and their impact on the crop (Lavorel and Garnier 2002; Garnier and Navas 2012; Navas 2012; Gaba et al. 2017).

Defining life history strategies based on traits can be an informative approach to characterising weeds functionally, given that they reflect a plant's resource capture rates and thus their competitiveness in a given situation (Reich 2014). Life history strategies have evolved in response to disturbance intensity and resource availability (Grime 1977; Westoby 1998; Bohn et al. 2014), both of which are strongly influenced by farm management in agroecosystems (Gaba et al. 2014). To the extent of current knowledge, two key dimensions appear to describe the majority of plant life history variation worldwide (Adler et al. 2014; Díaz et al. 2016; Fig. 6). The first of these is the 'fast-slow' economics spectrum (a whole-plant extension of the leaf economics spectrum; Reich 2014). 'Fast' plants are capable of rapid resource uptake and turnover but require high resource availability to sustain their physiology, while 'slow' plants can tolerate stress through resource conservation and recycling, but these mechanisms limit the rate at which they can capture resources (Adler et al. 2014; Reich 2014). The second dimension is the 'r/K selection' dimension (MacArthur and Levins 1967), with r-selected plants producing many small seeds (per unit biomass) that need a favourable environment for successful establishment, while K-selected plants produce fewer large seeds that are more capable of tolerating stress or competition (Moles and Westoby 2006). These two dimensions are reflected in Grime's (1977) 'ruderal/competitive/stress-tolerant' (R/C/S) life history triangle (Fig. 6). Ruderal species tend to be r-selected and competitive or stress-tolerant species K-selected, while stress-tolerant species have a slow physiology and both ruderal and competitive species tend to be 'fast'. On the global spectrum of plant strategies, weeds tend to follow 'ruderal', fast or 'r-selected' life strategies in response to the high disturbance frequencies and high resource availabilities that distinguish agroecosystems from natural ecosystems (Baker 1974; Smith 2015; Metcalfe et al. 2019). As agricultural intensity increases, in terms of increasing disturbance, resource availability and landscape simplification, then selection for 'faster' physiologies and 'r' reproduction strategies becomes more intense (Garnier and Navas 2012) and weeds with 'slower' stress-tolerant strategies become less common (Storkey et al. 2010, 2012; José-María et al. 2011; Bourgeois et al. 2019).

Agroecosystems that select strongly for ruderal and fast traits may increase weed competition with crops, given that fast life strategies confer competitiveness through rapid resource capture, which reduces resource availability to their neighbours (Reich 2014). Weeds that can establish before the crop are more competitive (Mohler 2001; Swanton et al. 2015), as are weeds that are taller than the crop (Storkey 2006; Gaba et al. 2017). 'Fast' traits may be particularly relevant in annual systems where annual harvest, weed control and crop sowing reset the 'race' for resources between crops and weeds each season (Smith 2015). In contrast, the least competitive weeds are expected to be species with a slow and more 'stress-tolerant' life strategy. These species would not only be less competitive with crops due to slower rates of resource uptake, but also more tolerant of the stress imposed by competition from crops (Andrew et al. 2015; Kunstler et al. 2016) and so more able to persist amongst crops to support biodiversity.

Blackgrass (*A. myosuroides*) and cleavers (*Galium aparine*) can be considered examples of fast weeds that would lie along the R-C axis of Grime's triangle (Fig. 6b). Both have relatively high early seedling growth rates (Storkey 2004), can extend above the crop canopy (Storkey 2006) and have a high competitive potential (12.5 and 1.7 plants per m^2 to reduce wheat yields by 5%; Marshall et al. 2003). In contrast, the relatively slow field pansy (*Viola arvensis*) is a short, shade-tolerant weed (Storkey 2006) that produces a relatively small number of seeds per unit biomass (Lutman et al. 2011) and has been shown to have a very low competitive ability (250 plants per m^2 to reduce wheat yields by 5%; Marshall et al. 2003). Field pansy would lie further along the R-S axis of Grime's triangle (Fig. 6c).

'Slow' weeds would be expected to occur more frequently under conditions of lower resource availability and low or intermediate disturbance (Fig. 6), and indeed short, late-flowering large-seeded weeds appear to have been disproportionately selected against as fertiliser and herbicide use has increased in recent decades (Storkey et al. 2010, 2012). However, reducing disturbance levels under high resource availability is likely to be problematic, as this would start to select for species with a more competitive strategy and shift weeds along the R-C axis of Grime's triangle (Fig. 6b). An increase in such 'competitive-ruderal' species, such as perennial herbs and grasses (Metcalfe et al. 2019), has been observed when tillage disturbance is reduced in organic farming systems (Armengot et al. 2015; Halde et al. 2015). Herbicides also represent a disturbance regime, and so herbicide resistance (i.e. loss of the herbicide disturbance) can also create a habitat niche for more competitive strategies. These competitive weeds may be particularly problematic due to their potential to outcompete both crops and rare weed species (Metcalfe et al. 2019).

It may also be possible to use functional traits and plant strategies to determine which types of weeds are most able to promote biodiversity and provide ecosystem services and thus enhance the environmental value of the weeds present. So far, however, it is not clear whether any particular traits consistently favour higher biodiversity, although Gaba et al. (2017) identified weeds that produce small seeds (but not too small) with a thin coat and a high seed lipid content may be most important for granivorous wildlife and more obviously that flowers and nectar resources support pollinators. There is some evidence that dicots typically support a wider range of invertebrates than monocots (Hawes et al. 2009), and plants with a high tissue nitrogen content and tender leaves may provide more resources to herbivores (Storkey et al. 2013). Given their typically faster rates of decomposition, such species may also promote nutrient cycling (Kazakou et al. 2016). The emerging pattern is therefore that the most beneficial weeds for biodiversity and ecosystem services lie along the ruderal (R) to stress-tolerant (S) axis of Grime's life history triangle (Fig. 6), and thus, management filters that select for these (in addition to promoting weed functional diversity) are likely to maximise both biodiversity and reduce competitiveness. There may be trade-offs between maximising beneficial biodiversity and promoting crop pests, although as long as the weed community is diverse and the majority of weeds are not from the same family as the crop, their potential to host crop pests should be low (Schellhorn and Sork 1997) and their value to natural enemies of pests should be high (Landis et al. 2005). Furthermore, the same management measures that limit weed abundance while promoting weed diversity, particularly in terms of management variation in time and space, can also be used to limit the populations of pests and pathogens (Storkey et al. 2019).

Currently, agricultural intensification is typically associated with increased disturbance, increased resource availability and increased landscape simplification and thus creates selection pressure for species positioned along the ruderal (R) to competitive (C) axis (Figs. 5 and 6). For example, Storkey et al. (2010) noted that taller, small-seeded early-flowering weeds become more common as agriculture intensified, while Bourgeois et al. (2019) identified that agricultural weeds tended to have a higher SLA, a higher affinity for resource-rich environments and more disturbance-tolerant life forms than non-weeds. Species along the R-C axis are more likely to compete with crops, while potentially providing fewer benefits to biodiversity and ecosystem service provision (Metcalfe et al. 2019). However, strategies that reduce resource availability and increase management and landscape diversity may be able to mitigate this effect and promote a greater diversity of weeds with traits that confer a lower competitiveness with crops (Fig. 6c).

3.2.3 Taking advantage of differences between weeds and crops

It may be possible to tailor management to either or both: (a) exploit trait differences between weeds and crops to suppress weeds while leaving the crop unharmed or (b) further reduce competition between crops and weeds by promoting divergence and complementarity in resource use in space and time. Mohler (1996 and 2001) suggests that the difference in seed size between crops and weeds could be key to giving crops an advantage over weeds in annual systems. Most weeds tend to have small seeds compared with most crops (with a few exceptions such as wild oats, *Avena fatua*), which means they produce smaller seedlings that are more demanding of resources and highly sensitive to competition. Crops tend to have larger seeds and larger seedlings and thus have a competitive head-start on weeds. This difference can be enhanced by increasing crop planting densities and the use of competitive cultivars or exploited by using filters that large seedlings can overcome, such as mulches (Mohler 1996).

Differences between weeds and crops however may also allow co-existence of a greater number of weeds at low levels of yield loss, consistent with ecological principles that explain species co-existence on the basis of resource supply and imbalance (Cardinale et al. 2009). For example, weeds that are much shorter than the crop tend to be much less competitive (Marshall et al. 2003; Storkey 2006), presumably due to reduced overlap by the weeds of the crop leaf canopy and rooting depth (Garnier and Navas 2012). Some management actions that directly select against tall species may thus shift the weed community to one composed of shorter species and so inherently less competitive with the crop, such as mowing in vineyards and orchards (MacLaren et al. 2019a) or the use of weed wipers in arable crops.

Crop choice could promote divergence between crops and weeds. According to the principle of limiting similarity (MacArthur and Levins 1967), competition imposed on weeds by crops should select for weeds that diverge from crops in their resource use, particularly if alternate resources are available (i.e. resources available in different chemical forms or at different times; Smith et al. 2010). In practice, however, studies indicate that filtering in agroecosystems tends to be sufficiently strong to select for weeds that mimic crops (Garnier and Navas 2012) and can actively select against the type of species expected to be less competitive and more valuable to biodiversity (Storkey 2006; MacLaren et al. 2019a). One concession that weeds seem to have made to adapt to crop competition is a relatively high shade tolerance (weeds tend to have a higher SLA and lower Ellenberg index for light than non-weeds; Bourgeois et al. 2019), but otherwise, the agronomic conditions created to favour crops also favour weeds with the same phenology and nutrient demands as crops (Fried et al. 2009; Perronne et al. 2015). If, however, the strength of filtering for crop-mimicking weeds is reduced in agroecosystems following the principles of diversity outlined above, then competitive crops may have a greater role to play in promoting divergent weed communities.

3.3 Ecological principles for sustainable weed management: beyond IWM

The relationships discussed in this and the previous section indicate that weed abundance and weed diversity have opposing responses to management consistency and resource availability (Fig. 7; Table 1). Intensive, simplified agroecosystems are characterised by high management consistency and high resource availability, and this tends to promote a high abundance but low diversity of competitive weeds. However, the opposite effect could be achieved by increasing management variability, reducing resource availability and increasing biotic interactions. This would be expected not only to result in more beneficial weeds (a diverse, less competitive weed community limited in abundance) but also to help manage pests and pathogens, as these are subject to many of the same population and community processes as weeds (Storkey et al. 2019).

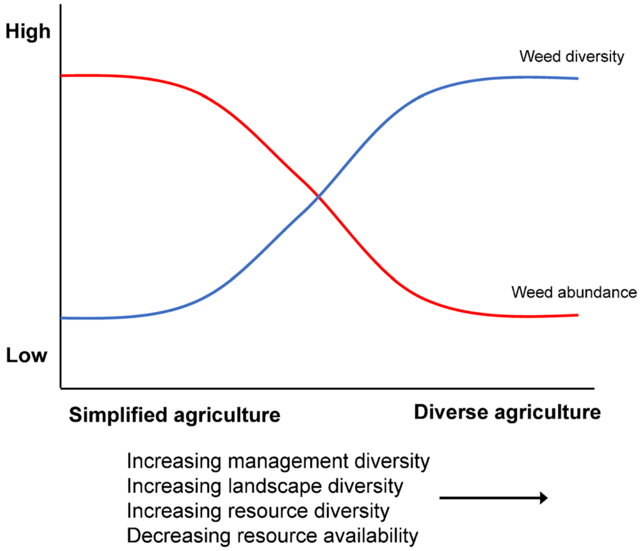

Fig. 7 Expected relationships between weed abundance, weed diversity and agroecosystem characteristics, based on the evidence reviewed. The exact nature of these relationships is not known, but sigmoidal rather than linear relationships were selected to represent the expected relationships because it is unlikely that weeds will ever reach zero abundance or diversity and impossible that they would reach infinity

Four key ecological principles for sustainable weed management arise from our review of the ecological properties and processes that influence weed abundance and diversity (Tables 1 and 2), and these principles can help to guide the design of agricultural systems that are resilient to weeds. These principles are to (1) increase diversity in all its forms, (2) reduce resource availability to weeds, (3) use 'little hammers not sledgehammers' and (4) take advantage of the positive effects of weeds. The meaning of each principle and their translation to practical agriculture in terms of cropping systems, livestock, fertilisers, soil and landscape management and weed management decisions (Table 2) are explored in the next section, in the context of their effects on weed ecology (Table 1).

Predecessors of our four principles can be seen in some previous reviews on weed management, for example, Harker (2013) discussed 'big hammers vs little hammers' and 'tactics that discourage weeds' while Bagavathiannan and Davis (2018) highlight the importance of 'multi-tactic weed management strategies'. Such ideas are usually presented as key elements of IWM and often in the context of avoiding herbicide resistance in order to conserve the utility of herbicides. Here, however, we emphasise that ecological weed management goes beyond IWM and herbicide stewardship. Our four principles prioritise the fundamental integrity and resilience of the agroecosystem at large spatial and temporal scales as the foundation to underpin any weed management strategy in a given field and year (Figs. 3 and 4). Our principles give rise to multiple synergies with other agroecosystem functions (such as pest management, yield stability and wildlife support; see Section 5.1) and are applicable to designing herbicide-free systems as well as to designing systems in which herbicides could be used judiciously in the long term.

4 From theory to practice: ecological weed management options

In this section, we explore potential practical opportunities for implementing our four principles of sustainable weed management (Table 2) from landscape to field scales (Fig. 8). We include some well-known and tried and tested practices, as well as identifying areas for further research. The list is not exhaustive; it is intended to be an illustration of how ecological theory can inform weed management, and we hope it can be expanded upon by others. Recent experimental evidence is reviewed to highlight the effects of various strategies in practice; however, further work is needed to definitively prove the effects of many of these practices and also to adapt them to the variety of conditions and farming systems around the world.

4.1 Increase diversity in all its forms

4.1.1 Crop and management diversity in time and space

Crop diversity can be increased temporally, through growing more different crops in rotation, or spatially, with different crops in different fields or together as intercrops and mixtures. There is substantial evidence that crop rotation (and the associated rotation of management practices) is a highly effective tool for reducing weed abundance and increasing weed diversity (Liebman and Dyck 1993; Anderson 2005; Davis et al. 2012; Adeux et al. 2019a), with a meta-analysis by Weisberger et al. (2019) reporting a 49% reduction in weed density in diverse compared with simple rotations. Rotations that incorporate management diversity both within and between years (Smith and Gross 2007; Bourguet et al. 2013; MacLaren et al. 2019b) and that use crops with different sowing dates each year are particularly effective (Mahaut et al. 2019; Weisberger et al. 2019).

Crop rotation reduces weed abundance and promotes weed diversity through altering the conditions experienced by weeds each year (Clements et al. 1994). Similarly, crop and management diversity in space at the landscape scale (i.e. different crops in different fields) can limit weed population spread by reducing suitable habitats available to each species and allow a more diverse weed community to persist due to reintroduction of species from different habitats through spillover. A recent cross-continent analysis of the effect of compositional and configurational crop heterogeneity on weeds reported that in-field weed diversity was higher in landscapes with a more heterogenous crop mosaic (Alignier et al. 2020). In addition, landscape-scale diversity reduces the area available for weeds to adapt to specific conditions and can thus slow the evolution of herbicide resistance (Neve et al. 2009).

Table 1 A summary of the ecological properties and processes of agroecosystems that influence weed abundance, diversity and competitiveness, as described in Section 3. Symbols at the top of each cell indicate whether a positive (+) or negative effect (−) is expected, although some depend on the context (+/−). Blank cells indicate a neutral effect

Ecological process or property	Effect on weed abundance	Effect on weed diversity	Effect on weed competitiveness
Filter strength (see Fig. 5)	+ / − Can temporarily reduce abundance by eliminating susceptible species, but may not affect abundance in the long term as tolerant species increase	− Reduces diversity by eliminating susceptible species	+ Strong filters aimed at promoting crop survival can select for crop-mimicking weeds
Filter diversity between years (see Fig. 5)	− Can reduce abundance by increasing chance that all species will be limited in some years	+ Can promote diversity by increasing chance that all species can reproduce in some years	− Promotes diverse weed communities which are typically less competitive
Resource availability (see Fig. 6)	+ Higher resource availability allows more weeds to grow and increase their reproductive output	− May limit diversity through favouring species with a 'fast' and r-selected life history at the expense of 'slow' species	+ Promotes 'fast' r-selected species adapted to rapid resource capture
Resource diversity		+ Promotes diversity through increasing resource-related niche space	− Provides opportunities for weeds to diverge from crops, reducing selection for crop mimics
Disturbance intensity (see Fig. 6)			+ / − Too much disturbance selects for 'fast' competitive species, too little allows for perennial weeds
Limiting similarity			− Reduces competition by promoting weeds that diverge from crops in their resource use
Biotic resistance	− Reduces abundance as other organisms can limit resource availability to weeds, and reduce survival through herbivory, seed predation etc		
Landscape heterogeneity	− Can promote biotic resistance through supporting natural enemies	+ Promotes diversity through increasing refugia for weeds that cannot survive certain filters	− Decreasing crop monocultures reduces the source population area for well-adapted weeds of those crops

Spatial crop diversity at the field scale, in terms of polycultures, intercrops and crop species and cultivar mixes, can contribute to weed suppression through increasing the resource use efficiency of a crop (Malézieux et al. 2009; Isbell et al. 2017). Incorporating different crop species with complementary patterns of resource use in space and time can minimise crop-crop competition and maximise the overall capture of light, water and nutrients in the field, thus reducing resource availability to weeds (Finn et al. 2013; Brooker et al. 2015).

4.1.2 Integrated crop-livestock systems

Various economic pressures have driven farms to specialise in either crops or livestock, as agricultural systems have intensified (Sanderson et al. 2013). However, livestock and forage crops can prove valuable for weed management in cropping systems (Hilimire 2011). MacLaren et al. (2019b) report a greatly reduced weed abundance and an increased weed diversity in systems where crops are rotated with grazed legumes, while Leon and Wright (2018) note a 75% reduction in palmer amaranth (*Amaranthus palmeri*) following grazed bahiagrass (*Paspalum notatum*). Doole and Pannell (2008) found that grazed lucerne (*Medicago sativa*) pastures can increase the profitability of cropping systems in the presence of severely herbicide-resistant weeds. Integrating livestock introduces grazing as a direct control method for palatable weed species, which may impose a distinct selection pressure on those weeds through continuous removal of biomass, rather than a single and more often lethal disturbance event imposed by tillage or herbicides (Fig. 4). Integrating livestock also increases the incentive for more diverse crop rotations by requiring

Table 2 A summary of potential weed management practices associated with each key ecological principle of sustainable weed management. All practices listed are considered to be promising elements of an ecological weed management strategy but are not necessarily proven. Some key references discussing underlying theory and/or possible application of these practices are noted, but see the main text (Section 3) for a full explanation of each strategy and the available evidence for each practice

Ecological principle	Management strategy	Possible practices	Key references
Increase diversity in all its forms	Crop and management diversity in time	Crop rotation	Liebman and Dyck (1993); Bagavathiannan and Davis (2018); Weisberger et al. (2019)
	Crop and management diversity in space	Crop mosaics; different crops in different plots or fields	Alignier et al. (2020)
		Intercropping, polycultures, agroforestry, cover crops and catch crops	Malézieux et al. (2009); Brooker et al. (2015); Isbell et al. (2017)
	Integrated crop-livestock systems	Multi-year grazed or cut leys Annual forage crops	Hilimire (2011); Döring et al. (2017)
		Grazing of orchard/vineyard floors	
	Landscape diversity and wild diversity	Habitat diversity to promote natural enemies	Landis et al. (2005); Trichard et al. (2013); Kulkarni et al. (2015)
		Reduced tillage and residue management to promote natural enemies	Menalled et al. (2007); Kulkarni et al. (2015)
		Crop rotation and crop mosaics	Clements et al. (1994); Neve et al. (2009); Alignier et al. (2020)
	Resource diversity	Use more fertilisers based on organic materials Integrate different resource sources such as legumes and livestock	Smith et al. (2010); Poffenbarger et al. (2015); Storkey and Neve et al. (2018)
Little hammers' not 'sledgehammers'	Avoid repeated use of strong hammers	Combine management tools and practices within years but rotate them between years (especially sowing date)	Bourguet et al. (2013); Mahaut et al. (2019); Weisberger et al. (2019)
		Combine multiple soft filters in the system rather than using single strong filters	Clements et al. (1994); Bagavathiannan and Davis (2018); Storkey and Neve et al. (2018)
	Reduce disturbance frequency	Include perennial crops	Davis et al. (2000); Smith (2015); Döring et al. (2017)
	Tailor filters for less competitive and beneficial weeds	Reduce resource availability and disturbance frequency to select for 'slow' weeds	Storkey (2006); Storkey et al. (2010); Garnier and Navas (2012)
		Use mowing or weed wipers to select for weeds shorter than the crop	MacLaren et al. (2019a)
		Manage non-crop habitats to select for 'slow' species and to provide herbicide refugia	Boutin et al. (2001); Bourguet et al. (2013); Metcalfe et al. (2018)
	Take advantage of differences between crops and weeds	Use mulches, shallow mechanical control, or moisture gradients, or allelopathy to disadvantage small-seeded weeds compared with large-seeded crops	Mohler (1996, 2001); Liebman and Sundberg (2006)
Limit resource availability to weeds	Resource capture by crops	Select competitive crop varieties	Andrew et al. (2015)
		Mix or intercrop complementary crops	Funk et al. (2008); Finn et al. (2013); Brooker et al. (2015)
		Cooperative crops or genetically diverse crops	Weiner et al. (2010); Bertholdsson et al. (2016)
	Covers and mulches	Mulches (preferably organic materials) or crop residue management	Mirsky et al. (2013); Steinmetz et al. (2016)

Table 2 (continued)

Ecological principle	Management strategy	Possible practices	Key references
		Cover crops and intercrops, perennial groundcovers	Blanco-Canqui et al. (2015); Brooker et al. (2015); Moore et al. (2019)
	Precision resource placement	Precision fertiliser and drip irrigation	Grattan et al. (1988)
Take advantage of the positive effects of weeds	Some weeds can be directly beneficial to the crop	Use weeds to stress crops (for crop quality), support natural enemies or deter pests where appropriate	Frank and Barone (1999); Landis et al. (2005); Gibson et al. (2017); Blaix et al. (2018)
	Allow weeds for other ecosystem services	Leave weeds where possible, and use management practices that promote a diverse weed community	Clements et al. (1994); Marshall et al. (2003); Storkey and Neve et al. (2018); Adeux et al. (2019b); Smith et al. (2020)

annual forage or hay crops or multi-year leys to be incorporated into rotations (Tracy and Davis 2009). Forage crops and leys can present an easier opportunity than cash crops to introduce both competitive crops and crop mixtures to a rotation. Forage crops are often selected for biomass production rather than grain yield, which can equate to a faster life history strategy and thus greater competitiveness with weeds, while crop mixes can be more efficient than monocultures at resource capture. Suter et al. (2017) report that weed survival reduced by half in a four-species mixture compared to monocultures, while Tracy and Sanderson (2004) identified a consistent negative relationship between forage pasture diversity and weed abundance across the north-eastern USA. Introducing multi-year (perennial) leys into an annual rotation can select against annuals and so promote a greater diversity of life forms in the weed community (Döring et al. 2017).

4.1.3 Landscape diversity and wild biodiversity

Increasing landscape diversity in terms of both crop diversity and habitat diversity may contribute to weed suppression through limiting the spread of weed species associated with particular crops (Neve et al. 2009) and through providing habitat to potential natural enemies of weeds such as herbivores and seed predators (Trichard et al. 2013; Kulkarni et al. 2015). Encouraging weed control by natural enemies reduces the effort farmers have to invest in weed control and so can reduce both economic and environmental costs. The loss of this 'regulating ecosystem service' through declining functional biodiversity in the landscape has increased reliance on chemical protection products and needs to be restored to increase the resilience of farming systems (Tscharntke et al. 2005).

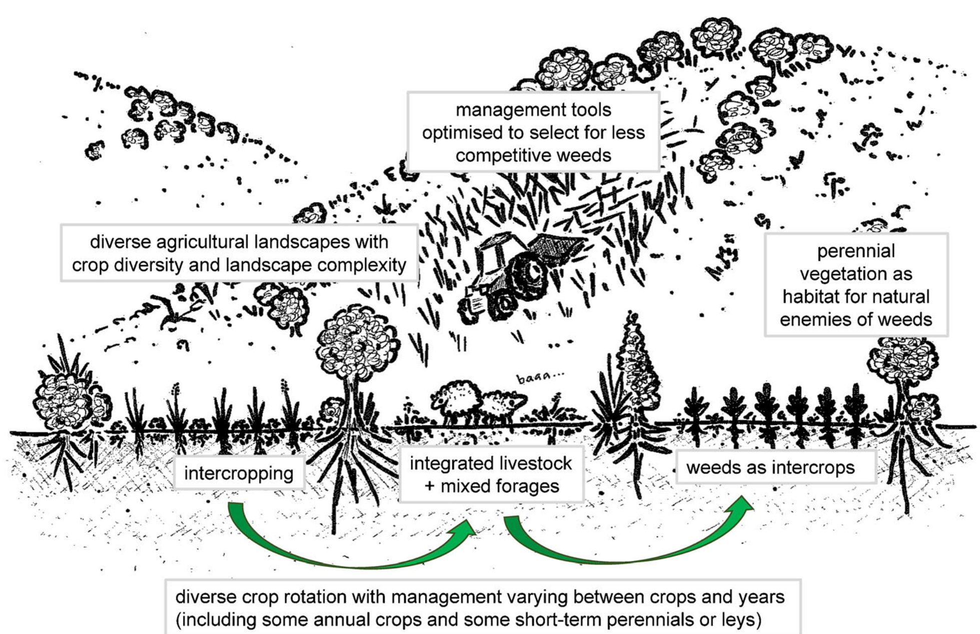

Fig. 8 An illustration of how different practices can be integrated into a systems-level ecological weed management strategy

Some natural enemies of weeds could also threaten crops, so it would be important to encourage either species-specific natural enemies or natural enemy activity at times when crops are less vulnerable. Enhancing weed seed predation (for example by carabid beetles) between cropping seasons may offer such an opportunity in arable systems, given that weed seeds must persist in the field to establish the next generation, while crop seeds are typically re-planted. Further research is required to establish how to ensure reliable seed predation, as for example, predation rates by carabid beetles can range from less than 5% up to 70% of all seeds produced in a season (Kulkarni et al. 2015) and may only occur at specific times under specific conditions (Davis et al. 2011). However, increased landscape complexity, crop and habitat diversity, no-till practices, retaining crop residues and increasing vegetation cover have all been found to encourage the abundance, diversity and activity of weed seed predators (Menalled et al. 2007; Meiss et al. 2010; Trichard et al. 2013; Petit et al. 2018). An advantage of encouraging natural enemies for weed suppression would be their capacity to respond in a density-dependent fashion. As weed populations increase, more natural enemies are drawn to the greater food resource, and thus, the pressure they apply to reduce that population is increased (Baraibar et al. 2012).

4.1.4 Resource diversity

According to the resource pool hypothesis (Smith et al. 2010), if multiple resource sources are available to weeds, then competition with crops will tend to favour weeds that use alternate resources, thus reducing weed-crop competition and selecting for a less competitive weed community over time. Systems fertilised with organic materials are thought to have greater resource pool diversity (in terms of time, space and chemical forms) than conventional systems (Smith et al. 2010), which may explain why several studies have identified that weeds are less competitive with crops per unit biomass in organic rather than conventional systems (Davis et al. 2005; Ryan et al. 2009). A pot trial by Poffenbarger et al. (2015) found evidence that resource partitioning does occur between crops and weeds, although it was not clear if this was due to plants accessing different chemical forms of nitrogen or accessing different areas of soil through different root structures. More research is required to understand this effect and explore whether it has consistent results across different agroecosystems, but if so, nutrient resource diversity could be increased through using legumes, crop residues, manure and compost-based fertilisers. It is also possible that this resource diversity could promote weed diversity through increasing the number of available resource-related niches, under which further reductions in competitiveness could be expected (Smith et al. 2010; Storkey and Neve 2018; Adeux et al. 2019b).

4.2 'Little hammers' not 'sledgehammers'

4.2.1 Avoid consistent use of strong filters

As discussed in the ecology section, the use of techniques that impose strong filters or 'sledgehammers' on the weed community will limit weed diversity but will not necessarily limit weed abundance, if suitably adapted species are present and able to multiply. For example, herbicide use intensity in the absence of crop rotation can be associated with higher weed abundance (MacLaren et al. 2019b) and higher prevalence of herbicide resistance (Hicks et al. 2018). The most promising approach thus seems to be to use multiple 'little hammers' within and between years and sites to reduce selection pressure for resistance and also to conserve weed diversity (Mortensen et al. 2012; Bourguet et al. 2013; Storkey and Neve 2018). Varying crop sowing and weed management timings between years can be particularly effective in this regard (Weisberger et al. 2019).

A step toward reducing filter strength would be the uptake of precision herbicide applications or precision mechanical weeding. Herbicides or mechanical control could be applied to areas with problematic weed patches while allowing a diversity of weeds to remain in other parts of the field (Metcalfe et al. 2018). The areas where these 'strong filters' are required would be expected to decrease as other practices in line with our four key ecological principles are identified and integrated into the system, and it becomes overall more resilient to problematic weeds.

4.2.2 Reduce disturbance frequency

Every disturbance that removes existing biomass and releases the resources captured by that biomass back into the environment presents an opportunity for new weeds (particularly ruderal species) to use those resources to establish (Smith 2015). The disturbance and subsequent resource flushes associated with the seedbed preparation, fertilisation and harvest of annual crops make agroecosystems inherently vulnerable to weeds (Davis et al. 2000). Incorporating multi-year leys into crop rotations can help to reduce the abundance of annual weeds (Döring et al. 2017), and the development of perennial field crops may present further opportunities to achieve this. Even if such crops only persist for 3 or 4 years, they substantially reduce disturbance and subsequent resource flushes. This limits opportunities for weed establishment compared to annual re-planting (Smith 2015). Breeding for perennial field crops for temperate regions continues, with 'Kernza' wheatgrass already commercially available in the USA (Lanker et al. 2019) and other crops in development (Schlautman and Miller 2018). Use of the few existing tropical perennial field crop species such as pigeon pea (*Cajanus cajan*) and sorghum (*Sorghum bicolor*) could also be upscaled (Peter et al. 2017). However, perennial crops still need to be utilised within diverse systems (either through long rotations that include perennials or through altering understory management techniques beneath perennials) or selection pressure will eventually promote a set of weeds more adapted to lower disturbance.

It seems intuitive that minimum tillage practices would also reduce disturbance and resource release, but this is not necessarily true. Minimum tillage can reduce soil turnover and light penetration into the soil during tillage operations and thus reduce germination of deeply buried seeds, but over time, it also results in weed seed accumulation at or near the soil surface. If there is no soil cover, then the depth of tillage does not affect the amount of light reaching the soil surface, nor the nutrients contained therein, which can be used by these weed seedlings to establish. Shifting from ploughing to minimum tillage thus selects for a different weed community, but not necessarily a better one (Armengot et al. 2016), and often results in an increase in weeds (although this is not always associated with a yield loss; Cooper et al. 2016). Any perceived or actual negative impacts from weeds under reduced tillage can lead to an over-reliance on herbicides due to the loss of tillage as an option to limit weeds. To avoid increased herbicide use, minimum tillage farmers need to maximise their uptake of the other strategies and practices to promote management diversity and reduce resource availability (Chauhan et al. 2012). Minimum tillage could contribute to reduced resource availability if it allows crop residues to be maintained on the soil surface to prevent germination through intercepting light (and this combination has been shown to be an acceptable method of weed management; Mirsky et al. 2013).

4.2.3 Tailor management practices to filter for beneficial weeds and avoid selection for crop mimics

In some farming systems, it may be possible to use management actions to directly select for weeds that are less competitive with the specific types of crop grown. In general, the evidence discussed so far suggests that strategies that involve limited disturbance and reduced resource availability would select for weeds with a slower life history, which are expected to be generally less competitive with crops. In contrast, increased disturbance frequency and resource availability would select for weeds with a faster life history (Fig. 6). Increased crop diversity can reduce competition through reducing the abundance of weeds adapted to grow alongside any particular crop, which tend to be competitive due to the need to match the crop's phenology and resource demands in order to avoid disturbances associated with sowing and harvest (see discussion in Section 3.2). Additional, specific solutions to increase weed-crop complementarity may also be possible for some systems, such as the use of mowing or weed wipers to promote weeds shorter than crops.

Similarly, it may be possible to reduce the seed rain of competitive weed species by altering management of non-cropped areas to avoid selecting for these species across so much of the landscape. For example, the spraying of fence lines or headlands to avoid these becoming 'reservoirs of weeds' consistently creates environments where only weeds adapted to establishing in bare soil and growing rapidly between spray events, or tolerating spray events, could survive. These may then act as a seed source of fast r-selected herbicide-resistant weed species that would impose high early-season competition on annual crops. In contrast, areas where weeds can survive without encountering herbicides (refugia) can also slow the spread of herbicide resistance through providing a source of susceptible alleles to the wider population (Bourguet et al. 2013). However, some types of neighbouring vegetation can prove a source of problematic weeds; Metcalfe et al. (2019) point out that grass margins can be a source of particularly competitive species, which may suppress both crops and other more desirable weeds if local management practices are not sufficient to limit their ingress into fields.

Habitats that are managed as differently as possible from farmed fields in terms of disturbance and resource availability would seem least likely to produce species that can thrive as weeds (Boutin et al. 2001; Metcalfe et al. 2019). Options could be restoring or conserving hedgerows or woodland or establishing grass and wildflower margins managed by mowing and/or tillage in ways that contrasts to the crop field management, although further research is required to verify which habitats consistently suppress rather than promote weeds (Boutin et al. 2001; Metcalfe et al. 2019). Managing such habitats also presents an additional cost to farmers that would need to be weighed against any beneficial effects on weeds. Other services provided by non-crop vegetation could make it more attractive, though, for example, Morandin et al. (2016) demonstrate that establishing hedgerows amongst tomato and walnut crops in California can provide a return on investment in 7 to 16 years through promoting beneficial insects and suppressing pests.

4.2.4 Take advantage of differences between weeds and crops

Tactics that specifically target weed's vulnerabilities may reduce the amount of energy and inputs required to remove them. Mohler (1996, 2001) suggests taking advantage of the fact that weeds typically have smaller seeds and smaller seedlings than crops in several ways. First, large-seeded crops can be planted more deeply when soil moisture is present at depth but not at the surface, so crops can germinate but weeds cannot. A similar effect can be achieved through the use of mulches that larger seedlings can germinate through. Superficial mechanical weeding could be used just after planting to disrupt weed seedlings on the surface while the crop remains below or to throw soil into the rows at the stage where crops have large enough seedlings to withstand this but weeds do not (Mohler 1996, 2001). The generally smaller size of weed seeds themselves may also make them more vulnerable to control at the seed or white thread stage, such as to allelopathic or other chemical disturbance (Liebman and Sundberg 2006). Weed seeds must also survive in the field between seasons, while crop seeds are re-planted each time. This may offer opportunities for increasing seed predation, decomposition or mortality due to exposure to moisture and temperature extremes, at times when crop seeds are not present. Quite how this would be achieved however remains to be explored.

4.3 Limit resource availability to weeds

4.3.1 Competitive and cooperative crops

Increasing a crop's capacity to capture resources is an effective means of reducing resources available to weeds and of promoting weeds that diverge from crops in their resource use. The choice of crop species and cultivar, as well as their timing, density and arrangement can affect resource capture and sequestration. Some crops are inherently capable of greater and more rapid resource capture and thus have a greater suppressive effect on weeds. In annual systems, these tend to be taller crops with extensive root systems and high early vigour (Andrew et al. 2015) and larger seeds (Mohler 1996). These traits suggest that crops with a faster, competitive life history strategy are more able to outcompete weeds in annual systems.

Increasing sowing density and using sowing arrangements that maximise crop resource capture in space, such as reduced inter-row spacing, can also suppress weeds (Mohler 1996; Colbach et al. 2014). Such effects could potentially be enhanced by breeding crops for traits that improve their cooperativeness, i.e. total crop resource capture and total yield rather than individual plant fitness (Weiner et al. 2010; Weiner 2017). Such 'cooperative crops' have yet to be developed, but an intriguing alternative that may be more attainable are 'composite cross populations' (CCPs), where multiple varieties are crossed and allowed to develop into a genetically diverse crop population over several generations in the same environment. This approach has been shown to result in cereal crops developing more competitive traits with weeds, such as increased height, early ground cover and root and shoot growth (Döring et al. 2015; Bertholdsson et al. 2016). Genetic diversity may also increase crop reliability in the face of climate variability, increasing the chance that the crop will produce sufficient biomass to suppress weeds regardless of the conditions (Döring et al. 2015). The first CCP is already available for sale as seed and flour in Europe (Organic Research Centre 2018; Hodmedod's 2020).

A similar effect could potentially be achieved through intercropping species with complementary use of resources in time and space (Brooker et al. 2015), as noted above in the section on crop and management diversity. It can, however, be difficult to predict which crop combinations will be successful in this regard (Finney et al. 2016). Evidence so far suggests that phenological diversity (Finn et al. 2013) is more effective than growth form diversity (MacLaren et al. 2019c) to increase resource capture and suppress weeds.

4.3.2 Mulches and covers (living and dead)

A widely used technique of reducing light availability to weeds is the use of covers and mulches. These can be composed either from organic materials (e.g. wood chips, straw, crop residues) or synthetic materials (e.g. plastic sheeting), or can be living plants, such as cover crops and intercrops. With regard to choosing a mulch type, it is important to keep in mind the systems approach. For example, in the quest for sustainable agriculture, plastic sheeting may not be optimal when one considers the impacts of its creation, degradation and disposal (Steinmetz et al. 2016). Plant-based biodegradable polymer sheeting may be a good option to reduce impacts (Shogren et al. 2019), while mulches of organic materials such as straw can also improve soil function and fertility (Tu et al. 2005).

Cover crops or intercrops (sometimes known as living mulches) can provide a variety of other functions in addition to limiting resource availability to weeds, such as nutrient management (e.g. nitrogen fixation or recovery), pest regulation, and additional crop yield (Blanco-Canqui et al. 2015; Brooker et al. 2015). Intercrops or cover crops are intended to use resources in the times and spaces when crops are not, so weeds that would be using those resources are effectively replaced by plants that provide more direct benefits to the farmer. Moore et al. (2019) propose maintaining a living perennial groundcover between rows in annual cropping systems to suppress weeds, an approach that would both limit disturbance to crop rows and would sequester resources away from weeds. It could also reduce inputs, increase yields and increase profits in the long-term through improving the biological functioning of the system (Moore et al. 2019). A different technique using annual cover crops is to terminate a cover crop through rolling it flat to create a thick residue mulch across a field and then use disc or tine openers to sow the crop, which limits the amount of soil and thus weed seeds exposed to light (Halde et al. 2017). Mirsky et al. (2013) discuss how residues from a rye cover crop can be used successfully manage weeds in organic no-till maize rotation systems.

4.3.3 Precision resource placement

Another approach to reducing resource availability to weeds is to supply only what is needed by the crop, when it is needed, and no more. Such approaches are typically referred to as 'precision agriculture' (Gebbers and Adamchuk 2010) and requires that resources such as fertiliser and irrigation are applied in locations and at times when they are more likely to be available to crops than weeds, and the resource supplied does not exceed crop requirements. An example is the use of drip irrigation rather than spray irrigation, which provides water to crop roots while avoiding wetting the areas between crop rows or the soil surface (Grattan et al. 1988). In horticulture and viticulture, fertiliser is often also applied via irrigation ('fertigation'), which may reduce nutrient as well as water availability to weeds. In arable and pasture systems, remote-sensing methods to monitor crop conditions and resource levels can also facilitate the application of resources only when and where needed by the crop (Diacono et al. 2013), although the effect of this on weeds has not yet been quantified.

4.4 Take advantage of the positive effects of weeds

Weeds perform a range of ecosystem functions in terms of soil quality and biodiversity support (Petit et al. 2015; Blaix et al. 2018; Gaba et al. 2020), which can help to sustain agroecosystem productivity in the long term. In some cases, weeds may also have direct positive effects on crop production. For example, Frank and Barone (1999) observed that some weeds attracted slugs and thus reduced slug damage to oilseed rape, while Gibson et al. (2017) have shown that weeds can be managed within a corn crop to promote grain quality. There is anecdotal evidence that under high rainfall conditions, weeds in vineyards can contribute to wine quality through reducing water availability as grapes ripen. Such observations suggest that on some occasions, the right weeds at the right time and in the right places could be considered volunteer intercrops that can reduce the need for pesticides and fertilisers and sometimes increase product value. When more is understood regarding how to select for more beneficial weeds, then weeds could perhaps be utilised as cover crops, given that the capacity of weeds to cover a field with no effort invested from the farmer may mean they could be a cost-effective way to protect and improve soil during crop-free periods (as long as these weeds were managed so as not to become a problem in subsequent crops). However, we expect examples where the direct positive effects of weeds on crops outweigh their negative impact are rare, and it is likely that greater benefits will be obtained for other ecosystem services, such as biodiversity support and soil health (Marshall et al. 2003; Blaix et al. 2018; Gaba et al. 2020; Smith et al. 2020). As we come to understand more about the biology and ecology of weeds, the more we may be able to identify opportunities to use weeds to improve agroecosystem sustainability.

5 Ecology as a guide for future weed science and management

5.1 Ecological approaches benefit the whole agroecosystem

The management practices summarised in the previous section illustrate a wide range of possibilities to implement our four principles to create farming systems that are resistant to problematic weeds yet capable of fostering weed diversity. Furthermore, the majority of these management practices tend to be synergistic with and have positive effects on other aspects of the agroecosystem. For example, many diversity-based ecological approaches are relevant not only to weeds but also to insect pests and pathogens (Ratnadass et al. 2012; Storkey et al. 2019), while strategies that increase soil cover (such as cover crops, intercrops, mulches and retaining weeds) can reduce soil erosion and run-off, while increasing soil health and carbon capture (Zhang et al. 2007; Power 2010; Blanco-Canqui et al. 2015; Moore et al. 2019). Systems that increase crop diversity can lead to higher yields, yield stability and soil fertility (de Cárcer et al. 2019; Bowles et al. 2020). Restoring ecological relationships and functions in order to manage weeds requires the conservation of both farmed and wild biodiversity, while also reducing the external energy and inputs (and associated pollution) required to limit weed-crop competition. Ecological weed management is therefore 'both sustained by nature and sustainable in nature' (Tittonell 2014).

These synergies between sustaining agricultural production and reducing impacts are a key advantage of taking an ecological systems approach over a focus on specific technologies for weed control. Global food production must increase substantially to feed the human population in coming decades, yet must also drastically reduce its environmental impact to avoid endangering that same population through climate change, pollution and biodiversity loss (Hunter et al. 2017; Rockström et al. 2017). In the words of Hunter et al. (2017), it is thus critical that 'applied agricultural research should focus on developing production systems that can meet both production and environmental targets while helping farmers adapt to a range of challenges'. A techno-fix focused future for weed science seems unlikely to achieve this, given that techno-fixes not only tend to lack synergies with environmental conservation but can also have direct negative impacts on agricultural production in the long term. In general, food systems that are narrowly focused on increasing yields and production efficiency at the farm level result in reduced efficiency and increased food waste, environmental impacts and human health challenges at the food system level (Benton and Bailey 2019). More specifically from a weed management perspective, tools applied specifically to remove weeds can have adverse effects on other elements of the agroecosystem, such as herbicides interfering with soil biota (potentially affecting nitrogen fixation and nutrient cycling; Druille et al. 2013; Rose et al. 2016) or tillage causing soil erosion (Montgomery 2007; Verheijen et al. 2009) and reducing soil carbon (Lal 2004b). A techno-fix approach can also have negative feedback on our ability to control weeds, for example, the over-use of herbicides promoting herbicide resistance (Varah et al. 2020) and the simplification of landscapes and reduction of plant diversity reducing the abundance of seed predators (Tscharntke et al. 2005).

In contrast, explicitly making systems-level ecology the foundation of weed research and management would result in agronomic solutions that are better able to address the multiple goals needed to achieve sustainability. In order to obtain such synergies, it is critical that the ecological management practices are designed at the farm or landscape scales and to account for long-term effects (Tittonell 2014; Altieri et al. 2017; Rockström et al. 2017). Many approaches currently presented as 'ecological' techniques for weed management are often little more than novel control techniques. For example, bioherbicides may pose less of a toxicity threat to humans and biodiversity (Bajwa et al. 2015), but there is no research to suggest that weeds will not be just as capable of evolving resistance to bioherbicides (Neve et al. 2009), and it remains a risk that applying unnaturally high concentrations of 'natural' chemicals to landscapes will have some negative impacts on biodiversity and soil functioning. Similarly, avoiding herbicides through the use of plastic mulches may not be objectively better for biodiversity, ecosystems and human health than judicious herbicide use (Steinmetz et al. 2016).

In general, farming practices that increase within-farm diversity and ecosystem functioning have potential substantial improvements in sustaining agricultural productivity and farm livelihoods, as well as wider biodiversity and ecosystem functioning (Altieri 2002; Kremen and Miles 2012; Tscharntke et al. 2012; Bommarco et al. 2013). More diverse agroecosystems are typically more resilient, provide more reliable yields, are less dependent on agrichemical inputs and support a higher quality of life for rural communities (Cabell and Oelofse 2012; Tittonell and Giller 2013; Altieri et al. 2017; Bowles et al. 2020). Overall, the evidence so far suggests that ecological weed management is the best way to ensure that agriculture can continue to meet our food, fuel and fibre needs without compromising other requirements for human survival and wellbeing.

5.2 Advancing ecological weed research and management

The potential advantages of ecological weed management outlined above raise the question of why existing practices are not more widespread and what can be done to encourage the introduction and adoption of new ecological practices. Arguably, the first change must be in the philosophy of weed science itself—we need to accept that simple answers for 'weed control' will inevitably fail if used too often and for too long. Instead, we should seek strategies that promote diverse weed communities that are minimally competitive to crops and beneficial to the wider agroecosystem, and we should aim to work with rather than against the rules of nature to ensure long-term stability. The particular approaches required to achieve this may seem at first to be highly complex and site-specific, given that ecological weed management often relies on multiple practices that have a limited effect in isolation but significant impact in concert. However, this review has presented a substantial body of literature that supports a range of ecological rules of thumb for weed management that can be adapted to reveal a great number of synergistic practices for different local contexts and farming systems (Tables 1 and 2). More such rules may await discovery if a greater number of weed scientists turned their attention to weed ecology.

However, as Liebman et al. (2016) point out, proof of concept for several ecological practices offering improvements in the sustainability of weed management has been present in the weed science literature for decades but has not been widely adopted in agriculture. They suggest that the major barriers are hostile policy and market environments, which for example limit the diversity of crops it is feasible for a farmer in a given region to grow. A lack of social infrastructure that would allow farmers to learn about and trial ecological practices in their particular systems may also pose a problem. Kleijn et al. (2019) further emphasise the gap between an abundance of theory on agricultural ecology in the scientific literature and a lack of evidence and recommendations for specific practices that farmers can expect to implement, their effects and the timescales over which these effects will occur. This indicates the need for a transition from input intensive to knowledge intensive cropping systems, which would allow farmers to better manage complex, diverse systems.

A potential route forward is modelled by the Long-Term Social-Ecological Research site, Zone Atelier Plaine & Val de Sèvre (LTSER ZA-PVS), in France. Since 1994, this landscape-scale research platform has been 'promoting nature-based solutions that integrate agricultural development and biodiversity conservation within resilient multifunctional landscapes' (Bretagnolle et al. 2018). It has produced several studies demonstrating benefits to food production and other ecosystem services that can result from managing agricultural land for high biodiversity (e.g. Petit et al. 2015; Catarino et al. 2019), including weeds (Gaba et al. 2020). Critically for increased adoption, however, the LTSER ZA-PVS has also enabled researchers to identify the practices and landscape configurations that best meet the needs of multiple local stakeholders, as well as the social infrastructure and policy instruments that can promote these. Governance that builds on the synergies between different stakeholder needs and different ecological practices seem most promising (Bretagnolle et al. 2018). Different practices and different policies are likely to be more or less effective in different regions, cultures and farming systems; however, the LTSER ZA-PVS illustrates that benefits to food production, environmental conservation and local communities can be achieved by putting ecological thinking at the heart of agricultural research and development and by working with local stakeholders to understand how best to translate ecological relationships into agronomic practice.

In terms of weed management, our article takes the first step of demonstrating how ecological theory can help to identify practices that are expected to be beneficial at the agroecosystem level and to be sustainable over the long term. The next step is to take these ecological concepts and practices, such as those outlined in this article, and explore how they can be applied to the variety of environments and farming systems around the world. Weed researchers have a key role to play in assisting farmers in addressing this challenge, through using their access to scientific knowledge to draw on global advances in ecological theory and weed science to design and test locally appropriate management techniques and approaches (Anderson 2005; Jordan et al. 2016; Liebman et al. 2016). Adapting ecological theory to farm practice is not always straightforward, and, given the risks involved, many farmers prefer to adopt new ideas only after having seen them successfully implemented in their own environments and farming systems. For example, this is seen in the increased adoption of new practices amongst farmers whose neighbours and social networks have previously adopted the practices (Läpple and Kelley 2015; Milne et al. 2015; Ward and Pede 2015). Scientists can help to introduce new practices by piloting potentially suitable approaches on demonstration farms and through farmer networks and by ensuring that results are both accessible and relevant to farmers (Liebman et al. 2016; Payne et al. 2016). This will require ecologists, applied weed scientists and agronomists to work more closely together to design and identify weed management practices that are effective and suitable at the agroecosystem scale (Ward et al. 2014; Neve et al. 2018). Further collaboration with psychologists, economists and social scientists could better clarify the conditions in which farmers would make positive changes to their practices (Doohan et al. 2010; Liebman et al. 2016; Moss 2019), while involving farmers themselves in the research can also be advantageous (Jordan et al. 2016). Local and traditional knowledge can offer a source of locally effective solutions, and farmers' input can streamline research toward strategies that address their everyday realities and are achievable with available tools (Snapp et al. 2003). Including farmers as well as the wider public in developing new approaches to agriculture could also help to drive democratic demand for the political and economic shifts required to facilitate sustainable food and farming systems.

6 Conclusion

Given the disadvantages of current mainstream weed management and of techno-fixes in comparison with the benefits offered by ecological weed management, it is clear in which direction we should steer the future of weed science. However, designing and implementing ecological weed management strategies at the level of the agroecosystem is not a simple task: a detailed understanding of complex ecological interactions is required, and theoretically relevant practices need to be tailored to meet the needs and constraints of the range of environments and farming systems around the world. To do this effectively, weed researchers will need to embrace interdisciplinary and transdisciplinary studies. This, however, should present an exciting challenge to weed scientists, agronomists and ecologists. Pursuing the ecological weed management will allow us to increase the diversity of ideas, theories, tools, practices and people that we work with and to link these together in novel ways to design resilient and sustainable farming systems.

Acknowledgments The authors wish to thank James Bennett, Julia Wright, Dana MacGregor and four anonymous reviewers for comments that improved earlier versions of this manuscript.

Authors' contributions Conceptualisation, C.M, J.S and K.D-S; investigation, C.M, J.S, A.M, H.M and K.D-S; visualization, C.M, J.S, A.M and H.M; writing—original draft, C.M; writing—review & editing, J.S, A.M, H.M and K.D-S.

Funding information During the development of this manuscript, CM was supported by a Coventry University Doctoral Scholarship and the European Commission EcoDry Project (612686 FP7-PEOPLE-2013-IRSES). HM and JS are partly supported by the Natural Environment Research Council (NERC) and the Biotechnology and Biological Sciences Research Council (BBSRC) research programme NE/N018125/1 LTS-M (ASSIST).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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