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Biodiversity-based options for arable weed management. A review

Sandrine Petit¹ · Stéphane Cordeau¹ · Bruno Chauvel¹ · David Bohan¹ · Jean-Philippe Guillemin¹ · Christian Steinberg¹

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Abstract

In the context of a shift towards pesticide reduction in arable farming, weed management remains a challenging issue. Integrated Weed Management currently recommends agronomic practices for weed control, but it does not integrate the use of biodiversity-based options, enhancing the biological regulation of weeds. Here, we review existing knowledge related to three potentially beneficial interactions, of crop–weed competition, weed seed granivory, and weed interactions with pathogenic fungi. Our main findings are the following: (1) promoting cropped plant–weed competition by manipulating cropped cover could greatly contribute to weed reduction; (2) weed seed granivory by invertebrates can significantly lower weed emergence, although this effect can be highly variable because seed predation is embedded within complex multitrophic interactions that are to date not fully understood; (3) a wide range of fungi are pathogenic to various stages of weed development, but strain efficacy in field trials does not often match that in controlled conditions. We present a framework that superimposes biodiversity-based options for weed biocontrol on a classical Integrated Weed Management system. We then describe the current state of knowledge on interactions between agronomic practices and the organisms at play and between the different biological components of the system. We argue that further advances in our understanding of biodiversity-based options and their performance for weed biocontrol will require farm-scale experimental trials.

Keywords Agroecology · Ecological intensification · Plant competition · Granivory · Cover plants · Pathogenic fungi · Cropping systems

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1 Introduction

Weed management remains a challenging issue that could restrict the move towards pesticide reduction in arable farming. Weed control still relies on the use of synthetic herbicides with 128 t of herbicides sold in EU-28 in 2014, i.e., 33% of pesticide sales (Eurostats 2016—<http://ec.europa.eu/eurostat/>) despite widely acknowledged, detrimental environmental and ecological impacts (Stoate et al. 2009) and major issues of herbicide resistance (Heap 2014). There is, therefore, an urgent need to move towards more sustainable weed management strategies that are much less reliant on herbicide use.

Recently, studies have begun to assess the sustainability of Integrated Weed Management (IWM) practices designed to combine a low reliance on herbicides with current knowledge on the influence of cropping systems on weed demography (Swanton et al. 2008). Particular combinations have been shown to produce long-term control of arable weeds and a significant reduction in herbicide use (Chikowo et al. 2009). Some of these novel cropping systems reconcile agricultural crop production, weed control, and weed biodiversity (Mézière et al. 2014; Petit et al. 2015) and are more energy-efficient (Lechenet et al. 2014). A recent analysis of a network of 946 conventional arable French farms with contrasting levels of herbicide use demonstrated that low herbicide use is generally not in conflict with high productivity and profitability and that methods to reduce herbicides are already available to farmers in most production situations (Lechenet et al. 2017). However, Lechenet et al. (2017) found that rates of herbicide application remained high even when pesticide use was low, suggesting that herbicides remain, above all, the pesticide that is most difficult to reduce in conventional agriculture.

Moving IWM towards biodiversity-based, agroecological approaches, to further reduce herbicide use, will require the use of beneficial biotic interactions that naturally regulate weeds (Wezel et al. 2015; Duru et al. 2015). Scientists have argued that the reliance on pesticide inputs could be considerably reduced by better employing biotic interactions (Rusch et al. 2010; Ekström and Ekbohm 2011). The biodiversity of agroecosystems has declined markedly in recent decades with the intensification of agricultural management (Stoate et al. 2009; Bommarco et al. 2011) with concomitant falls in agroecosystem functioning and notably in the natural regulation of crop pests (Geiger et al. 2010; Cardinale et al. 2012; Oliver et al. 2015). Enhancing beneficial biodiversity and their interactions in agriculture through the integration of a combination of agricultural techniques at different spatial and temporal scales (biodiversity-based systems) remains a highly promising avenue of research that is still largely unexplored (Mézière et al. 2011; Gaba et al. 2015). The main challenge for such agro-ecological approaches to engineering the agro-ecosystem is to design a compatible set of agricultural practices even while the necessary ecological knowledge is often incomplete (Lescouret et al. 2016).

In this paper, we consider three biodiversity-based interactions that could increase the biological control of weeds. The first interaction is competition provided by a “cover” of specifically sown plants directed at the weeds (Teasdale 1996; Zimdahl 2007a,b). The second interaction is granivory of weed seeds by arthropods (Westerman et al. 2003), which can be enhanced through appropriate in-field and off-field management (Kulkarni et al. 2015). The third interaction is a set of interactions that occur between plant pathogenic fungi and weeds (Charudattan 2010; Bailey 2014). For each of these three interactions, we review the existing knowledge on (a) the ecological processes at play, (b) the field-based evidence that they regulate weeds, and (c) the agricultural practices that can be used to enhance these interactions, for which we highlight existing knowledge gaps and future challenges. We then present a hypothetical integrated weed management system that incorporates biodiversity-based options to deliver weed regulation and discuss issues related to implementation of this system.

2 Weed biological control by weed–crop competition

That cropped plants can be manipulated in order to interfere with weeds is not a novel conjecture (Robinson and Dunham 1954), but this hypothesis has received renewed attention lately. Weed–crop competition occurs when individuals share the same limited resource and spatial and temporal niches (Zimdahl 2007a,b). The degree of competition experienced by an individual plant is determined by its species’ characteristics, density and spatio-temporal distribution of other surrounding plants and also the identity of the crop, and its density (spacing between rows and in the row) and phenology (Bleasdale 1960). The addition of a third competitor, like cover crops, makes the study of the system more complex, but, in essence, the main drivers of the competition outcome remain the same. The present review focuses on non-harvested cover crops (i.e., companion crops and cover crop) even if increasing the number of crop species or varieties in the field (intercropping cash crops) could increase weed suppression (Corre-Hellou et al. 2011).

Weed biocontrol can be based upon interference that sown plants can deliver to weeds by competition for resources, such as light, water, and nutrients, as well as by allelopathy. Allelopathy encompasses the effects of chemical compounds produced mainly from the secondary metabolism of plants, microorganisms, viruses, and fungi and that influence the growth. The use of allelopathy for weed control has been the subject of a recent review (Jabran et al. 2015), and we will focus here on weed biological control mediated by competition.

2.1 Description of processes at play at various weed stages

Above-ground, weed–crop competition for light can regulate seed germination as well as many aspects of plant growth, i.e., it can reduce root and shoot biomass and seed production. The intensity of this competition depends on light duration, quantity, and quality. Neighboring plants directly intercept the light supply and thus affect, by shading, the quantity and quality of light transmitted into the canopy.

At least half of all arable annual weeds require light for seed germination (from Juroszek and Gerhards 2004), and leaf canopy-imposed germination inhibition has been demonstrated in a range of small-seeded weeds (King 1975; Silvertown 1980), including light-sensitive and dark-germinating species (Gorski et al. 1978). The cover provided by the crop canopy reduces the red:far-red ratio of light reaching the seed and thus affects the plant phytochrome, a system of photoreceptors that drive the breaking of seed dormancy (Kruk et al. 2006). Red light promotes the phytochrome system whereas far-red light inhibits the system, such that increased light interception promotes seed dormancy. Changes in the light environment predominantly affect seeds at the soil surface as no light penetrates the soil deeper than a few millimeters (Cordeau et al. 2015a). For growing plants, the ability to compete for light varies according to a number of phenotypic traits, such as plant height (Barnes et al. 1990), leaf angle (Hikosaka and Hirose 1997), leaf area (Walker et al. 1988), and the vertical distribution of leaves (Munier-Jolain et al. 2013). Crop and weed species differ in their shade tolerance (Sutherland 2004), and many weed species are well-adapted to compete for light. Summer-germinating weeds, such as *Solanum ptycanthum* Dunal, *Amaranthus albus* L., or *Xanthium strumarium* L., are most photosynthetically efficient under low irradiance (Regnier et al. 1988). Many other weeds acclimate to low irradiance by plastic responses that reduce the growth-limiting effects of shading (Holt 1995). In addition, some weed species, such as *Galium aparine* L. (Bain and Attridge 1988), *Convolvulus arvensis* L., *Solanum dulcamara* L., or *Ipomoea sepiaria* Koenig Ex. Roxb, have climbing and twinning habits that enable them to develop leaves above the crop canopy.

Below ground, weeds can be impacted by competition for nutrients and water, as crop and weed species that coexist require these resources at the same time. Because of early emergence, weeds are however often more successful than crop plants in obtaining nitrogen. This success is highly dependent on the growth response of the weed species to soil-nitrogen availability often described as the N- Ellenberg score (Ellenberg et al. 1992). This nitrophilic status is closely related to some weed ecophysiological traits, such as plant biomass and plant leaf area (Moreau et al. 2013). The amount of competition between weeds and crops is also affected by the

spatial niche overlap of their respective root systems. For example, rhizotron experiments have shown that legume roots grow in the superficial soil layer whereas *Brassica* species, like oilseed rape, grow in the deepest soil layer (Cortés-Mora et al. 2010). In some situations, plant species may not target nitrogen in the same nutrient form. For instance, in N-poor soil, legume species will target nitrogen derived from biological nitrogen fixation (Mylona et al. 1995) and rhizodeposition (Fustec et al. 2010).

Plants compete for water, and the ability of weeds to out-compete crops for water resources is related to their above-ground biomass (Norris 1996). Competition for water is determined by the relative root volume occupied by the competing plants and is greatest when roots closely intermingle within the same soil volume (Wilson 1988). Water use efficiency is also related to the C3/C4 photosynthetic category (Spitters and Aerts 1983), C4 having a general advantage over C3 species in dry conditions.

The competition processes at play to obtain light, nutrients, and water are non-independent. First, when any one of the resources is limiting for a plant, other resources cannot be used efficiently. For example, the deleterious effects of water competition might be amplified by a lack of nutrient uptake. Second, the outcome of the competition for a given resource will impact the plant requirements for additional resources. Nitrophilic weed species markedly increase plant leaf area in response to increased available soil-N (Moreau et al. 2013) and as such become highly demanding in water. In addition, it is generally assumed that there is a trade-off between above-ground and below-ground competitive abilities (Aerts et al. 1991) because of allocation patterns of biomass. Growth of shoots results in a higher competitive ability for light, whereas growth of roots results in a higher competition ability for nutrient and water uptake.

2.2 Evidence of weed biological control by other plants

Current evidence that cropped plants could regulate weed populations mostly stems from experimental trials that have assessed the potential of plant species or combinations of species that are grown before the crop is grown (fallow cover crop) or alongside the crop (intercropped from the sowing or undersown later in the crop cycle) to regulate weeds (Fig. 1 and Fig. 2). Living mulches are plant species sown mostly in the fallow period and kept alive after the cash crop sowing. Existing studies have demonstrated two broad classes of effect, i.e., a decrease of weed emergence or a decrease of weed biomass.

First, plant covers have been shown to decrease weed emergence and thus weed density. Legume cover crops sown in the fallow period (*Medicago polymorpha* L., *Medicago truncatula* Gaertn., *Trifolium alexandrinum* L., and *Trifolium*



Fig. 1 A legume-based cover crop being destroyed by a roller before crop sowing

pratense L.) reduce weed emergence in the succeeding crop by 41 to 78% compared to no cover crop control (Fisk et al. 2001). Hairy vetch (*Vicia villosa* Roth.), crimson clover (*Trifolium incarnatum* L.), but also non-legume cover crops such as rye (*Secale cereale* L.) or barley (*Hordeum vulgare* L.), suppress the emergence of *Solanum ptycanthum* Dun. (Creamer et al. 1996). *Brassica* cover crops were shown to delay and reduce weed emergence by 23 to 34% in the succeeding crop compared with no cover crop control (Haramoto and Gallandt 2005). In oilseed rape crops, undersowing with pea (*Lathyrus oleraceus* Lam.), berseem clover (*Trifolium alexandrinum* L.), common vetch (*Vicia sativa* L.), and mixtures of these species decreased weed density in the oil seed rape by 20–75% compared to sole crop (Lorin et al. 2015). Further studies also suggest that this weed regulation varies greatly with weed species. Weeds such as *Euphorbia helioscopia* L., *Geranium dissectum* L., and *Cyanus segetum* Hill., for example, were shown to have similar emergence rates under cover crops than without cover crops (Cordeau et al. 2015a). These species are not photosensitive, and exposure to light or changes in light quality do not break their dormancy.

Second, a plant cover can limit weed biomass. Cordeau et al. (2015a) showed that the presence of cover reduced weed biomass of all 14 tested weed species, in average by –87.2%. Intercropping companion species, such as pea, berseem clover, common vetch, and mixtures of common vetch/faba bean/berseem clover, have been shown to reduce, by up to 70%, the biomass of annual weeds in comparison to situations of an oilseed rape crop alone (Lorin et al. 2015). To limit the growth of perennial weeds, undersowing a companion crop can also be used with limited impact on the crop productivity. For example, undersowing red fescue (*Festuca rubra* L.) in wheat was shown to have no impact on wheat production but reduced the biomass of rhizomes of *Elytrigia repens* (L.) Desv. ex Nevski by 40% (Bergkvist et al. 2010). Intercropping companion crops was also

shown to limit weed biomass in 90% of 55 trials reported in the literature (Liebman and Dyck 1993). Dead mulches of hairy vetch and cereal rye have received most attention over the past thirty years, but other species, such as subterranean clover, *Trifolium subterraneum* L., have also been tested as living mulches to suppress weeds (Enache and Ilnicki 1990). These studies have focused on weed dynamic during the fallow period and in the succeeding crop, even if living mulches are expected to impact weeds after crop harvest. *T. subterraneum* mulches were found to reduce weed biomasses by between 53% and 94% during the fallow period and by 11% and 76% in the succeeding maize crop (Enache and Ilnicki 1990). Residues from living mulches have been shown to be weed-suppressive, particularly when used at high rates (Mohler and Teasdale 1993). The presence of overwintering annual or permanent living mulches helps control weeds such as *Cyperus* (Hartwig 1977) and may slow down or even prevent the invasion of new weeds such as *Taraxacum officinale* F.H. Wigg. (Hartwig 1989), which might otherwise have become a problem. A recent meta-analysis of 476 experiments showed that legume companion plants significantly decreased weed biomass, by 56 and 42% relative to control treatments with no weed and weed control measures, respectively (Verret et al. 2017).

2.3 Management options promoting weed regulation by other plants

Increasing plant species diversity, via various spatial and temporal manipulations of plant organization in the field (Fig. 2), is a potential tool for suppressing weeds (Liebman and Dyck 1993; Malezieux et al. 2009).

In Fig. 2, the reference system is a winter crop/spring crop succession where the fallow period is left unsown, such as for stubble in no-till systems or bare soil after tillage. The fallow period can be short, between winter cash crops (winter wheat/winter barley, oilseed rape/winter wheat), or long, between winter and spring/summer cash crops (winter wheat/maize, winter wheat/spring barley, durum wheat/sunflower). Fallow cover crop is established during the fallow period, typically in summer time after the harvest of the preceding crops and before rain. When sowing is delayed, even by few weeks, the probability of producing high amount of cover crop biomass decreases (Mirsky et al. 2017). Even if the weed suppression effect was not tested in the latter study, there is clear evidence in the literature that increasing cover crop biomass decreases weed growth (Gebhard et al. 2013). Fallow cover crops established during a short fallow period target weed communities that could emerge in the succeeding winter crop. However, the effect of cover crop is not visible in the succeeding crop when cover crops are terminated by broad-spectrum herbicide that kills the existing weed flora (e.g.,

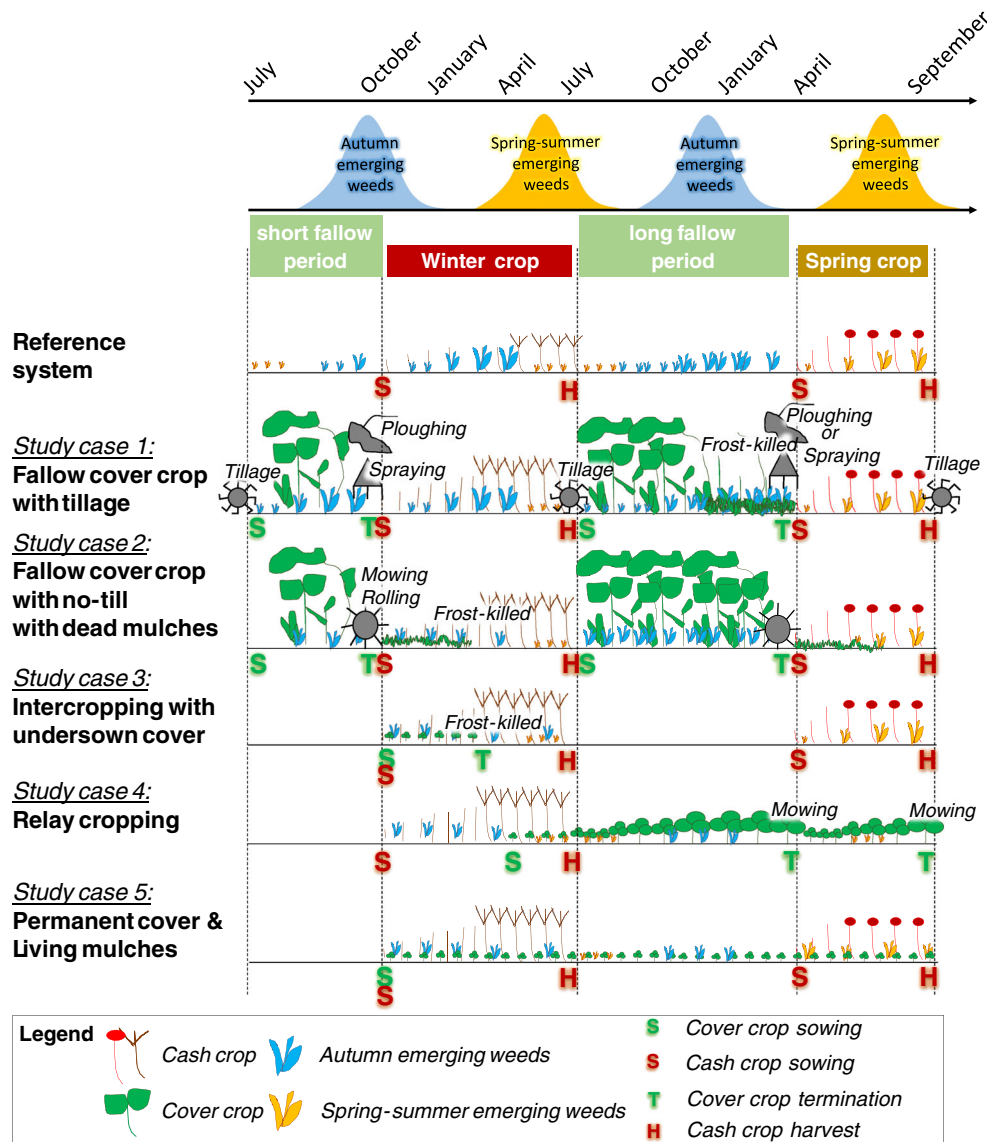


Fig. 2 Spatial and temporal arrangement of cover crops (in green) in cropping systems to target the biological regulation of autumn- (in blue) and or spring-/summer-emerging (in yellow) weed species, according to

glyphosate) or tillage (Fig. 2; study case 1), which stimulates the establishment of other weed seedlings (Cordeau et al. 2017). In regions with hard winters, farmers often use frost-sensitive cover crop species (e.g., *Phacelia tanacetifolia* Benth., *Guizotia abyssinica* (L.f.) Cass., *Fagopyrum esculentum* Moench, *Helianthus annuus* L., *Sorghum bicolor* (L.) Moench, *Camelina sativa* (L.) Crantz, *Raphanus sativus* var. *longipinnatus* L.H. Bailey) so that the cover destruction does not require the use of herbicides and the succeeding cash crop is not infested with cover crop volunteers.

In no-till systems, when cover crops are mechanically terminated, by mowing, roller crimping (Wallace et al. 2017), or root undercutting (Creamer et al. 1996), dead mulches remain on the soil surface (Fig. 2; study case 2) and can limit weed emergence in the succeeding cash crop (Teasdale and Mohler

their patterns of emergence, the timing of sowing (S), harvest (H) of cash crops (in brown), and termination (T) of cover crops (in green)

2000). If established during a long fallow period, cover crops suppress autumn-/winter-emerging weeds by competing for resources so that their effect will not be visible in the succeeding spring crops where mainly spring-/summer-emerging weeds will be present (Fried et al. 2008). In some cases, non-frost-sensitive fallow cover crops established in summertime can be maintained during the winter and terminated in spring to target early spring-emerging weeds and then a summer cash crop can be directly sown (Liebert et al. 2017).

Farmers using tillage (e.g., stale seedbed) to manage summer- or early autumn-emerging weeds, during the fallow period, can undersow living mulches either with the crop (Fig. 2; study cases 3 and 5) or following weeding operations (study case 4) (Hartwig and Ammon 2002; Rasmussen 2004). Living mulches sown within a winter cash crop target autumn-

emerging weeds and are often frost-killed, such as frost-sensitive legumes established in wheat or oilseed rape (Lorin et al. 2015). Permanent living mulches that survive the winter will also suppress spring-emerging weeds. Living mulches may compete with the cash crop (Teasdale 1996), and indeed, most studies have reported a decrease in cash crop yield (Carof et al. 2007; Pedersen et al. 2009; Picard et al. 2010), although a few others have reported no yield loss (Ilnicki and Enache 1992), particularly when living mulches are legumes (Verret et al. 2017). Yield losses were predominantly due to the presence of the cover crops during crop establishment, particularly during spring (Carof et al. 2007; Hiltbrunner et al. 2007). Intercropping frost-sensitive cover crops appears to be a less risky option (study case 3) compared to permanent cover (study case 5) and could release nitrogen for the cash crop needs during spring (Jones 1992; Thorsted et al. 2006) or the following year (White and Scott 1991).

2.4 Knowledge gaps and future challenges in weed control by cover plants

Competitive relationships within a multi-species cover One aspect that is crucial but still poorly documented is the outcome of crop–weed competition during the summer period, when fallow cover crops are established and the in-field situation is characterized by low availability of nitrogen and water. Cover crop mixtures usually include species with various root system types, including taproot, elongated taproot, tuberoid root, and branched root forms. Competition for water and nutrients will result from spatial niche occupation, and thus, studying the role of root architecture and below-ground competition is becoming crucial (Dunbabin 2007). In fallow cover crop as well as in relay cropping or undersowing companion cover crops, understanding the competitive relationships between each component of the system is crucial.

Cover crop species traits: addressing the trade-off between high weed suppression and low yield loss Farmers have tested a range of cover crop species over the last decades and have identified opportunities for breeding cultivars adapted to their needs (Wayman et al. 2017). However, large-scale adoption of cover cropping is currently limited by a lack of varieties that are adapted to different regions and meet farmer needs. The current variety options for cover crops are low in comparison to cash crops, and this problem is particularly acute for organic farmers. To ensure that cash crop and cover crop combinations can be an effective tool for weed regulation, it is urgent that we identify and develop ideotypes of cover crop species that are highly weed-suppressive but have little effect on cash crop productivity. Traits that convey these functions, such as the degree of cold tolerance for winter survival, low specific leaf area for reduced soil water depletion, and high root:shoot ratio for residual nitrogen uptake, are increasingly described (Wilke

and Snapp 2008; Tribouillois et al. 2015). Since current cultivars do not achieve the required multi-factorial level of performance, such as being highly productive and tolerant to pests, one possible option is to consider and select ideotypes of mixes of cultivars or species. This would require designing and evaluating new cultivars not as pure stands but in mixture or intercropped with cash crops.

To conclude, although results from available trials provide evidence that cover plants regulate weed species, there is currently a lack of genericity. The current consensus is that promoting plant–plant competition by manipulating cover crops can greatly contribute to weed regulation (Liebman and Dyck 1993), but it remains unlikely to lead to substantial reductions in herbicide use if used alone (Teasdale 1996). When combined with other management practices, such as tillage, cover crops have been demonstrated to be efficient in managing weeds in conventional and organic systems (Teasdale et al. 2012; Mirsky et al. 2013; Jernigan et al. 2017)

3 Weed biological control by granivory

To date, the best-documented example of weed regulation by granivory of arable weeds is that provided by seed-eating carabid beetles. Many carabid species are known to be seed predators and may therefore represent valuable agents for the bio-control of weeds in agro-ecosystems (Honěk et al. 2003; Kulkarni et al. 2015).

3.1 The process of weed seed consumption

Carabid beetles are generalist predators that are very abundant in arable fields and can produce substantial post-dispersal weed seed predation (Honěk et al. 2003). Predation occurs in brief and intense periods of seed consumption (pulses), which follow recurrent weed seed rain episodes, prior to the seeds being protected by burial by rain and wind (Westerman et al. 2009; Davis and Raghu 2010). Seed-eating carabids have been shown to aggregate spatially in response to the sudden inputs of trophic resources (Diehl et al. 2012).

Seed-eating carabid is a general term encompassing both omnivorous and granivorous species and within these trophic guilds, sub-groups can be identified that differ in their association with weed species (Brooks et al. 2012). Cafeteria tests conducted in the lab suggest that individual carabid species exhibit preferences in the seeds they consume (Honěk et al. 2003; Petit et al. 2014). Weed preference is shaped by the size of seeds and the size of predators, e.g., larger carabids consume larger weed seeds (Honěk et al. 2007). Other factors such as the nature of resources stored in the seed and the thickness of the seed coat appear, at least anecdotally, to be key. The consequences of preferential weed seed predation are two-fold: (a) not all weed species are consumed by carabids

and (b) it is the composition of carabid communities that determines the weed species that are the most impacted by seed predation (Fig. 3).

In field conditions, complex multitrophic interactions influence the fate of weed seeds. The hypothesis that increasing seed-eating carabid abundance may lead to enhanced weed suppression in many agricultural systems is widely accepted (Gallandt et al. 2005; Westerman et al. 2005; Petit et al. 2017) and illustrated with data on *Viola arvensis* predation in 67 winter wheat fields in North-east France in Fig. 4. Carabid diversity may also drive the amount of seeds consumed in arable fields (Gaines and Claudio Gratton 2010; Trichard et al. 2013), possibly because increased species richness leads to an increase in the diversity of carabid body sizes and therefore an increase in the range of seeds consumed (Honěk et al. 2007). It is likely that density-dependent effects are at play (Cardina et al. 1996; Cromar et al. 1999). Carabid satiation during periods of peak weed seed rain could limit the potential of seed-eating carabids to control weeds at certain times (Davis and Raghu 2010). Overall, seed consumption will therefore likely be impacted by the densities of both of weed seeds and carabids (Frank et al. 2011). Intra-guild predation in carabid communities may be another limiting factor (Currie et al. 1996). Omnivorous carabids prey upon one another, and there are likely to be additional in-direct (non-trophic) effects. Small carabids might alter their behavior, in response to the risk of intra-guild predation, by lowering their level of activity or by leaving prime foraging locations, in order to reduce their individual risk (Prasad and Snyder 2004; Smith et al. 2008). Finally, several studies suggest that seed-eating carabid species shift their diet during their activity period (Marino et al. 2005; Mauchline et al. 2005; Brooks et al. 2012). For example, *Amara similata*, described as mainly phytophagous, has been shown to feed mostly on pollen beetle and stem weevil larvae in oilseed rape fields in early spring (Haschek et al. 2012). Other seed-eating species, such as *Pterostichus melanarius*, feed on slugs (Bohan et al. 2000). The spatio-temporal distribution of alternative prey may therefore play an important role in the delivery of weed seed predation.



Fig. 3 The carabid *Pseudophonus rufipes* feeding on *Cyanus segetum* seeds

3.2 Evidence of weed biological control by granivory

Given the episodic nature of weed seed predation, field estimates of seed predation are highly variable in time but repeated measurements have allowed the calculation of annual seed losses due to predation (Westerman et al. 2003). From ten published datasets, Davis et al. (2011) estimated that annual losses due to invertebrates averaged 40% of the total number of seeds produced by the plants, over a range from 8 to 70% depending on the weed species and the agronomic context. The annual rate of seed depletion by invertebrate predators can therefore be substantial, but the impact of seed predation on weed regulation and control is still poorly documented. In other words, the evidence that rates of predation reported in the literature may significantly affect the demography of particular weed species is still scarce. A few modelling studies have addressed this question. Results suggest that an annual seed loss of 25–50% may be enough to substantially reduce weed population growth and maintain weed population to a stable size (Firbank and Watkinson 1985; Westerman et al. 2005). Empirical evidence of effective weed regulation by carabid beetles is even scarcer. A recent national scale survey detected a significant but small negative relationship between the abundance of seed-eating carabid beetles and the weed seed bank turnover, suggesting a regulation effect of carabids on weeds (Bohan et al. 2011). Seed predation by invertebrate was shown to reduce the emergence of *Abutilon theophrasti* Medik. and *Setaria faberi* F. Herm. by 4 to 13% (White et al. 2007). A recent experimental trial using differential predator exclusion showed a 38% reduction in seedling emergence and 81% reduction in weed biomass for *Chenopodium album* L. in fallow plots, suggesting that invertebrate seed predators suppress weeds (Blubaugh and Kaplan 2016).

The general lack of empirical evidence for weed regulation remains the key information gap to be filled and represents the primary scientific obstacle for a wider use of weed seed predation in agriculture.

3.3 Management options promoting weed seed granivory

To date, a limited number of studies have assessed the effect of agricultural practices and/or of the characteristics of off-field features or landscape properties on the amount of weed preyed upon in-field. However, because of well-established links between observed seed predation levels in-field and the richness, diversity, and abundance of seed-eating carabids (Fig. 4), it is possible to provide useful management guidelines for carabids. The evidence currently available suggests that both local and landscape scales can be used, in combination or not, to enhance the amount of seed predation in arable fields.

3.3.1 Local scale

In-field management Direct assessments of weed seed predation variations in response to agricultural practices show that seed predation tends to be higher in no-tilled fields, with an effect of time since conversion (Fig. 4) (Cromar et al. 1999; Menalled et al. 2007; Petit et al. 2017) as well as in fields with important (crop and non-crop) vegetation cover (Gallandt et al. 2005; Meiss et al. 2010; Sanguankeo and Leon 2011). However, several studies failed to detect any effect of in-field management on weed seed predation, particularly in organic farming (Diekötter et al. 2010; Jonason et al. 2013), and there is a need to identify more precisely agricultural practices that impact weed seed predation. Studies focusing on the spatial distribution of carabids indicate that crop type is a major driver (Kromp 1999; Eyre et al. 2013; Labruyere et al. 2016a). This crop effect mostly relates to the cover that is provided at certain times of the year, the microclimate (temperature, humidity) prevailing at the ground surface (Honěk and Jarošík 2000; Holland and Luff 2000) and prey availability (Diehl et al. 2012; Labruyere et al. 2016b). Differences in cropping systems, tillage regimes, and pesticide use can also drive the composition of carabid communities (Holland and Luff 2000; Thorbek and Bilde 2004; Hatten et al. 2007; Trichard et al. 2014).

Field margins Non-crop habitats that are directly adjacent to arable fields may provide carabids with alternative prey and a refuge from agricultural disturbances that occur in-field (Landis et al. 2000; Pfiffner and Luka 2000). Some carabid species also overwinter in field boundaries or grassy habitats and recolonize the adjacent crop field during the crop growing season (Wissinger 1997). As a result, the presence of grassy field margins, wildflower strips, and beetle banks can enhance the abundance of seed-eating carabids in the adjacent crop

(Lys and Nentwig 1992; Hof and Bright 2010). The presence of a non-crop habitat has also been shown to enhance the fitness of individuals within the adjacent crop (Zangger et al. 1994; Labruyere et al. 2016b).

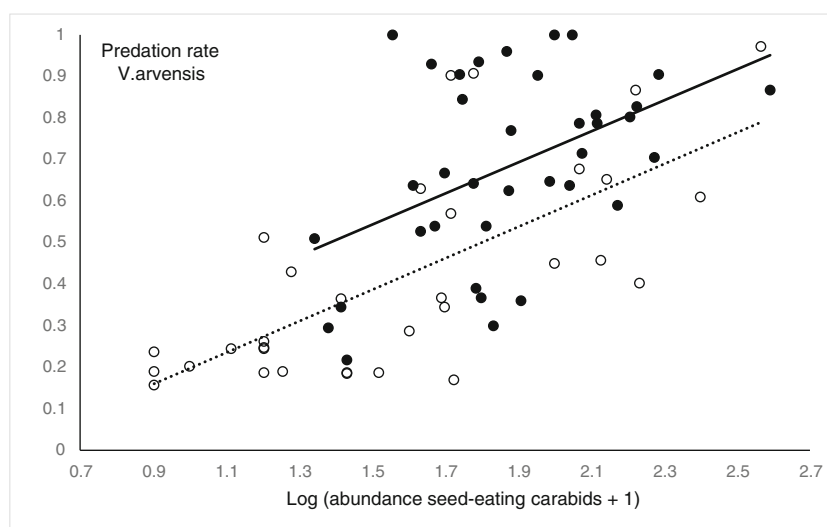
3.3.2 Landscape scale

Landscape context At landscape scales, the amount of particular habitats and the complexity in spatial arrangement of those habitats can have an important effect on weed seed predation but results appear to be context-dependent (Menalled et al. 2000; Trichard et al. 2013; Jonason et al. 2013). There can be conditional effects, such as when predation is enhanced in organic fields in complex landscapes whereas predation is only enhanced in conventional fields in simple landscapes (Fischer et al. 2011). Seed predation can also be highly dependent on the landscape context in fields recently converted to conservation agriculture, but independent of landscape in fields converted more than four years previously (Petit et al. 2017). Landscape-scale effects on carabids have been well-described and show that beyond the effects of compositional and structural properties of the surrounding landscape, landscape-scale management can also drive carabid communities. For example, the proportion of organic farming at the landscape scale was shown to enhance the activity and the body size of granivorous carabid species, thus enhancing their potential to control arable weeds (Diekötter et al. 2016).

3.4 Knowledge gaps and future challenges in weed seed granivory

Identifying the combination of in-field agricultural practices and landscape properties that can sustain intense and stable weed seed predation levels will require more precise quantification of trophic feeding links between carabids, weeds, and

Fig. 4 Relationship between the abundance of seed-eating carabids and the predation rate of *Viola arvensis* in 67 winter cereal fields during spring. Empty circles represent fields under the Conservation Agriculture for less than 4 years, and filled circles represent field under the Conservation Agriculture for 4 to 7 years. Data derived from Petit et al. (2017)



alternative prey species and a better understanding of the agronomic factors influencing seed predation. Current multiplex PCR primers allow many prey species to be screened simultaneously and sampling carabid gut contents can now be done non-destructively (Wallinger et al. 2015). The use of new-generation sequencing approaches also offers the potential for widening the assessment of prey species beyond those already known or suspected to potentially any plant species that exists within DNA sequence databases (Traugott et al. 2013). In parallel, there is a growing understanding of the importance of non-prey items in the diets of invertebrates serving as natural enemies (Lundgren 2009). This is a key issue because management strategies aiming at supporting carabids across a farmland landscape will likely also benefit other organisms (Gonthier et al. 2014). Any increase in the range of alternative prey available for carabids may allow prey switching and thus weaken their impact on weeds. Recent progress in the area of ecological networks, reconstructed from DNA data (Bohan et al. 2013; Vacher et al. 2016), is a promising avenue of research for separating out the multiple, simultaneously occurring interactions.

4 Weed biological control by fungi

Microorganisms in general but here, where we will focus on fungi, interact in different ways with plants, and this is in trying to decipher such interactions that putative bioherbicidal activities have been detected. Thus, biological control of weeds with pathogenic fungi has been the subject of various studies and then of many reviews including book chapters these last decades (TeBeest et al. 1992; Bailey 2014; Hershenthorn et al. 2016).

4.1 Biotic interactions between fungi and weeds at various weed stages

Above-ground Most interactions between weeds and fungi refer to pathogens causing aerial symptoms, although these can have a soil-borne phase during their life cycle. The mode of penetration used and the symptoms these fungi cause are similar to those described in crops. Pathogenic agents enter the plant tissues through stomata, specialized host cells, sites of mechanical injury or after other organisms have broken down the skin barrier. Symptoms include leaf staining, leaf curl, necrosis and premature leaf drop, early drying, fruit rot, cankers caused by different fungi (powdery mildew, rusts), and oomycetes (mildew) as in the case of ragweed, *Ambrosia artemisiifolia* L. for example, whose leaves can be infected with *Alternaria* sp. and *Rhizoctonia solani* (Runion et al. 2014) and *Plasmopara* sp. (Choi et al. 2009). Strains of *Sclerotinia sclerotiorum* and *S. minor* have been tested for their virulence against dandelion *Taraxacum* sp. (Riddle

et al. 1991). Similarly, strains of the same pathogenic fungi (Quimby et al. 2004) and of *Verticillium dahliae* (Skipp et al. 2013) were also tested for their ability to control Canada thistle *Cirsium arvense* (L.) Scop.

Secondary metabolites of fungi can have bioherbicidal effects. Metabolites produced in culture medium by *Ascochyta caulina*, *Drechslera gigantean*, and *Diaporthe* sp. were successfully tested for their phytotoxic activity against crabgrass, *Digitaria sanguinalis* (L.) Scop. (Evidente et al. 2006), *Chenopodium album* L. (Vurro et al. 2012), and horseweed, *Conyza* sp. (Pes et al. 2016). However, these promising results have been obtained under controlled conditions and have yet to be validated under natural conditions to guarantee the efficacy of these metabolites as mycoherbicides. Moreover, the control of *Xanthium occidentale* Bertol. using a combination of actions of the pathogenic agent, *Alternaria zinniae*, and a low concentration of brefeldin A, a secondary metabolite produced by the fungus during its growth, provided improved results because on one side, plant defense reactions including phenylalanine ammonia-lyase induction were blocked and on the other side *Alternaria zinniae* pathogenicity was enhanced (Vurro et al. 1998).

Below-ground Soil fungi are involved in seed decomposition, but whether this mechanism is a pathogenic trait involving a relative specificity of the pathogen–host interaction or simply a random and opportunistic saprotrophism between a fungus and an organic substrate integrated in the soil is not clear. Recent studies have shown that *Fusarium tricinctum* selects non-dormant seeds of cheatgrass *Bromus tectorum* L. and disregards dormant seeds, suggesting that exudates produced by non-dormant seeds attract and stimulate *Fusarium tricinctum* activity (Franke et al. 2014). Several strains of *Fusarium oxysporum* inhibit the germination of the parasitic weed broomrape, *Phelipanche ramosa* (L.) Pomel, or disturb its interaction with the crop host plant (Müller-Stöver et al. 2009). *Epicoccum purpurascens*, isolated from *Echinochloa* spp., inhibits seed germination of this weed and damages its leaves (Motlagh 2011). Strains of *Fusarium avenaceum* were however also shown to trigger the release of activated forms of polyphenol oxidases, a set of plant defense enzymes by dormant seeds of wild oat *Avena fatua* L. although this effect disappears in the presence of the oomycete *Pythium ultimum* (Fuerst et al. 2011). It is therefore quite likely that signal molecules are produced both by seeds, whether dormant or not, and by fungi, whether they are pathogenic or not.

Soil-borne pathogenic fungi can attack weeds during the germination and emergence of the seedling (Lamichhane et al. 2017). These damping-off attacks are made by fungi, such as *Rhizoctonia solani* and *Fusarium* spp., and oomycetes, such as *Phytophthora* spp. and *Pythium* spp.; the host spectrum of which being particularly wide can include weeds as well as crops (Agrios 1997; Berestetskiy 2004; Pane et al. 2011; Ray and Vijayachandran 2013).

Finally, the root system of weeds may also be subject to soil-borne fungal and oomycetic attacks during the entire plant cycle. Strains of *Fusarium solani*, *F. oxysporum*, and *F. tricinctum* cause severe root necrotic lesions and crown rot in the invasive *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Caesar et al. 2002). Strains of *Fusarium* sp. cause root rot of ragwort *Senecio jacobaea* L. but can also be responsible for root rot of the cultivated clover (Pearson et al. 2016).

Table 1 presents some examples of weeds pathogenic fungi whose targets may be aerial parts, root parts, or seeds. In some cases, the relevant phytotoxic secondary metabolites have been identified.

4.2 Evidence of weed biological control by fungi

The specificity of the plant–pathogen interaction is not always complete. The pathogenic fungus responsible for the death of a target weed species may also be pathogenic to other plant species, including the crop. In addition, unlike chemicals, the infectious activity of pathogens takes place over time, depending on the phenological stage of the plant, which is not always compatible with the expectations of producers wishing a visible, rapid effect.

Evidence of successful weed biocontrol in field trials is still scarce although there are some success stories in North America and Australia. Seed infection by inundative applications of the seed-borne pathogen *Pyrenophora semeniperda* was demonstrated on several annual grass weeds (*Bromus diandrus* Roth., *Avena fatua* L., *Lolium rigidum* Gaudin, *Hordeum leporinum* Link., *Vulpia bromoides* (L.) Gray), with for example more than 70% of *B. diandrus* seeds infected by the pathogen. The inoculation of conidia suspensions is generally more effective than that of propagule mixtures and leads to an absence of germination in most weeds and to a significant reduction in the viability of those having germinated (Medd and Campbell 2005). Chandramohan et al. (2002) proposed to use combination of three fungi, *Drechslera gigantea*, *Exserohilum longirostratum*, and *Exserohilum rostratum*, to control a complex of seven weedy grasses. Control efficacy of the mixture ranged from 32 to 98% and 74 to 100% depending on the year and was equivalent to the additive efficacy of each fungal species but with the benefit that a mixture is easier to use. In many instances, the bioherbicidal effect of particular isolates is only delivered under specific conditions (host specificity, crop tolerance, efficacy, temperature, and moisture spectrum). For example, *Stagonospora convolvuli* was found to control the bindweeds, *Convolvulus arvensis* L. and *Calystegia sepium* (L.) R. Br., in maize crops provided the selection and formulation of the fungal inoculum met the required conditions (Défago et al. 2001). In the field trial, bindweed cover in the *Stagonospora*-treated plots (two to five applications at 40–160 ml/m² and 5.10⁶ conidia/ml) remained low at 14.6% and the weed necrotic leaf area reached 78%

(45.4% of leaves dead), while in the control plots (treated with the fungicide benomyl), bindweed cover increased by 115%, and necrotic leaf area was 13.8% (6% of leaves dead). The experience was successfully repeated several years in succession. However, the same level of control was not achieved from one year to the next (Boss et al. 2007). This efficacy was further enhanced by the combined use of the fungal inoculum and the insect *Melanagromyza albocilia*, the latter facilitating the penetration of the fungus into the weed stem (Défago et al. 2001). Different accessions of *Convolvulus arvensis* L. originating from different regions in North America and Europe were tested for their susceptibility to *Phomopsis convolvulus*. The fungus caused nearly half of the *C. arvensis* seed death observed and reduced the bindweed foliar biomass from 65 to 100% depending on the accession, indicating that control of *Convolvulus arvensis* using *Phomopsis convolvulus* might be achieved across geographic regions (Vogelgsang et al. 1999).

In many instances, there are issues with transferring the infectious activity detected under controlled conditions into field situations. For example, *Phomopsis amaranthicola* and *Microspheariopsis amaranthi* were shown to control *Amaranthus* spp. under controlled conditions in greenhouses but much less in the field, although field trials revealed that the combination of the two fungi had more pathogenic effect than the use of a single isolate (Roskopf et al. 2005; Moran and Showler 2007). In the Netherlands, combinations of *Ascochyta caulina* conidia, fungal phytotoxins, nutrients, and low doses of chemical herbicides provided promising results to control *Chenopodium album* L., but the efficacy of the *Ascochyta caulina* strain was too limited for the development of a bioherbicide (Netland et al. 2001). Strains of *Fusarium oxysporum* that reduced the parasitic incidence of *Phelipanche ramosa* (L.) Pomel under controlled conditions could reduce the biomass of *Phelipanche ramosa* shoots between 30 and 70% when tested in tobacco fields, but these results were not reproducible from one year to the next. Subsequent experiments revealed fungistatic effects of the field soil that partly explained the reduced efficacy of field experiments (Kohlschmid et al. 2009). Reasons for such a gap between greenhouse trials and field applications are multiple and not necessarily always well-known. They might be due to the wide variety of weed survival strategies, the poor ecological fitness of fungal candidates introduced into a not-always welcoming biotic environment, and the particular edapho-climatic conditions. In combination, these factors likely determine the success/failure of the weed–pathogen interactions (Kohlschmid et al. 2009; Swope and Stein 2012). Improving inoculum formulations appears to be a necessary step to ensure fungal survival when faced with environmental stresses and to assure pathogenic activity towards target weeds (Quimby et al. 2004).

Table 1 Some examples of weed pathogenic fungi whose targets may be aerial parts (1), seeds (2), or root (3) parts. In some cases, phytotoxic secondary metabolites have been identified (4).

| Target weed species | Causative pathogenic fungi and oomycetes | References |
|--|--|---|
| (1) Attacks on stem or foliage | | |
| <i>Amaranthus</i> spp. | <i>Phomopsis amaranthicola</i> / <i>Microspheariopsis amaranthi</i> | Roskopf et al. (2005)/Moran and Showler (2007) |
| <i>Ambrosia artemisiifolia</i> | <i>Alternaria</i> sp.; <i>Rhizoctonia solani</i> / <i>Plasmopara</i> sp. | Runion et al. (2014)/Choi et al. (2009) |
| <i>Calystegia sepium</i> | <i>Phomopsis convolvulus</i> | Vogelgsang et al. (1999) |
| <i>Chenopodium album</i> | <i>Ascochyta caulina</i> | Netland et al. (2001), Ghorbani et al. (2006) |
| <i>Cirsium arvense</i> | <i>Verticillium dahliae</i> , <i>Phoma</i> sp. | Skipp et al. (2013) |
| <i>Convolvulus arvensis</i> | <i>Staganospora convolvuli</i> / <i>Myrothecium verrucaria</i> | Défago et al. (2001)/Millhollon et al. (2003) |
| <i>Fallopia japonica</i> | <i>Mycosphaerella polygoni-cuspidati</i> , <i>Puccinia polygoni-amphibii</i> | Kurose et al. (2009, 2012) |
| <i>Rumex dentatus</i> | <i>Alternaria alternata</i> | Siddiqui et al. (2010) |
| <i>Senecio vulgaris</i> | <i>Puccinia lagenophorae</i> | Kolnaar and van den Bosch (2001) |
| <i>Taraxacum</i> sp. | <i>Sclerotinia sclerotiorum</i> / <i>Sclerotinia minor</i> / <i>Phoma macrostoma</i> | Riddle et al. (1991)/Li et al. (2010)/Bailey (2014) |
| <i>Tradescantia fluminensis</i> | <i>Cercospora apii</i> , <i>Rhizoctonia solani</i> , <i>Uromyces commelinae</i> | Macedo et al. (2016) |
| (2) Seed germination inhibition | | |
| <i>Avena fatua</i> | <i>Fusarium avenaceum</i> + <i>Pythium ultimum</i> | Fuerst et al. (2011) |
| <i>Bromus tectorum</i> | <i>Fusarium tricinctum</i> / <i>Pyrenophora semeniperda</i> | Franke et al. (2014)/Ehlert et al. (2014) |
| <i>Bromus diandrus</i> , <i>Avena fatua</i> , <i>Lolium rigidum</i> , <i>Hordeum leporinum</i> , <i>Vulpia bromoides</i> | <i>Pyrenophora semeniperda</i> | Medd and Campbell (2005) |
| <i>Echinochloa</i> spp. | <i>Epicoccum purpurascens</i> | Motlagh (2011) |
| <i>Phelipanche ramosa</i> | <i>Fusarium oxysporum</i> | Müller-Stöver et al. (2009) |
| (3) Root and crown rot | | |
| <i>Abutilon theophrasti</i> , <i>Setaria faberi</i> | <i>Pythium</i> sp. | Davis and Renner (2007) |
| <i>Centaurea diffusa</i> , <i>C. maculosa</i> | <i>Fusarium solani</i> , <i>F. oxysporum</i> , <i>F. tricinctum</i> | Caesar et al. (2002) |
| <i>Lepidium draba</i> | <i>Rhizoctonia</i> spp. | Caesar et al. (2014) |
| <i>Senecio jacobaea</i> | <i>Fusarium</i> sp. | Pearson et al. (2016) |
| <i>Tradescantia fluminensis</i> | <i>Sclerotium rolfsii</i> | Macedo et al. (2016) |
| (4) Mode of action based on the production of fungal phytotoxins | | |
| <i>Carthamus lanatus</i> , <i>Cirsium arvense</i> | <i>Pyrenophora semeniperda</i> , <i>Stagonospora cirsii</i> | Cimmino et al. (2015) |
| <i>Digitaria sanguinalis</i> | <i>Ascochyta caulina</i> | Evidente et al. (2006) |
| <i>Xanthium occidentale</i> | <i>Alternaria zinnia</i> | Vurro et al. (1998) |
| <i>Chenopodium album</i> | <i>Drechslera gigantean</i> | Vurro et al. (2012) |
| <i>Conyza</i> sp., <i>Echinochloa</i> sp. | <i>Diaporthe</i> sp. | Pes et al. (2016) |

4.3 Management options for weed regulation by fungi

There are two approaches to implement weed biological control by fungi (Tebeest et al. 1992; Barton 2004; Charudattan 2010; Hershenhorn et al. 2016).

The first, described as “classical,” consists of locally introducing fungal pathogen(s) of the weed, isolated from symptomatic weeds plants in their region of origin. In principle, classical biological control is economical and relatively

simple to implement, although it must satisfactorily address the strict criterion that the specific host–pathogenic interaction be reproduced in an environment in which the plant had no natural enemy (Charudattan 2010). If successful, this approach should lead to a gradual reduction of the weed population and therefore can only be envisaged under special conditions involving, in particular, vegetative propagation of the plant in areas not targeted for control, such as adjacent grasslands or forested areas. Classical biological control has been used in Brazil, South Africa, Australia, and New Zealand,

where many invasive weeds originating from other continents threaten the native biodiversity (Grice 2004; Scott and Morin 2012). Nearly 40 fungal biocontrol agents have been or are still being successfully used to control invasive weeds in Australia (Barton 2004; Hershenthorn et al. 2016). One of the reasons for the success of this approach is undoubtedly related to spatial and time scales. In these countries, environmental managers aim at controlling invasive plants in large natural areas and the process is spread over several years, the resilience of the (eco)system providing both biological and legislative regulation. In the EU, although invasive weeds represent a clear issue, legislative problems have limited classical biocontrol based on the release of exotic biocontrol agents including fungi (Shaw 2003; Kurose et al. 2006).

The second approach is referred as “inundative” or “bioherbicide strategy.” It consists in applying massive and repeated doses of phytopathogenic agents to suppress weeds, so that applications are thought of in the same ways as the application of chemical pesticides (TeBeest et al. 1992; Charudattan 2010; Harding and Raizada 2015). Bioherbicides can be formulated as complexes of biocontrol products, including phytopathogenic fungi applied in combination with vegetable or fungal metabolites (Hershenthorn et al. 2016). Massive inoculation of a mixture of 20% canola oil emulsion with 10^7 conidia/ml of *Alternaria alternata* was successfully used to control *Rumex dentatus* L. in wheat under field conditions in the Philippines (Siddiqui et al. 2010). Two applications of a mixture of rice hulls and bran and *Sclerotinia rolfsii* were shown to control broad-leaved weeds in rice fields in China (Tang et al. 2011). Such results are promising, but it remains to establish whether resistances to bioherbicides have appeared among weeds. A massive use of microorganisms as biocontrol agents represents a risk of future emerging weeds resistant to pathogens used to control them (besides that these weed pathogens can also be or become pathogenic to plants of agronomic and environmental interest). This is why it seems preferable to use metabolites which, unlike synthetic xenobiotics, are naturally biodegradable and should not exert continuous pressure on the target plants.

As bioherbicides typically consist of native pathogens, they do not face to same regulatory burden of proof of safety that exotic pathogens must bear. However, bioherbicides require a capital outlay for industrial R&D, commercial backing, a willing registrant, as well as customers (Charudattan 2010). Ten to twelve mycoherbicides are currently on sale, but none of them is from Western Europe, and only three have achieved any measure of success in the marketplace (Charudattan 2010; Dagno et al. 2012; Bailey 2014).

4.4 Knowledge gaps and future challenges in weed control by fungi

Weed control by fungi remains underused, especially in Europe, and addressing some of the current practical

limitations as well as more fundamental knowledge gaps is necessary to increase the use of bioherbicides in weed management strategies; so, bioherbicides should be combined with other weed management tools.

In practical terms, one limitation to the adoption of weed control by fungi is the poor documentation of the outcomes of biological control programs. It is thus important to improve the long-term evaluation of agent efficacy as well as the long-term evolution of fungi introduced into the environment, and notably possible changes in the specificity of their pathogenic activity (Morin et al. 2009; Bailey 2014). Notably, this involves ascertaining the host spectra, so as not to affect the crops and to measure the impact of inundative inoculation of a strain or set of fungal strains on the wider environment. It can be derived from field observations but also by using of predictive models designed to assess the risk of misuse of a pathogen to control a weed (Barton 2012; Berner and Bruckart 2012). This evaluation should also focus on estimating the cost/benefit ratio of biocontrol versus chemical and/or mechanical approaches. The search for bioherbicide niche markets and improved collaborations between researchers and R&D industries to develop formulations would be valuable (Kremer 2005; Bailey et al. 2011). Finally, more effective communication with farmers and the public is required to remove their doubts and fears about the mutability of pathogens, putative genetic recombination, unpredictable nontarget attack, mycotoxin accumulation, or environmental buildup (Charudattan 2010).

In addition, there are scientific challenges. First, many questions arise about impacts of fungal inoculum introduction in agrosystems; persistence and activity of fungal inocula in fields, ecological fitness of these inocula interacting with communities already present in the environment and with the cultural practices (e.g., fertilization, ...), and effects on weed plants (e.g., defense reactions, ...), on weed population demography and on the other communities (microbial, insects, ...). All of these impacts should be described. The data acquired should feed into models to predict the bioherbicide and weed population fate under different edapho-climatic conditions and cropping systems (Berner and Bruckart 2012; Berner and Cavin 2012; Colbach et al. 2014). Second, research should focus on broad-spectrum rather than solely on highly host-specific bioherbicides. This can involve mixing strains whose host specificities are different and correspond to co-occurring weed species in given cropping systems or by mixing fungal strains and phytotoxic secondary metabolites of fungal and/or plant origin (Vurro et al. 2012). The use of phytotoxic metabolites towards weeds, mimicking already used herbicide approaches, might accelerate the development of weed bio-control. In classical biological control, solutions may emerge from combined use of fungi and arthropods, especially of insects, or fungi and secondary metabolites of microbial or plant origin, so that a host–parasite-like equilibrium

may develop over time. Finally, only limited attention has been paid so far to the possibilities of targeting the seedbank to control weeds. Studies are needed to identify fungal and/or soil microfauna functional groups naturally present in the soil and able to decay weed seeds. These might be either specific weed seed pests, which remain to be identified, or opportunistic saprotrophs capable of hydrolyzing caryopses and other seed coats, thus preventing their germination. The next step would then be to assess how the activity of such beneficial groups could be enhanced by agricultural practices.

5 Towards an integrated management promoting the biological control of weeds

5.1 Presentation of the framework

In this paper, we have argued that classical IWM-based cropping systems could be widened to integrate additional management practices specifically promoting the biological regulation of weeds. Figure 5 represents a system incorporating these components for enhancing weed biological regulation.

In a classical IWM-based cropping system, the set of selected agricultural practices is used to increase crop yield and decrease weed abundance (Fig. 5), which in turn has a positive feedback effect on crop yield (Quinio et al. 2017). However, these agricultural practices also impact the composition of natural communities in the agroecosystem, including seed-eating arthropods (Kromp 1999) and fungal communities (Trognitz et al. 2016). As stated in Section 3, interactions between agricultural practices and seed-eating carabids are well described in the literature. However, individual practices that are combined in a cropping system can have opposite effects on the abundance or diversity of carabid communities. Conversely, the impact of agricultural practices on fungal communities is hardly documented and further research should be developed to fill in this large knowledge gap.

Additional management practices can be superimposed on the classical IWM system to enhance the biological regulation of weeds (Cordeau et al. 2016). This is illustrated in Fig. 5, with two levers represented by green lozenges: (a) the inundative use of bioherbicides and (b) in-field plant diversification in space and time with the introduction of cover crops. The addition of these two levers and the explicit account of natural communities involved in weed biocontrol complexify the number of potential interactions between the components of the framework, which are either effects of practices on communities and weed biocontrol or interactions between organisms that are present in the system, including the crop. In this section, we describe this framework and identify available knowledge and current knowledge gaps.

Applications of bioherbicides are expected to decrease the abundance of weeds, as long as IWM practices do not impede

the expected effects of bioherbicide applications. Inundative release of bioherbicides may potentially affect fungal communities that are naturally present, but there is to date limited knowledge on such interactions (Hoagland et al. 2007). Bioherbicides may also impact seed-eating arthropod communities, but we have little evidence of such potential effects.

In-field plant diversification is expected to have a direct weed suppression effect through cropped plant–weed competition and, in some instances, and for some weed species, through allelopathy. In-field plant diversification is also likely to lead to changes in communities that naturally occur within cultivated fields (Lichtenberg et al. 2017). Increasing in-field plant diversity can be implemented through different management options (see the five case studies presented in Fig. 2) that will imply modifications of the initial cropping system and associated agricultural practices. Table 2 presents the body of available field-based evidence on impact of the five case studies of in-field plant diversification on weed seed-eating carabid abundance and fungi pathogenic to weeds, as well as on the intensity of the related weed biocontrol. For all five case studies, there is a strong support that increasing in-field plant diversity in space and time promotes weed seed depletion by seed-eating carabids (Table 2). Indeed, the higher the vegetation ground cover, the higher the seed predation (Galland et al. 2005). In-field plant diversification can also impact fungal communities and their pathogenic activity towards weeds, but available knowledge is very limited so that no general statement can be made (Table 2). A final aspect likely to be important in the delivery of weed biocontrol is potential interactions between biocontrol agents (e.g., fungal communities and seed-eating arthropods), and these are yet to be described. It is also possible that enhancing natural communities delivering weed biocontrol impacts crop growth or crop health.

5.2 Implementation of the framework

The description of this framework reveals a significant degree of uncertainty and/or gaps in our understanding of the relations between farming practices and the dynamics of organisms playing a role in weed biocontrol. It is for example unclear if (and if so, which) specific IWM practice should be avoided when biodiversity-based options are mobilized because it counteracts expected weed biocontrol. The nature of the biological interactions that would develop in a biodiversity-based system and their consequences on weed biocontrol, but also more broadly on crop production, are not yet clearly understood. Significant advances in our understanding of biodiversity-based systems are thus required if such options are to be adopted by farmers. A first step could be the implementation of the framework on experimental farms, with two major objectives requiring two complementary approaches (Cordeau et al. 2015b).

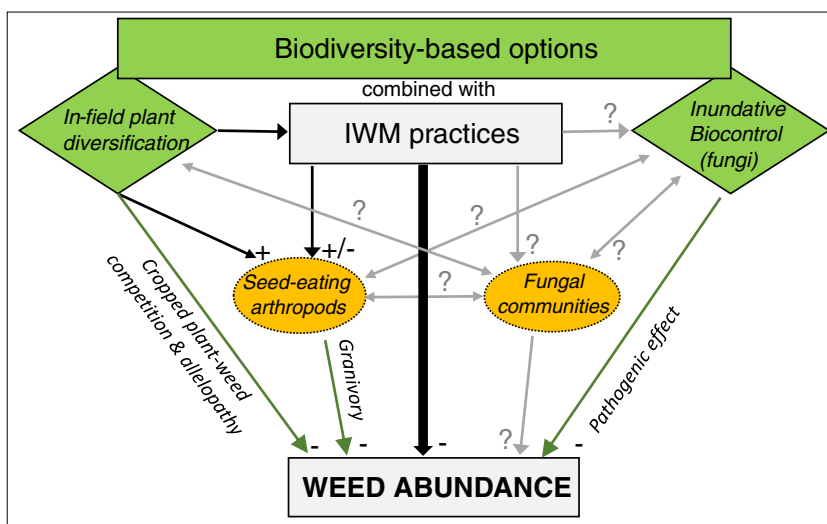


Fig. 5 General framework presenting the different components and interactions between components of a biodiversity-based management system. Here, two biodiversity-based options for weed biocontrol (green lozenges) are superimposed on an Integrated Weed Management

(IWM) system. IWM practices (thick black arrow) and biological control (green arrows) have a negative impact on weed abundance. Many interactions coexist in the framework that are either well-documented in the literature (black arrows) or largely not documented (grey arrows)

A first generic goal would be to assess the level of weed biocontrol that can be achieved with a biodiversity-based system (system’s approach). This would involve monitoring the long-term effects of the overall management system on beneficial communities and subsequent weed regulation, which

could take some time to establish. It should also include an assessment of the implemented system on “detrimental” organisms that negatively affect crop production and that could thrive in biodiversity-based systems, for example rodents and slugs that could benefit from in-field plant diversification. The

Table 2 Effects of cover crop type on weed biological agent (carabids, fungi) and their biological control. Main references are mentioned in each cell of the table.

| | Biological control agent | | Intensity of biological control | |
|--|---|---|--|------------------------------|
| | Carabid abundance | Pathogen fungi | Weed predation by carabids | Pathogenic activity on weeds |
| SC1 Fallow cover cropping with tillage | ↗ Boojij et al. (1997) ↗ Gallandt et al. (2005) ↗ Shearin et al. (2008) ↗ Ward et al. (2011) | ↘ <i>Verticillium</i> sp. França et al. (2013) ↗ Balota et al. (2014) | ↗ Gallandt et al. (2005) 0 Ward et al. (2011) | ? |
| SC2 Fallow with no-till & dead mulches | 0 Trichard et al. (2013) 0 Quinn et al. (2016) ↗ Petit et al. (2017) | ? | 0 Trichard et al. (2013) 0 Quinn et al. (2016) ↗ Petit et al. (2017) | ? |
| SC3 Intercropping with undersown cover | ↗ & ↘ Dixon et al. (2004) ↗ Holland (2004) ↗ Prasifka et al. (2006) ↗ Depalo et al. (2017) ↗ Dunbar et al. (2017) | ↘ <i>Fusarium</i> sp. Verrell et al. (2017) | ↗ Davis & Liebman (2003) ↗ or 0 Heggenstaller et al. (2006) | ? |
| SC4 Relay cropping | ↗ Xu et al. (2011) | ↗ & ↘ Specific responses <i>Pythium</i> sp. & <i>Rhizoctonia</i> sp. Sumner et al. (1995) | ? | ? |
| SC5 Perennial cover & living mulches | ↗ Carmona and Landis (1999) ↗ Hurej and Twardowski (2006) ↗ Fox et al. (2013) | ? | ↗ Meiss et al. (2010) ↗ Fox et al. (2013) ↗ Blubaugh et al. (2016) | ? |

The effects are described as follows: ↘, decrease; 0, no effect; ↗, increase; ?, not known

biological monitoring of the implemented biodiversity-based system will enable adaptive management, i.e., a continuous adjustment of practices to pilot the different ecological equilibrium at play.

A second objective would be to describe interactions that take place in biodiversity-based system that are to date either not documented or not fully understood (analytical approach). Experimental research could test hypotheses on potential interactions between individual IWM or biodiversity-based practices and weed biocontrol agents and their dynamics. One key question is that of antagonisms, where a particular management option will simultaneously enhance beneficial and detrimental organisms. Analytical studies could also be developed to identify the mechanisms and the agroecological consequences of interactions between different communities co-occurring in biodiversity-based systems.

6 Conclusion

Although this review provides evidence that biotic interactions could significantly alter weed species development at different stages of its life cycle, the implementation of an integrated biodiversity-based management system delivering the ecosystem service of weed regulation remains challenging. Planning and long-term monitoring of field trials are required to document the trajectories of the different biological components of the system, to assess weed regulation that is effectively delivered and to ensure that the system meets the other criteria of sustainability.

Compliance with Ethical Standards

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

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