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Review article

Weeds in agricultural landscapes*. A review

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Abstract – There is currently an increasing societal and political shift towards more sustainable agricultural systems to provide both food production and ecological biodiversity levels. This shift has recently modified scientific questioning and brought up new research challenges for agro-ecological research. This is the case in particular for weed management, where issues have so far largely focused on the conflict between weeds and crop productivity. Here, we review recent findings that have led to a changing perception on weeds in agro-ecosystems and upcoming areas in terms of weed management options. Our main findings are that weeds have numerous interactions with other organisms and, in turn, some of these interactions can have direct, either negative or positive, effects on the functioning of the agro-ecosystem. Many interactions are species-specific, and therefore assessing the role of weed communities in the agro-ecosystem would benefit from further development in the functional grouping of weed species. In terms of weed management our review shows that alternative cropping systems can deliver both good levels of crop productivity and of weed management at the field level. Weeds respond to landscape attributes and there is a need to fully assess the scope for utilizing the spatio-temporal organization of cropping systems and uncultivated habitats as a tool for minimizing weed infestations. Weeds are also submitted to biological regulation through the predation of their seeds and further research is required to assess the effect of cropping systems and landscape on levels of weed natural enemies, and therefore on the potential contribution of biological regulation in the management of weeds.

ecosystem services / trophic web / biodiversity functions / integrated weed management / landscape scale / biological regulation / seed predation / sustainable agriculture

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1. INTRODUCTION

Agriculture can be conceived as the management of terrestrial ecosystems to divert their productive capacity to serve human needs (Millennium Ecosystem Assessment, 2005). As such, agro-ecosystems provide benefits for humankind, i.e.

“ecosystem services”, mostly in the form of primary production such as food, feed, timbers, fibers and other natural products. Recent research has shown that there is often a fundamental conflict between the increasing needs of agriculture and the maintenance of services other than primary production. Reliance on chemical inputs has well-known impacts on soil and groundwater quality (Arias-Estevéz et al., 2008). There is also a great deal of evidence about how agricultural changes pose a threat to biodiversity in agricultural landscapes (Petit et al., 2001), and influence species richness

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and abundance of taxa (Benton et al., 2003; Tschardt et al., 2005), and a consensus that pressures of agricultural intensification on biodiversity act on different spatial scales, i.e. land cover, landscape management and crop management (Firbank et al., 2008). It is also becoming obvious that the loss of some organisms has in turn consequences for agriculture, e.g. through the loss of natural enemies of crop pests or pollinators (Isaacs et al., 2009) or through the loss of microorganisms that are vital for the maintenance of soil health (Kibblewhite et al., 2008). This shows how crucial it is today to identify land management options that can provide both food production and levels of biodiversity that are sufficient to ensure the ecological functioning of the agro-ecosystem (McNeely and Scherr, 2003). Finding such options is the remit of agro-ecology (Wezel et al., 2009).

Weed diversity has declined drastically in farmed landscapes over the last decades (Andreasen et al., 1996; Sutcliffe and Kay, 2000; Hyvönen, 2007; Baessler and Klotz, 2006; Fried et al., 2009). We believe weeds are an excellent illustration for the current shift in paradigm that has resulted from the societal and political will to move towards a more sustainable agriculture. This paper describes and reviews available information on new questions of interest in relation to weeds in agro-ecosystems as a result of the move away from a solely productive agricultural objective and the emergence of the functional biodiversity concept. We also believe that there are a number of emerging challenges, in relation to the future management of arable weeds, given the 50% reduction in herbicide use expected to occur within the coming 10 years in France (Anonymous, 2008). In this paper, we review current knowledge on the role of weeds in agro-ecosystems, as well as upcoming challenges in three complementary areas that we deem the most promising for delivering sustainable weed management: integrated weed management at the field level, landscape management at different spatial scales and biological control.

2. THE CHANGING PERCEPTION ON WEEDS IN AGRO-ECOSYSTEMS

The role of biodiversity in the functioning of agro-ecosystems has been argued for many years (Altieri, 1995, 1999), but it is only recently that the concept of the functional group (cluster of genes, species or habitats) has boosted research on the relationship between biodiversity and its role in ecosystems (Hooper et al., 2002). A recent literature review reveals that little is known on the functional value of organisms in the agro-ecosystem (Moonen and Barberi, 2008) and one of the consequences is a relatively weak case for biodiversity conservation in cultivated landscapes (Jackson et al., 2007). This lack of knowledge partly results from the fact that many studies carried out in agro-ecosystems have focused on assessing the bioindicator value of organisms (in response to agricultural practices, e.g. Albrecht, 2003) rather than on their role in processes (Moonen and Barberi, 2008). Yet, the gap between the two approaches needs to be bridged as it is the effect of agricultural practices on functional diversity, and hence the

provision of services, that is of interest if we are to promote sustainable agriculture.

Weeds have numerous interactions with other organisms and some of these interactions can have direct effects on the functioning of the agro-ecosystem. Apart from the vast literature on weed-crop competition (Bastiaans et al., 2000), the best documented role of weeds results from their primary producer status, which places them at the basis of the agro-ecosystem food web. In particular, weeds are important as main food sources for animals such as pollinators that maintain rare plant species (Gibson et al., 2006), earthworms (Thompson et al., 1994), granivorous and omnivorous arthropods such as carabid beetles (Hawes et al., 2003), ants (Jacob et al., 2006), pollinators, e.g. bumblebees associated with particular weed species (Backman and Tiainen, 2002), farmland birds (Wilson et al., 1999; Gibbons et al., 2006), and mammals (Manson and Stiles, 1998).

Weeds also serve as an indirect resource for predatory species (Hawes et al., 2003). They can provide alternative food sources for organisms that play a role in pest control, e.g. omnivorous carabid beetles that also feed on aphids and slugs (Kromp, 1999). Most taxa feeding on weeds exhibit consumption preferences that are specific (Alignier et al., 2008; Thompson et al., 1994). Weeds may provide other services that may be beneficial or detrimental to a number of processes in the agro-ecosystem, but these have been less studied and quantified. Weed cover supports both primary and secondary consumers in the invertebrate community (Bohan et al., 2007) and thus supports the services provided by different guilds of invertebrates. More generally, weeds can significantly influence crop disease incidence by acting as vectors or reservoirs of plant pathogens (Wisler and Norris, 2005). They can be host plants for parasitic organisms, e.g. *Orobanche ramosa* L., which attacks winter rape fields and causes severe yield losses (Gibot-Lerclerc et al., 2003) or infectious fungi, e.g. ergot *Claviceps purpurea* (Mantle, 1977), and many viruses (Lavina et al., 1996). The seeds of weed species also have either beneficial or negative impacts on ecosystem functioning (Franke et al., 2009). Impacts can be indirect through trophic interactions, e.g. weed seeds provide food for earthworms which in turn improve soil quality, providing a habitat for seed-associated microorganisms and promoting their antifungal activity.

This review is not comprehensive but it highlights the fact that weeds have strong relations to other groups of organisms and that these interactions are usually species-specific. It means that the services provided by a weed community will strictly depend on the set of individual species and on their respective abundances within the community, or at least that these functions will depend on sets of species grouped according to the types of biotic interactions they have with other organisms. However, functional group approaches in weed communities have been scarce so far, mostly because of knowledge gaps; trophic-based approaches have been applied using published information on the (quantity/quality of) trophic links exhibited by some individual weed species, e.g. with birds, pollinators, beneficial insects and associated pests (Marshall et al., 2003; Hyvönen and Huusela-Veistola, 2008). More recently,

the identification of generic and robust links between invertebrate trophic groups and weed groups in large-scale datasets has validated trophic-based approaches (Bohan et al., 2007; Hawes et al., 2009). Functional approaches have also been developed based on eco-physiological weed traits to account for the pattern of weed productivity and weed competitive ability and thus their negative impact on crop yield (Storkey, 2006). Combining both approaches has led to the identification of weed groups allowing both biodiversity provision and crop production, i.e. species of high trophic value with a low impact on crop yield (Storkey, 2006). Yet, in the light of the large set of beneficial and detrimental 'services' listed above, it would be valuable to either compile existing information or conduct more research in order to rank individual arable weed species along a scale of provision of positive through to negative services. This would also help to assess whether the specific services rely on many or few species (i.e. the application of the concept of ecological redundancy to weed species).

3. SUSTAINABLE MANAGEMENT OF ARABLE WEEDS: EMERGING CHALLENGES

3.1. Alternative weed management at the field level

The conflict between crop productivity and weeds has so far mainly been managed through the sole use of herbicides, but relying solely on chemicals can be unsustainable when weed populations develop resistance to herbicides (Mace et al., 2007), and because of the environmental impacts of herbicides and their residues. One alternative is the application of current knowledge on the effects of agricultural practices on weed populations to design novel cropping systems (integrated weed management or IWM) that would require few herbicides to manage weeds. IWM combines the use of crop rotation design and adapting cultural practices such as type of soil tillage, sowing dates and densities, competitive cultivars, and mechanical weeding (Bastiaans et al., 2008). IWM relies on weed management principles that have proved to have satisfying efficiency for long-term weed containment in organic farming for decades (Bärberi, 2002). However, IWM systems differ from organic ones by several aspects. Crop mineral nutrition is not a limiting factor in IWM, as mineral fertilization is not restricted, so yielding potential is higher in IWM as compared with organic (in fact lying in between current systems with high inputs and organic farming; see Butault et al., 2010), which is an important issue in the current context of the world global food shortage for the next decades. However, early and high nutrient availability might also be advantageous to weeds, which are usually able to take up nutrients more quickly and efficiently than crops (Liebman and Davis, 2000; but see different results by Jørnsgård et al., 1996). IWM currently does not benefit from price premiums compensating yields lower than the local agricultural potential, hence restricting the feasibility of costly agro-ecological management options (e.g. growing crops with low direct economic profitability for expected agro-ecological future services, including weed population containment). However, limited use

of herbicide is possible in IWM, thus reducing the risk of severe weed infestations affecting crop yields, as frequently observed in organic farming with weed species poorly controlled by weed management measures (e.g. *Cirsium arvense*, cited in many organic field surveys; see Ulber et al., 2005).

The central question here is whether adopting such IWM-based cropping systems can deliver outcomes that are compatible with sustainable agriculture without side effects on the productivity and overall economic performance of the system (Gerowitt, 2003). Some IWM cropping systems seem to lead to higher levels of weed infestation (Koocheki et al., 2009). Other results derived from a few long-term farming system experiments seem to indicate that some combinations of IWM techniques allow weed control with low herbicide use or even no herbicide use, i.e. organic farming (Chikowo et al., 2009). Combinations of prevention strategies and control tactics have proved to be efficient enough to avoid any significant crop yield loss due to weed competition (Anderson, 2007). However, more research is needed to address concerns over possible seed return which may increase the weed burden in following crops (Storkey and Westbury, 2007). Furthermore, some measures that may be included in IWM strategies might have indirect impacts on crop productivity. For example, diversifying crop rotation is likely to mean moving away from crop sequences chosen by the farmer to maximize the gross return in the specific local environment. Modifying crop sowing dates to escape weed emergence flushes might also affect crop yielding potential. In addition, IWM principles tend to increase the system complexity (Bastiaans et al., 2008), hence hampering their feasibility at the farm level because of (i) possible bottlenecks in labor organization (Pardo et al., 2010), (ii) possible impediments due to the organization of the market of agricultural products, and (iii) lack of farmers' knowledge.

Research on IWM faces methodological difficulties owing to the long time scales needed to take account of cumulative processes. Moreover, real IWM cropping systems are scarce in commercial farms, so surveys of weed infestations in fields managed according to IWM for a long time are almost impossible. At the moment, the main challenges for IWM research relate to the following key issues.

Firstly, there is a need to increase knowledge of the consequences of alternative cropping systems not only for weed management, but also for other factors challenging crop production (Mouron et al., 2006; Pimentel et al., 2005). Multi-criteria assessments of IWM should be performed considering diverse issues such as pesticide contamination of the environment (Bockstaller et al., 2008), economic profitability, energy input and emission of greenhouse gases (Nemecek et al., 2008), and feasibility and acceptability for farmers (Pardo et al., 2010). Considering a wide range of aspects will help in demonstrating possible trade-offs among evaluation criteria (e.g. decreased herbicide use versus increased labor input per hectare). This kind of knowledge will be of particular importance for policy-makers and farmers in the future.

A second important issue is the question of risk assessment in IWM-based systems, a question which has seemingly not been addressed so far. Various risks might be considered, including: (i) the risk of insufficient weed control after a number

of satisfying years; (ii) the risk of a shift in weed community due to the replacement of currently dominating weed species by other harmful ones more adapted to the new crop management system; and (iii) unsuspected multiplicative problems as IWM became a dominant practice over the landscape. For example, the IWM measure of delaying fall sowings to escape fall peaks of weed emergence might increase the risk of unfavorable sowing conditions that can affect yielding potential in some years (Pardo et al., 2010). Risk assessment can be based on experimental networks, providing high amounts of data that make it possible to quantify the frequency of any accidental event. However, when available, models are also useful tools for risk assessment, as they can be used to simulate contrasting climatic scenarios (Debaeke and Aboudrare, 2004). Models of weed community demography accounting for the interaction between cropping system components, climatic conditions and weed life-history traits (Storkey and Cussans, 2007) could be used for predicting long-term changes in weed communities and the optimal combination of plant traits that could be selected by a given innovative cropping system. However, such simulation of “virtual” weed species should be complemented by research on comparative ecology analyzing the distribution of life traits among real weed species.

Finally, IWM research should integrate the links between weeds and other organisms. Insecticides and insect management measures might indirectly affect weed communities if non-target seed-eating insects are affected. This question of biological regulation, which is discussed in detail below, requires multidisciplinary agro-ecological approaches at both field and landscape scales, to address the great complexity of agro-ecological systems.

3.2. Weed management at the landscape level

Weed species composition is strongly influenced by environmental heterogeneity, which is itself partly related to crop type and management practices (tillage, fertilization and herbicide use). Data suggest that weed assemblages that span a large diversity of management treatments (a mosaic of crops and management regimes) tend to display a more complex structure than assemblages restricted to a more homogenous habitat, e.g. one large management unit. Increasing management heterogeneity leads to a shift from a unimodal to a multimodal species abundance distribution pattern and the most noticeable impact is a decreased abundance of aggressive and dominant problematic weeds (Dornelas et al., 2009).

Beyond the field level, there is also scope to increase environmental heterogeneity and therefore enhance complex weed communities (Petit et al., 2003). Indeed, many arable weeds develop outside the cultivated field per se (Fig. 1). Crop edges shelter a high diversity of arable weeds (Wilson and Aebischer, 1995), some of which have become gradually restricted to these habitats as land-use intensity has increased within the core of fields (Fried et al., 2009). Fertilizer-free management of crop edges in agri-environmental schemes has indeed proved successful for arable weed conservation

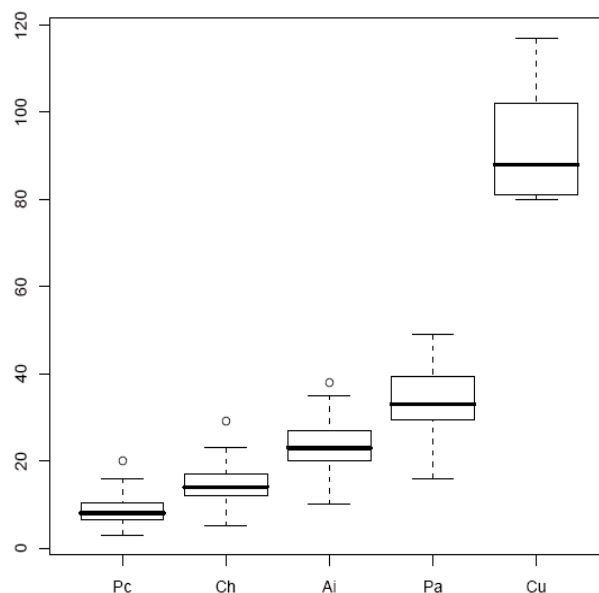


Figure 1. Increase in weed species richness from the core of the field to the landscape level. Pc = field core area; Ch = cultivated field (i.e. Pc + crop edge); Ai = Tilled zone (Ch + tilled area not sown); Pa = extended field (i.e. Ai + field margin); Cu = all the extended fields in the area grown with the same crop species. Sampled area for all plots is 2000 m² (after Fried, 2007).

(Walker et al., 2007). Field margins and disturbed semi-natural habitats embedded in the agricultural mosaics provide additional habitats for at least some arable weed species (Marshall and Arnold, 1995). There is surprisingly little knowledge about the level of exchanges between these adjacent habitats and therefore on the impact of introducing new suitable habitats on the dynamics of weed populations at the mosaic level. There is often concern among farmers that introducing new habitats for weeds may lead to greater infestation of fields. However, results show that introducing grassy margin strips along crop edges usually reduces weed populations in crop edges and therefore within the core of the field (Marshall, 2009), depending upon management type and intensity in the core field.

The effect of environmental heterogeneity on weeds has rarely been considered on scales larger than the field and its surrounding margins. Overall, it has been found that weed diversity in arable fields is higher in complex and heterogeneous landscapes. However, studies have compared landscapes that were highly contrasted in terms of structure, e.g. mixed landscapes with hedges versus open-field areas (Fried et al., 2008) or have followed a gradient of landscape complexity, e.g. arable landscape through to mixed-farmed landscape (Gabriel et al., 2005), with a resulting mix of many confounding effects. There is, on the other hand, little data on weed responses to the landscape context within a single landscape or in a set of landscapes that would be comparable in terms of composition and structure. Marshall (2009) could not detect an effect of field

size and landscape structure on weed diversity in a set of sites under agri-environmental schemes. Another study which compared the weed flora of 125 winter wheat fields within the same landscape showed that smaller parcels surrounded by a small-grain pattern or diversified mosaics of land-use types tended to harbor higher levels of weed diversity and richness (Petit et al., 2009). Both studies agree that the spatial extent to which landscape composition and structure would impact the arable flora is likely to be local, i.e. within a 300-m radius of the focal point. Landscape management options should therefore be considered at the crop and non-crop mosaic level even though it is recognized that some weed species can disperse over long distances and that anthropogenic dispersal is an important factor (Benvenuti, 2007).

This review illustrates that weed communities that are found within arable fields are influenced by the spatial context of the cultivated field and this appears valid at different scales. This indicates that, despite the high degree of disturbance experienced on the field scale, the landscape context of arable weeds is nevertheless an important factor, as found for plant assemblages in less disturbed habitats, e.g. extensively managed grassland (Pacha and Petit, 2008; Cousins and Aggmir, 2008) or woodland (Petit et al., 2004). Scales on which farmers and land managers can most realistically act are the immediate vicinity of cultivated fields (i.e. core of the field and associated crop edge, tilled area and field margin) and the fine scale of landscape mosaics, i.e. a group of adjacent cultivated and associated uncultivated habitats. Fully assessing the scope for utilizing the spatio-temporal organization of crops and uncultivated habitats as a tool for minimizing weed infestations within such mosaics will require: (i) identification of groups of weed species that exhibit comparable distribution patterns and population functioning in heterogeneous mosaics, and (ii) a quantification of the reproductive success of different weed species groups in the different habitats that compose agricultural mosaics. This will require methodological development at the interface between landscape ecology and agronomy in order to realistically represent in space and time the mosaics of agricultural practices that are relevant to weeds.

3.3. Biological regulation and weed management

The regulation of pests resulting from the activity of naturally present predators (natural enemies) is frequently cited as a potentially important ecosystem service in agro-ecosystems (Losey and Vaughan, 2006). In terms of weed demography, it has been suggested that an annual seed loss of 25–50% may be enough to slow down weed population growth substantially (Firbank and Watkinson, 1985). The same applies to low herbicide situations where a seed loss rate of 40% per year was deemed sufficient for stabilizing *Abutilon theophrasti* population densities (Westerman et al., 2005). The main seed predators in arable fields are rodents, ants, carabid beetles and birds, and the relative impact of the different taxa seems to vary according to the crop type and the context of studies. This means that weed seed predation may potentially contribute to weed

management (as well as deplete seeds of useful weeds) and studies exploring the natural predation of weed seeds are currently proliferating.

Within the range of available studies, predation rates observed in the field and attributed to carabids often appear sufficient to impact weed population densities (Brust, 1994; Tooley and Brust, 2002; White et al., 2007). Such findings are supported by large-scale studies showing a generic and robust association pattern between granivorous and omnivorous carabid species and weed seed abundance, while this pattern does not exist for species that are predators of invertebrates (Brooks et al., submitted). So far, few field studies have simultaneously recorded the activity-density of carabids and weed seed predation rates. Some studies provide evidence for a spatio-temporal correspondence between the activity-density of granivorous and omnivorous carabids and seed predation rates (Honek et al., 2003; Gallandt et al., 2005; Menalled et al., 2007) although other studies did not detect such a relationship (Mauchline et al., 2005; Saska et al., 2008). Patterns of seed consumption are shaped by the size of seeds and the size of predators, e.g. larger carabids consume larger weed seeds (Honek et al., 2007), and in general laboratory experiments show that carabids exhibit preferences in the seeds they consume (see Tab. I). However, little information has been gained so far on the identity of predators and the consumption rates experienced by specific weed species. This information would be valuable, especially for the most pernicious weed species.

In arable fields, predation rates are influenced by farming systems (Navntoft et al., 2009), vegetation cover provided by the crop (Cromar et al., 1999; Gallandt et al., 2005; Meiss et al., 2010) or in adjacent habitats, e.g. wildflower strips (Kollmann and Bassin, 2001), and specific agricultural practices such as tillage (Cardina et al., 1996; Cromar et al., 1999; Menalled et al., 2007), irrigation (Baraibar et al., 2009) and harvest (Heggenstaller et al., 2006). These effects are thought to result from changes in the abundance and activity of predators in response to crop growth or particular practices. It appears important to assess more comprehensively the impact of the crop management system on the abundance and activity of granivorous and omnivorous species, and on predation rates. Such knowledge would make it possible to include strategies for maximizing the predation of weed seeds by natural predators when designing cropping systems with low reliance on pesticides.

In the same way, the spatial context can affect predation rates through its impact on the distribution and abundance of predators. It might be expected that predation rates are higher (1) at the within-field level near the relatively undisturbed field margin and (2) at the landscape level within mosaics that are more complex and where semi-natural habitats are well represented. Indeed, few studies have so far explored the effect of the spatial context on weed seed predation, and results are often inconclusive (Menalled et al., 2000; Saska et al., 2008; Booman et al., 2009). This short review shows that although the scope for using seed predation as a control tool is probably important, weed seed predation is a complex process and further research is needed before its potential application to weed control can be fully assessed.

Table I. The 12 weed species that have been the focus of 2 or more studies on seed predation by carabid beetles. Weed species name, literature with number of carabid species tested in brackets, carabid species consuming these weeds in descending order of seed consumption. Carabid genus abbreviations: H = *Harpalus*; A = *Amara*; C = *Calathus*.

Weed species	Paper (number of carabid species)	Species (in descending order of seed consumption)
Capsella bursa-pastoris	Honek et al. (2003) (22)	<i>A. similata</i> , <i>A. aenea</i> , <i>H. distinguendus</i> , <i>H. affinis</i> , <i>A. ovata</i> , <i>C. ambiguus</i> , <i>H. signaticornis</i> , <i>A. familiaris</i> , <i>H. tardus</i> , <i>Ophonus azureus</i> , <i>H. rufipes</i> , <i>Trechus quadristriatus</i> , <i>Dolichus halensis</i> , <i>A. aulica</i> , <i>P. cupreus</i> , <i>A. consularis</i> , <i>Anchomenus dorsalis</i> (0), <i>C. fuscipes</i> (0), <i>H. atratus</i> (0), <i>Pterostichus melanarius</i> (0), <i>Stomis pumicatus</i> (0)
	Saska et al. (2008) (8)	<i>A. spreta</i> , <i>A. plebeja</i> , <i>A. aenea</i> , <i>H. distinguendus</i> , <i>A. familiaris</i> , <i>H. rufipes</i> , <i>H. affinis</i> , <i>A. muelleri</i>
	Goldsmith and Toft (1997) (3)	<i>H. rufipes</i> , <i>P. cupreus</i> , <i>P. versicolor</i>
	Martinkova et al. (2006) (2)	<i>H. affinis</i> , <i>H. rufipes</i>
	Honek et al. (2006) (2)	<i>H. affinis</i> , <i>H. distinguendus</i>
Taraxacum officinale	Honek et al. (2005) (28)	<i>A. montivaga</i> , <i>A. eurynota</i> , <i>A. convexiuscula</i> , <i>Zabrus tenebrioides</i> , <i>A. similata</i> , <i>A. ovata</i> , <i>Anisodactylus signatus</i> , <i>A. aenea</i> , <i>A. ingenua</i> , <i>A. bifrons</i> , <i>A. littorea</i> , <i>H. affinis</i> , <i>A. sabulosa</i> , <i>A. apricaria</i> , <i>A. anthobia</i> , <i>H. luteicornis</i> , <i>H. signaticornis</i> , <i>H. rufipes</i> , <i>A. consularis</i> , <i>C. ambiguus</i> , <i>Parophonus maculicornis</i> , <i>A. aulica</i> , <i>A. familiaris</i> , <i>H. atratus</i> , <i>Acupalpus meridianus</i> , <i>C. fuscipes</i> , <i>Ophonus azureus</i> , <i>Trechus quadristriatus</i>
	Honek et al. (2006) (2)	<i>H. affinis</i> , <i>H. distinguendus</i>
	Martinkova et al. (2006) (2)	<i>H. affinis</i> , <i>H. rufipes</i>
	Jorgensen and Toft (1997) (1)	<i>H. rufipes</i>
Cirsium arvense	Honek et al. (2003) (23)	<i>H. rufipes</i> , <i>Anisodactylus signatus</i> , <i>H. affinis</i> , <i>A. aulica</i> , <i>H. tardus</i> , <i>H. distinguendus</i> , <i>A. similata</i> , <i>A. ovata</i> , <i>A. littorea</i> , <i>A. aenea</i> , <i>H. signaticornis</i> , <i>P. cupreus</i> , <i>H. atratus</i> , <i>Pterostichus melanarius</i> , <i>Ophonus azureus</i> , <i>A. consularis</i> , <i>Anchomenus dorsalis</i> , <i>Dolichus halensis</i> , <i>A. familiaris</i> , <i>C. ambiguus</i> , <i>C. fuscipes</i> , <i>Trechus quadristriatus</i> (0), <i>Stomis pumicatus</i> (0)
	Honek et al. (2006) (2)	<i>H. affinis</i> , <i>H. distinguendus</i>
	Martinkova et al. (2006) (2)	<i>H. rufipes</i> , <i>H. affinis</i>
Stellaria media	Saska et al. (2008) (8)	<i>H. rufipes</i> , <i>A. aenea</i> , <i>A. familiaris</i> , <i>H. distinguendus</i> , <i>H. affinis</i> , <i>A. spreta</i> , <i>A. plebeja</i> , <i>A. muelleri</i>
	Honek et al. (2006) (2)	<i>H. affinis</i> , <i>H. distinguendus</i>
Amaranthus retroflexus	White et al. (2007) (3)	<i>H. pennsylvanicus</i> , <i>Anisodactylus sanctaecrucis</i> , <i>A. aenea</i>
	O'Rourke et al. (2006) (3)	<i>H. pennsylvanicus</i> , <i>P. lucublandus</i> , <i>P. chalcites</i>
	Honek et al. (2006) (2)	<i>H. affinis</i> , <i>H. distinguendus</i>
Abutilon theophrasti	White et al. (2007) (3)	<i>H. pennsylvanicus</i> , <i>Anisodactylus sanctaecrucis</i> , <i>A. aenea</i>
	O'Rourke et al. (2006) (3)	<i>H. pennsylvanicus</i> , <i>P. lucublandus</i> , <i>P. chalcites</i>
Chenopodium album	Tooley, F. Williams (1999) (3)	<i>H. rufipes</i> , <i>A. aenea</i> , <i>Pterostichus melanarius</i>
	Honek et al. (2006) (2)	<i>H. affinis</i> - <i>H. distinguendus</i>
Melandrium album	Honek et al. (2006) (2)	<i>H. affinis</i> - <i>H. distinguendus</i>
	Martinkova et al. (2006) (2)	<i>H. affinis</i> , <i>H. rufipes</i>
Polygonum persicaria	Tooley, F. Williams (1999) (3)	<i>H. rufipes</i> , <i>Pterostichus melanarius</i> , <i>A. aenea</i>
	Jorgensen and Toft (1997) (1)	<i>H. rufipes</i>
Thlaspi arvense	Honek et al. (2006) (2)	<i>H. affinis</i> - <i>H. distinguendus</i>
	Martinkova et al. (2006) (2)	<i>H. rufipes</i> , <i>H. affinis</i> ,
Tripleurosp. inodorum	Honek et al. (2006) (2)	<i>H. affinis</i> - <i>H. distinguendus</i>
	Martinkova et al. (2006) (2)	<i>H. affinis</i> , <i>H. rufipes</i> ,
Viola arvensis	Tooley, F- Williams (1999) (3)	<i>H. rufipes</i> , <i>Pterostichus melanarius</i> , <i>A. aenea</i>
	Jorgensen and Toft (1997) (1)	<i>H. rufipes</i>

4. CONCLUSION

This paper offers a review on the role of weeds in agro-ecosystems and on possible ways to manage arable weeds within the context of productive and sustainable agriculture. It shows that there is substantial evidence for interactions between weeds and other organisms but the challenge remains to exploit these interactions further in the context of complex anthropogenic pressures, mainly cropping systems and their organization within the agricultural landscape.

In terms of ecological services potentially provided by weeds, the key questions are: (i) whether all services listed in this paper are compatible and can or should co-exist within the same landscape; (ii) how we measure such services, and (iii) what the trade-offs in the provision of services can be in different contexts. The follow-up is whether we could identify a combination of management factors that would enhance all the biotic interactions we wish to enhance simultaneously.

This review also shows that ecological processes involved in weed interactions are interrelated, such that management options need to be complementary. For example, IWM should take into account the fact that while weed seed predation is dependent on the abundance of seed predators, this is itself affected by the landscape context of cultivated fields. As the processes act at different spatial scales, this calls for a multi-scale approach to weed management aimed at combining field-scale management systems into a composite landscape-scale management strategy. Integrating the diversity of ecological services within a multi-objective arable crop production framework that also produces goods and provides economic returns is definitely a huge challenge for the near future.

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