



Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge

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Summary

Integrating principles of ecological intensification into weed management strategies requires an understanding of the many relationships among weeds, crops and other organisms of agro-ecosystems in a changing context. Extensively used during the last two decades in weed science, trait-based approaches have provided general insights into weed community response to agricultural practices, and recently to understanding the effect of weeds on agro-ecosystem functioning. In this review, we provide a holistic synthesis of the current knowledge on weed response and effect functional traits. Based on the literature and recent advances in weed science, we review current knowledge on (i) weed functional groups and ecological strategies, (ii) weed functional response

traits to cropping systems and (iii) weed functional effect traits affecting agro-ecosystem functioning. For each functional trait, we explicitly present the assumptions and evidence on the linkage between trait values and ecological functions, in response to either management practices, for example tillage, sowing and herbicides, or biotic interactions, for example crop–weed competition and pollination. Finally, we address and discuss major research avenues that may significantly improve the use of traits and the knowledge of functional diversity in weed science for the future, especially to design and implement more environmentally sustainable weed management strategies.

Keywords: agro-ecology, ecological intensification, functional ecology, cropping system, biodiversity.

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Introduction

Arable weeds comprise the set of wild plants found in agro-ecosystems that are well adapted to disturbed

environments and have been associated with crop production since the origin of agriculture (Mazoyer & Roudart, 1997; further references cited in Supporting Information S1). The ecological role of weeds can be seen in very

different ways, depending on one's perspective. On the one hand, weeds are perceived as noxious because they compete with the crop for resources and can favour a set of crop pests, thus causing yield losses (reviewed in Oerke, 2006) exceeding \$33 billion per year (Pimentel *et al.*, 2005). On the other hand, weeds are valuable agro-ecosystem components that provide ecosystem functions and services that may, to a certain extent, support crop production, for example by maintaining pollinators (Bretagnolle & Gaba, 2015). Weeds can also reduce soil erosion (Ruiz-Colmenero *et al.*, 2013) and provide food and shelter for rodents, insects and birds (Marshall *et al.*, 2003).

Concerns over herbicide resistance (Délye *et al.*, 2013), environmental and health hazards of herbicides (Waggoner *et al.*, 2013) and the decline in agricultural biodiversity (Tilman & Lehman, 2001), are challenging the existing paradigm of weed management strategies based solely or mainly on herbicide use. Nowadays, several alternatives co-exist. Integrated weed management combines herbicides with other agricultural practices (e.g. tillage, mechanical weeding, diversified crop sequences and modified sowing dates, adapted sowing densities and inter-row widths, competitive cultivars) to prevent crop yield losses while reducing negative environmental impacts (Liebman & Gallant, 1997; Lechenet *et al.*, 2014). Another commonly used alternative is organic farming, where synthetic agrochemical inputs are excluded. Many studies have assessed the potential benefits of organic farming relative to conventional farming, and showed an overall positive effect of organic farming on agricultural biodiversity (Hole *et al.*, 2005; Henckel *et al.*, 2015), but this is generally associated with a reduction in crop yield (Gabriel *et al.*, 2013; Tück *et al.*, 2014). More recently, ecological intensification has been proposed that optimises the natural functionality provided by ecosystems to maintain crop production while reducing chemical inputs (Bommarco *et al.*, 2013). One key assumption of this concept is that agriculture could benefit from an enhancement of ecological processes and functions to protect crops against pests, such as weeds, while reaching environmental, social and economic objectives. The transition from conventional cropping systems to these alternatives requires a shift from strategies considering the effects of management techniques on weeds viewed as noxious species, to strategies considering webs of relationships among weeds, between weeds and organisms at the field and landscape scales. Emphasis is therefore placed on knowledge and understanding of the relationships between weed species, weed and crop species, weed species and other organisms in the agro-ecosystems (e.g. parasites, pollinators, seed-eating organisms), and weed species dynamics in response to cropping systems and agricultural landscapes.

However, managing weeds based on these ecological intensification principles is far from straightforward. Although weeds commonly share several ecological attributes, they are by no means a homogeneous group of species. Weed floras comprise hundreds of weed species, making impossible a detailed analysis of the ecological properties of each weed species in varying environmental and management conditions. To partly overcome this issue, the response–effect traits approach (Lavorel & Garnier, 2002; Fig. 1) is a promising framework for quantifying weed responses to environmental factors (*sensu lato*) and evaluating weed effects on the ecosystem functioning. This conceptual approach describes species by their biological characteristics through the measurement of functional traits, that is features measurable at the individual level that contribute to fitness either directly (performance traits *sensu* Violle *et al.*, 2007) or indirectly (functional traits *sensu* Violle *et al.*, 2007). One major contribution of this conceptual approach to wider plant ecological theory is the definition of the worldwide leaf economics spectrum (LES), which describes strong correlations between multiple leaf functional traits (e.g. leaf lifespan or leaf mass per area) underlying resource allocation and fluxes in plants (Wright *et al.*, 2004). The trait-based approach also provides an integrated method to determine the influence of community assembly mechanisms, such as environmental filtering, niche differentiation and competitive hierarchies (Kraft *et al.*, 2015). Under this community assembly framework, management practices and biological interactions can be considered as filters limiting or allowing the establishment, growth and persistence of distinct weed species that may disperse from a reference species pool to a specific site (Booth & Swanton, 2002). Extensively used during the last two decades in weed science, trait-based approaches have provided general insights into weed community response to agricultural practices (Storkey, 2006; Fried *et al.*, 2009a; Gardarin *et al.*, 2010a; Storkey *et al.*, 2010; Gunton *et al.*, 2011; Fried *et al.*, 2012; Colbach *et al.*, 2014; Perronne *et al.*, 2015; Armengot *et al.*, 2016), to environmental properties characterising field boundaries (Cordeau *et al.*, 2012; Perronne *et al.*, 2014) and to landscape heterogeneity (Fried *et al.*, 2009b; Alignier *et al.*, 2012). A deeper understanding of how weed traits shift across climatic and management intensity gradients, at both global and local scales, however requires the appropriate 'core' traits to be identified as well as the translation of management practices into gradients of resources and disturbances.

Weed plants differ from other herbaceous plants by being more likely to have an annual life cycle with a fast growth rate, high seed production, fruits that persist on the plant, widely dispersed seed, high seedling

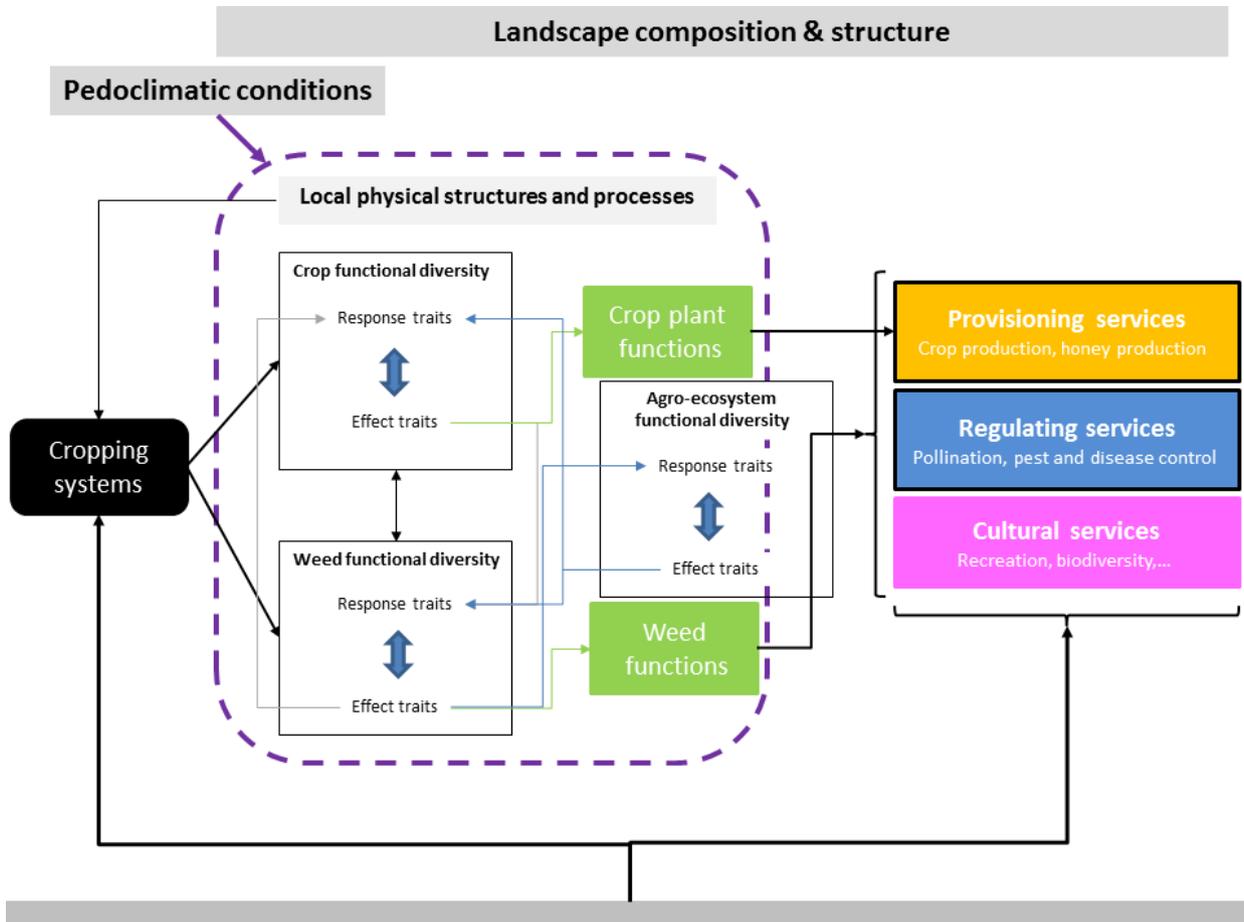


Fig. 1 Response–effect conceptual framework adapted to weed ecology in agro-ecosystems. Weed traits are affected by local pedoclimatic conditions, the cropping systems and the biotic interactions with the crop (effect traits). Resource levels and disturbances related to cropping systems vary with the local physical structures processes, which also affect the choice of cropping systems. Agro-ecosystem functional diversity responds to crop and weed effect traits alone or as interactions. Three groups of ecosystem services can be delivered by the crop and the weeds. All the relationships vary with the landscape composition and structure, and the socio-economic conditions.

vigour and fast vegetative spread (Kuester *et al.*, 2014). Recently, a conceptual framework has been proposed to characterise cropping systems on the basis of properties that affect plant performance, that is resource and disturbance levels, hence allowing for comparative studies and prediction of weed assembly (Gaba *et al.*, 2014a). Gaba *et al.* (2014a) also explored the relevance of the classic ‘core functional plant traits’ to analyse weed response to anthropogenic drivers of communities (e.g. tillage, herbicide applications) and identified a set of more specific traits. Robust stable links across wide gradients of disturbances and spatial variation have been established between the functional traits of weeds and carabids, and their trophic interactions (Brooks *et al.*, 2012). However, while weed response traits to management has been widely investigated (see for instance Storkey *et al.*, 2015), no study, to our knowledge, has proposed a holistic synthesis of the current knowledge on weed response and effect functional traits (Fig. 1).

In this article, we present such a holistic synthesis by reviewing current knowledge on (i) weed functional groups and ecological strategy, (ii) weed functional response traits to cropping systems and environmental conditions and (iii) weed functional response and effect traits related to biotic interactions. Consequently, our work extends the work of Navas (2012) and focuses on arable agro-ecosystems under temperate climate. For each trait, we explicitly present the assumptions on the linkage between trait values and ecological functions. After a section on functional groups and strategies, we synthesise current knowledge on response and effect traits and conclude by identifying new research avenues.

Weed functional groups and ecological strategies

Traits can be used to group plant species into functional groups based on ecological strategies (Lavorel *et al.*, 1997). For example, grouping species by life

form (such as trees, shrubs, forbs and graminoids) represents a functional classification, even if these represent very raw functional groups with an important range of variations among other traits within each life form. Identifying functional response groups, that is groups of species with a similar response to a particular environmental factor (Lavorel *et al.*, 1997; Lavorel & Garnier, 2002), is a long-standing practice in weed science used to optimise weeding, although it was only recently expressed in ecological terms. Historically, De Candolle (1832) proposed adapting mechanical weed control techniques according to life forms, with various recommendations for annual, biennial and perennial weeds. A century later, the finer plant-life form classification proposed by Raunkiaer (1934) provided a more suitable framework for studying arable weed communities facing regular below- and above-ground disturbances. As it is based on the description of bud position during seasons with adverse conditions, it allows weed responses to soil tillage and mowing to be predicted. As an example, mouldboard ploughing prevents the establishment of phanerophytes, chamaephytes and most of the hemicryptophytes, while no-till or reduced-tillage systems tend to promote biennial and perennial species (Froud-Williams *et al.*, 1983; Trichard *et al.*, 2013). In addition, soil disturbance may also explain the spatial pattern of plant-life form distribution from field centre to field margin (José-Maria *et al.*, 2011).

A more complex classification based on a series of traits appeared with the Grime's CSR strategy (Grime, 1974). Grime (1974) considered three basic determinants of vegetation: competition, stress and disturbances. Combinations of these drivers have led to the evolution of three distinct strategies in plants: competitors (C), stress-tolerators (S) and ruderals (R), each being characterised by a distinct set of traits. Height, lateral spread, flowering onset and duration, as well as three foliar traits, can be used to ordinate any species in the CSR triangle, each corner representing one extreme of these strategies (Hodgson *et al.*, 1999). Given that most plant species are adapted to intermediate intensities of competition, stress and disturbance, Grime (1974) also defined 16 secondary strategies (e.g. SR, C/CR, CSR). Although more accurate, this classification still remains too broad when considering most arable weeds, as they tend to predominantly be ruderals, or at least as partly ruderals (Gaba *et al.*, 2014a). At the community level, however, Gunton *et al.* (2011) showed that the dominant strategy shifts from ruderal weeds under graminoid crops to competitor-ruderals under single-stemmed crops. In addition, a long-term analysis of weed flora trajectories showed that many declining species were mostly characterised by an SR

strategy (e.g. *Adonis flammea* Jacq., *Legousia speculum-veneris* (L.) Chaix), while species increasing in frequency over time had an R or a mixed R/CR strategy (e.g. *Chenopodium album* L., *Lapsana communis* L., *Rumex crispus* L., *Sorghum halepense* (L.) Pers) (Fried *et al.*, 2009a). Finally, from a broader perspective, both life form and Grime's CSR strategy may be useful when studying weed survival at the scale of an agricultural landscape (Lososova *et al.*, 2006), including field margins and boundaries, as well as other semi-natural habitats (Cordeau *et al.*, 2012; Carlesi *et al.*, 2013).

Other species descriptors have been developed, such as ecological indicator values. Based on the compilation of a huge set of field observations and measurements, these values score the ecological species preferences (Landolt, 1977; Ellenberg *et al.*, 1992). They may be suitable, therefore, for predicting the impact of management practices and environmental factors on weed communities in arable fields and agricultural landscapes. Although Ellenberg scores cannot be considered as traits *sensu* Violle *et al.* (2007), they synthesise relevant information on weed ecology by summarising the optimal response of a species along an environmental gradient. There are six original Ellenberg indicators based on the response to various factors, that is light, temperature, continentality, soil moisture, nutrient and salinity, initially defined for plants under Central Europe conditions (Ellenberg *et al.*, 1992). These indicators were then calibrated for British (Hill *et al.*, 1999) and French vegetation (Julve, 2013) with the inclusion of two additional indicators, that is atmospheric humidity and soil texture. In weed ecology, two indicators have been mainly used, Ellenberg-L (response to light) and Ellenberg-N (response to soil-nitrogen). Ellenberg-L can potentially discriminate weed response to crop sowing density or row spacing, which increase competition for light (Gunton *et al.*, 2011; Fried *et al.*, 2015), as well as influence of the tillage regime (Armengot *et al.*, 2016). Ellenberg-N can reflect the response of plant growth to soil-nitrogen availability (Moreau *et al.*, 2013) and is assumed to appropriately account for the response of weed communities to soil enrichment through regular fertilisation (Fig. 2). Several temporal studies indicated that, compared with the 1970s, weed communities in the 2000s have changed towards more nutrient-demanding species (among others Fried *et al.*, 2009a,b) probably due to their higher competitive ability for both nitrogen and light (Moreau *et al.*, 2014), abundant weeds being more demanding of nutrients than rare species (Lososova *et al.*, 2008).

Although these classification schemes have their uses in weed science, the potential of the functional

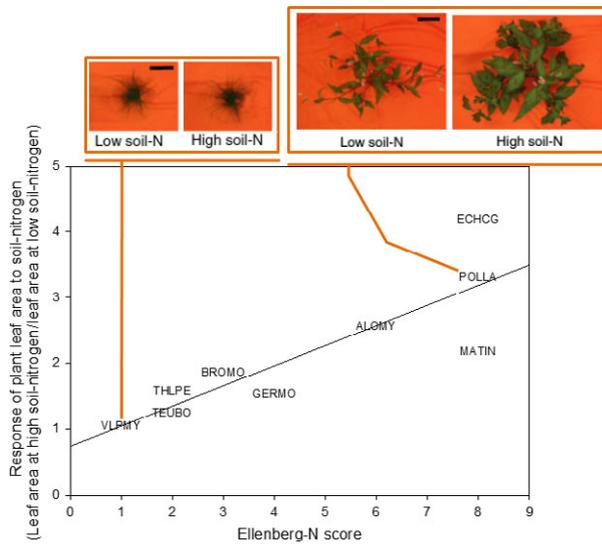


Fig. 2 Relationship between plant leaf area response to soil-nitrogen and Ellenberg-N score for nine weed species identified by their EPPO code. Reproduced with permission of Dr. Eric Lichtfouse, Editor-in-Chief of *Agronomy for Sustainable Development* (Moreau *et al.*, 2013).

group concept to predict weed community composition in arable fields remains limited (Gunton *et al.*, 2011). First, the composition of weeds in a field may reveal a history of dispersal from adjacent fields and reservoirs. Second, weed communities are shaped by a high number of factors, including the diversity of weed management and agricultural practices and their related disturbances, as well as the different potential limiting resources (nutrients, light, water) and their particular dynamics. In such a complex environment, the probability for species to survive and persist might be related with several contrasted ecological strategies, and therefore with contrasted combinations of functional response traits.

Functional response traits related to cropping systems and environmental conditions

Seed persistence in the seedbank: the key role of morphological and biochemical seed traits

Because weeds are dominated by therophyte species (Jauzein, 1995) growing in frequently disturbed cropping systems, their regeneration is particularly determined by seed traits that are crucial for weed adaptation. In particular, seed traits are related to processes affecting the often highly persistent, weed seedbank in the soil (Burnside *et al.*, 1996; Lutman *et al.*, 2002). These traits can give important insights into weed strategies (as presented below). However, one might

keep in mind the existence of ecological trade-offs that underpin the relationship between traits and processes. One of the most well-known trade-offs is the ‘colonisation–competition’ trade-off (Moles & Westoby, 2006), in which seed mass sits at the crux of a trade-off between two strategies: ‘producing a large number of small seeds, each with low establishment ability’ and ‘producing fewer, larger seeds, each with a higher chance of successful establishment’ (Westoby *et al.* 2002).

Two processes are involved in temporal seed dispersal: seed dormancy and seed survival. Seed dormancy is a strategy to delay seed germination over time, thus contributing to species persistence in unpredictable environments (Venable & Lawlor, 1980). Most weed species display cyclic dormancy, being dormant in one season and non-dormant in another, thus optimising their chance to establish in a favourable environment. Seed survival mainly depends on embryo ageing, avoidance of predation and microbe attacks.

Seed mass and seed shape are both related to seed persistence and seed dormancy (Rees, 1993; Thompson *et al.* 1993). Small and compact seeds tend to be more persistent than larger ones, a finding which is however controversial. Although an analogous relationship has been found in various other floras (see Hodkinson *et al.*, 1998; Fenner & Thompson, 2006), this pattern is not universally observed (e.g. Leishman *et al.*, 2000). Small seeds are often more spherical than larger ones and tend to penetrate more easily into the soil in untilled habitats. Hence, they often persist longer simply because their increased burial depth delays their germination (Thompson *et al.*, 1993; Bekker *et al.*, 1998; see section ‘Seed traits and seed-eating species’ for further details). The relationship between dormancy properties and seed shape and seed mass values are less straightforward (Leishman *et al.*, 2000). An analysis of a subset of weed species revealed that species with elongated or flattened seeds were usually less dormant than spherical ones (Gardarin & Colbach, 2015). Small seeds are expected to be more dormant (Rees, 1993) and some empirical data support this hypothesis (Thompson *et al.*, 1993), although some others do not (Jurado & Flores, 2005). The ambiguity of such relationships could result from the existence of covarying factors with seed mass and dormancy, and from evolutionary constraints of the species (Jurado & Flores, 2005). For instance, Volis and Bohrer (2013) found in theoretical models that seed mass and dormancy may evolve independently and that the nature of the environment, in terms of predictability and quality, can select different combinations of optimal attributes for these two traits.

From a process-based point of view, dormancy has also been shown to increase with seed coat thickness

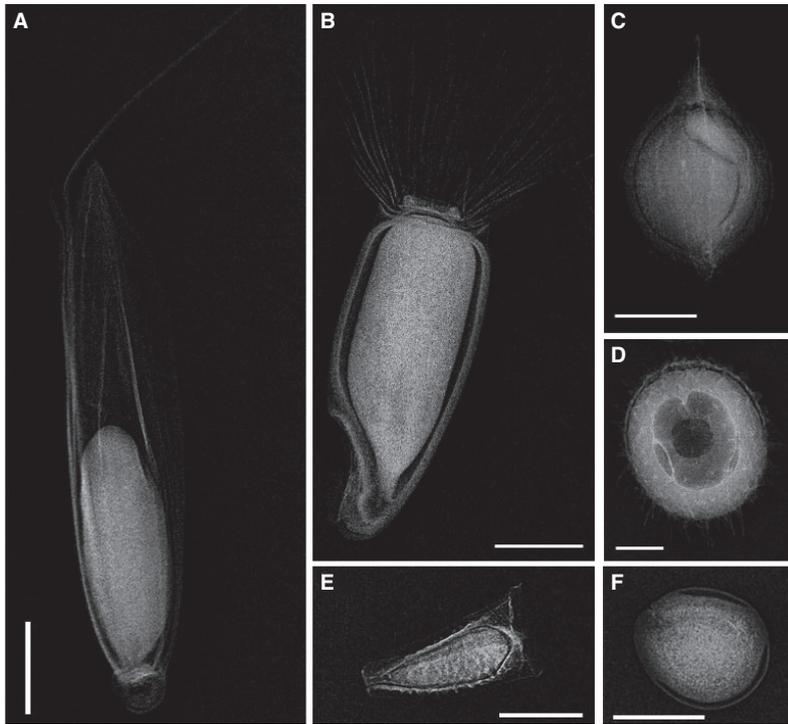


Fig. 3 X-ray images of seeds of six weed species with contrasted seed coat thickness. (A) *Alopecurus myosuroides*; (B) *Cyanus segetum*; (C) *Fallopia convolvulus*; (D) *Galium aparine*; (E) *Tripleurospermum inodorum ssp. maritimum*; (F) *Amaranthus hybridus*. Scale bars represent 1 mm. (photograph credits: Antoine Gardarin, INRA and Station Nationale d'Essai de Semences).

(Gardarin & Colbach, 2015), acting as a chemical or physical barrier (Fig. 3). In recent studies, however, Paulsen *et al.* (2013, 2014) questioned the traditional seed coat thickness–dormancy hypothesis and formulated the idea that physical dormancy has mainly evolved to hide seeds from predators. The seed coat barrier preserves the seed and the embryo from granivorous and parasite attacks as well as temperature and water fluctuations (Paulsen *et al.*, 2013, 2014; Fig. 3). As a consequence, seed coat thickness is negatively correlated with seed mortality rate in the soil due to post-dispersal predation (Davis *et al.*, 2008; see section ‘Seed traits and seed-eating species’ for further details) or due to ageing (Gardarin *et al.*, 2010a).

Finally, *seed persistence* may also significantly depend on the nature of the reserves and secondary compounds in the seeds. It is often suggested, although rarely demonstrated, that biochemical traits such as carbohydrate, protein and oil contents, and the relative proportions of saturated and unsaturated fatty acids, may affect seed ageing, embryo chemical activity and the speed of mobilisation of the reserves for energy production (Priestley *et al.*, 1985; Linder, 2000). The nature of seed-storage compounds may influence many aspects of seed biology, such as energy disposal, seed viability, the timing and speed of germination and the seedling growth rate (Levin, 1974; Linder, 2000). The energy density of fatty acids is higher than of carbohydrates. Hence, a weed species with a lipid seed-storage strategy should supply more energy for germination per unit of weight and volume than a species with a

carbohydrate strategy, although this has been poorly quantified (Lüttge, 2012; Bretagnolle *et al.*, 2016). However, oily seeds have to prevent oxidation of their energy stores during seed dormancy, a process that could reduce seed longevity (Sattler *et al.*, 2004) or need thicker and less permeable seed coats.

Spatial dispersal: strategies and diaspora traits

In addition to seed persistence over time in the seed-bank, spatial dispersal is another key process for the maintenance of arable weed species. Agricultural landscapes are highly dynamic in time and space. For a weed species, a field can be a favourable environment in a given year, but not the next one, whereas the adjacent field might be favourable. Consequently, species with higher spatial dispersal abilities will increase the likelihood of finding favourable environments in the agricultural landscape, ensuring the survival and growth of the population. Several studies have highlighted the importance of landscape structure and composition on weed species assembly (Gabriel *et al.*, 2005; Gaba *et al.*, 2010). Although spatial patterns of weeds seem not to be directly related to their seed dispersal type (Alignier *et al.*, 2012), weed spatial dispersal has also been suggested to be the main driver of rare weed species persistence, allowing rare weed species to persist in convention fields surrounding with high proportion of organic fields (Henckel *et al.*, 2015). Furthermore, spatial dispersion can also favour the persistence of small-seeded species by allowing the avoidance of local

intraspecific competition due to local high seedling densities. Several mechanisms can underlie spatial dispersion. Most weed species are characterised by a lack of specific dispersal strategy, that is barochory. However, 10–30% of weed species show dispersal strategies such as anemochory, that is wind dispersal, epizoochory or endozoochory, that is animal dispersal, with sometimes specific organs such as elaiosome to ensure attractiveness (see below), or active dispersal by explosive dehiscence, such as ballistic autochory (Benvenuti, 2007). In addition, anthropochory, that is dispersal by agricultural practices (humans) (Benvenuti, 2007), can occur within arable fields directly by soil or plant material displacement (Heijting *et al.*, 2009), indirectly by adhesion to the elements of the machinery (Barroso *et al.*, 2006), or between fields from grain trailer losses along the roads (Bailleul *et al.*, 2012) or due to recurrent soil erosion (Lewis *et al.*, 2013).

Many diaspore (i.e. dispersal unit) traits, including seed mass and the reproductive height of the parent plant, are related to the primary dispersal distance of seeds (Thomson *et al.*, 2011). The efficacy of animal dispersal is greatest when the height of the reproductive structure of the weed is approximately similar to that of the animal (Benvenuti, 2007) and reproductive height is crucial to define true anemochorous species in arable fields. Thomson *et al.* (2011) noted that seed mass is negatively correlated with the dispersal distance for a constant reproductive height, thus highlighting the importance of considering canopy height not only for anemochorous species. Finally, seed chemical or morphological features can contribute valuable information on the dispersal abilities of some weeds. For instance, the nutrient-rich appendages characterising some seeds can promote myrmecochory, that is dispersal by ants (Azcárate & Peco, 2006), while elongated appendages such as pappus or wings promote anemochory (Benvenuti, 2007). In perennials, clonal growth is also an important way of dispersal, especially in no-till cropping systems where these species are abundant (Froud-Williams *et al.*, 1983; Trichard *et al.*, 2013). Conversely, other perennials such as *Elytrigia repens* (Légère & Samson, 2004) spread better when their multiplicative organs are fragmented and dispersed by tillage. Indeed, the ability to regrow from small fragments, that is resprouting capacity (Baker, 1965), is an important trait of perennial weeds that determines both short- and long-distance dispersal within fields (Andujar *et al.*, 2012).

As part of a secondary dispersal (i.e. any significant movement of viable seeds following initial primary dispersal), the dehiscence time and seed retention are also crucial; weed plants shedding their seeds before crop harvest are dispersed shorter distances than weed

plants that shed their seeds during harvest (Heijting *et al.*, 2009). Indeed, when seed retention occurs, seed production can be collected by the grain harvester before being evenly redistributed across the arable field in the chaff fraction (Walsh *et al.*, 2013). Although machinery-induced secondary dispersal is currently known to extend the infield dispersal distance (Barroso *et al.*, 2006), its relative importance, compared with the primary dispersal, is still difficult to estimate and greatly depends on the species and the cropping system (Heijting *et al.*, 2009). Machinery-induced secondary dispersal of weeds would play an important role, as seeds collected in combine harvesters usually come from a large number of species and disseminate within arable fields (Shirtliffe & Entz, 2005). In many weeds, both primary and secondary dispersal mechanisms usually contribute to population expansion; for example, seeds of *S. halepense* are largely released at short distances from the mother plant and only a small percentage is dispersed by combine harvester, while soil tillage spreads rhizomes (Ghersa *et al.*, 1993; Andujar *et al.*, 2012). Depending on morphological similarities between crop and weed seeds, weed seeds can still be difficult to sort from the harvest and become impurities in crop seed that will be unintentionally resown (Fried *et al.*, 2015), either at the regional level (in the fields of the same farmer) or even at the continental level (traded seeds; Castejon *et al.*, 1991).

Germination and emergence: complementarities between hard and soft traits

The phenology of weeds is widely recognised to determine their success during the cropping cycle, as it is related to their ability to escape weed management as well as the competition with the crop (Bagavathiannan & Norsworthy, 2012). Seed germination and seedling emergence occur when seeds become non-dormant under favourable soil temperature and humidity (Benech-Arnold *et al.*, 2000), as well as light spectral composition and irradiance (Battla & Benech-Arnold, 2014). They can be described either by soft traits (i.e. traits that are relatively easy and quick to measure, Hodgson *et al.*, 1999) such as the onset and end of germination and emergence periods (Forcella *et al.*, 2000), or by hard traits (i.e. features that are more accurate indicators of plant functions, but which are more difficult to quantify, Hodgson *et al.*, 1999) such as the base temperature and the base water potential for germination (Grundey *et al.*, 2000).

Germination and emergence onset and season

Weeds, and more generally annual species, can be classified according to their germination seasons into

autumn-germinating species, spring-germinating species, summer-germinating species or all-year-round germinating species, that is species germinating throughout the season (Crawley, 2004). The period of optimal germination has long been recognised as a key characteristic explaining some of the greatest differences in weed floras (e.g. Fryer & Evans, 1968); the most successful and noxious weeds in a given crop germinate and emerge more or less simultaneously with the crop (Milberg *et al.*, 2000; Gunton *et al.*, 2011; Perronne *et al.*, 2015), and the relative timing of crop-weed emergence greatly influences competition (Peters, 1984; Knezevic *et al.*, 1997) and therefore weed survival and reproductive success (Forcella *et al.*, 2000). Weed germination seasons are broadly known and available in several databases (Fitter & Peat, 1994; Klotz *et al.*, 2002; Kleyer *et al.*, 2008; Gaba *et al.*, 2014b). Nonetheless, specific information on weed phenology according to crop type and environmental conditions is still needed for a better understanding of weed assembly and dynamics (but see Sans & Masalles, 1995), including the characterisation of the response to temperature in a measure that allows it to be used over diverse situations such as a sum of cumulated degrees above a base reference.

Emergence is also a crucial stage for weeds, and most of them can extend the flushes of germination over several weeks or months, from 40 to 290 days during the year (Grundy, 2003). In Northern hemisphere temperate countries, most weeds are able to germinate during two seasons, that is from March to May and from September to November

(Munier-Jolain *et al.*, 2005; Fig. 4). Several weeds can also emerge and flower indifferently all year round, but still present distinct emergence periods (e.g. three emergence periods for *Capsella bursa-pastoris* L., Aksoy *et al.*, 1998; Fig. 4). This substantial intraspecific variability in phenological traits emphasises the need to take into account both the onset and the duration of the emergence period when using weed phenology in a trait-based analysis. Such data are usually available for most weed species, based on expert knowledge and compilations of observations. As an example, the onset and duration of emergence periods have been collected on a multiyear monitoring of the weed flora for 214 annual and perennial weed species observed in the Burgundy region (Munier-Jolain *et al.*, 2005). This monitoring has provided phenological data for about 62 autumn-emerging, 46 spring-emerging, 21 summer-emerging and 49 annual weed species emerging throughout the growth cycle of winter cereals in the Burgundy region. In this French region, over the 178 annual species monitored, the mean duration of emergence period was estimated at around three months (with a standard deviation of 40 days; Fig. 4). What remains largely unknown is how the germination preferences adapt to regional climate variations. According to the commonly seen trend of mimicking crops, weeds from lower latitudes should germinate earlier than their equivalent from higher latitudinal spots. The partition in the adaptive process between response to external factors and internal genetic determinism remains largely unknown.

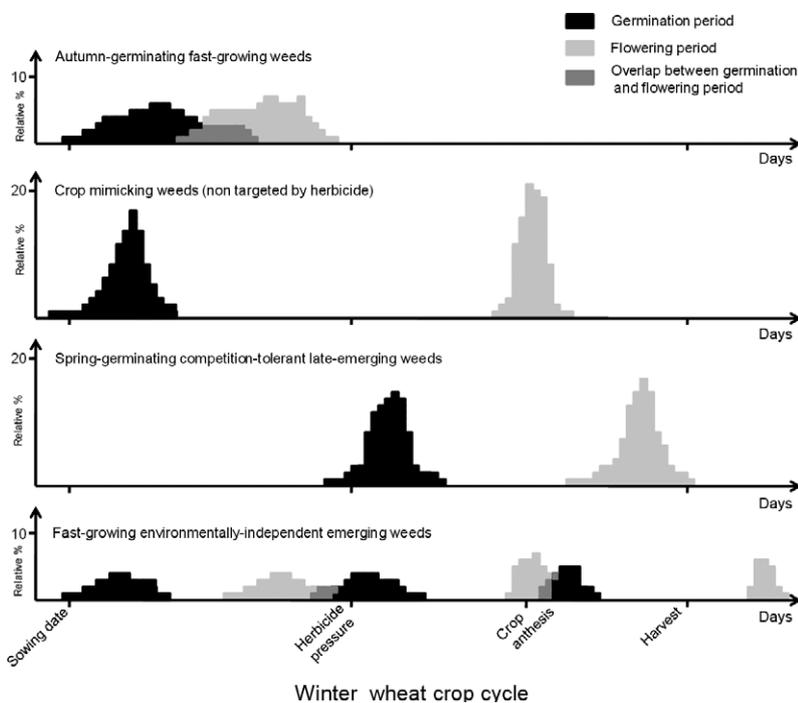


Fig. 4 Schematic representation of the germination and flowering patterns of the four main phenological guilds observed in winter cereals. Although showing very distinct patterns, the species constituting these four guilds are likely to produce seeds before the harvest. However, the crop mimicking weeds generally include most species which could cause significant yield losses. The relative percentage of individuals of a species showing a particular phenological stage at each time step along an entire cropping cycle is along the y-axis. Some species, including fast-growing environmentally independent emerging weeds, may have several cohorts during one cropping cycle.

Response of germination and emergence to temperature and water potential

Germination is mainly dependent on soil temperature (Baskin and Baskin, 1998) and water potential (Don-
 een & MacGillivray, 1943). Germination generally
 occurs when soil temperature and water potential
 exceed the species base values of these two parameters.
 The base values are frequently estimated as the x-inter-
 cept of a linear regression of the germination rate with
 temperature or water potential (Gummerson, 1986).
 Such standardised values provide valuable information
 about the soil conditions for any weed establishment
 and are a requisite for modelling the dynamics of plant
 growth and development as a function of climate.
 Rough estimates of base temperature for germination
 have been inferred from the main period of germina-
 tion (autumn, spring or summer) or at least from the
 period of emergence for a large range of species.
 Thereby, semi-quantitative ranges from 0 to 2°C, 2 to
 6°C and 5 to 13°C were proposed for autumn-, spring-
 and summer-emerging arable weeds in France respec-
 tively (Guillemin *et al.*, 2013). Conversely, few data of
 base water potential are available. Although a positive
 trend between base temperature and base water poten-
 tial has been suggested (Gardarin *et al.*, 2010b), analy-
 ses of a wider range of cultivated and wild plant
 species revealed that it was still not robust enough for
 accurate predictive purposes (Dürr *et al.*, 2015).

Effect of morphological and biochemical seed traits on rate of germination

The rate of germination has been related to morpho-
 logical and seed reserve traits with different underlying
 hypotheses. Larger seeds usually take more time to
 germinate than smaller ones, which could be mainly
 the result of biophysical constraints; larger seed surface
 area to mass ratio could lower water absorption capac-
 ity, or thicker seed coats could delay germination by
 limiting oxygen exchange, or by acting as a physical
 constraint to embryo growth (Ritchie *et al.*, 2000).
 Earliness of germination is also generally positively
 correlated with seed lipid content in some weed species
 (Gardarin *et al.*, 2011) and with higher amounts of
 unsaturated fatty acids, although the latter is modu-
 lated by temperature (Linder, 2000). Indeed, seeds with
 high amounts of unsaturated fatty acids can germinate
 earlier and faster, as the melting point of unsaturated
 fatty acids is much lower than in saturated fatty acids.
 These species would thus gain a competitive advantage
 under cold environmental conditions. Conversely, seeds
 with a higher proportion of saturated fatty acids would
 be positively selected under condition of high tempera-
 tures for germination, because they can supply more
 energy than unsaturated fatty acids.

Seed traits related to the effects of depth, soil struc-
 ture and soil cover on germination and emergence –
 Among agricultural practices, tillage directly affects
 weed germination and emergence by modifying both
 the soil properties and the seed distribution in the soil
 (Colbach *et al.*, 2005). Seed mass negatively correlates
 with the intensity of tillage, while seed mass and seed
 energy reserves were positively correlated with the abil-
 ity to emergence at greater depths (Gardarin *et al.*,
 2010c; Guillemin & Chauvel, 2011). Indeed, the major-
 ity of weed seeds (generally small-seeded species) ger-
 minate and emerge in the first centimetre depth (e.g.
 Boyd & van Acker, 2003) while only a few of them are
 able to emerge when deeply buried (e.g. 10 cm depth
 for *Ambrosia artemisiifolia* L., Guillemin & Chauvel,
 2011; up to 30 cm for *A. fatua*; Gardarin *et al.*,
 2010c). Another factor affecting emergence is the soil
 structure causing pre-emergent mortality. Seedling fate
 in the context of the resistance of the soil depends on
 both their emergence force, which is positively corre-
 lated to seed diameter and seed mass (Gardarin *et al.*,
 2010c) and on the risk to be trapped in small cavities
 (Dürr & Aubertot, 2000), which depends on the shoot
 morphology (differing between hypogeal and epigeal
 emerging species, Gardarin *et al.*, 2010c).

In no-till cropping systems, most weed seeds remain
 on the soil surface. The rate of emergence of some
 weed species decreased for unburied seeds compared
 with slightly buried (0.5 cm) seeds. This lower emer-
 gence can be explained by low soil–seed contact and/or
 by high fluctuations both in humidity and temperature
 on the soil surface (Boyd & van Acker, 2003). Indeed,
 cover or crop canopies have been shown to decrease
 the emergence of several weed seeds on the soil sur-
 faces in glasshouse experiments (Cordeau *et al.*, 2015),
 in a field experiment under a wheat canopy (Kruk
et al., 2006) and in no-till systems under lucerne
 canopy (Huarte & Benech Arnold, 2003).

Sensitivity to herbicides

Herbicides are the most effective weeding technique.
 As such, they have been commonly used across the last
 60 years in intensive cropping systems. Weeds can be
 ranked according to their sensitivity to specific active
 ingredients alone or in association. Mamarot and
 Rodriguez (2003) proposed a semi-quantitative scale
 with four classes of sensitivity from high, that is more
 than 95% control, to very low, that is less than 70%
 control. In each country, a sensitivity index has usually
 been estimated on the basis of available herbicide trials
 under standard conditions and provided to farmers.
 While herbicide selectivity is generally quantified at the
 species level, the additional use of functional traits can

complement herbicide sensitivity profiles of weeds (Gaba *et al.*, 2014a).

Plant morphology can affect weed sensitivity to herbicides, because erect shoots retain less spray than the nearly horizontal leaves commonly observed in dicotyledonous plants (Davies *et al.*, 1967). Leaf surface traits, including the cuticle (epicuticular wax, pectin and cutin), the hairiness (density of trichomes) and the surface cells (density of stomata and cell size), strongly affect the wetting (Nairn *et al.*, 2011) and the penetration (Schreiber, 2010) of foliar applied herbicides and therefore their bioavailability within the plant. These traits vary between species, but also within species with leaf age and development (Hess, 1985; Wanamarta & Penner, 1989). Among surface leaf traits, the epicuticular wax plays a crucial part in the wetting of the treated plants by the spray (Holloway, 1970). In addition, the attachment of spray droplets decreases when crystalline epicuticular waxes are present (Holloway, 1970), leading to a reduction in herbicide quantity in contact with the leaf surface (Hess & Falk, 1990). This, together with erect plant morphology, underlies the selectivity of some auxin-like herbicides towards maize (Gauvrit & Gaillardon, 1991). Leaf hairs can either retain herbicide droplets increasing foliar uptake, or conversely decrease it by holding the droplets away from the leaf surface. Hairy species are usually considered more difficult to control with herbicides, but there are many confounding effects such as life cycle variation or contrast in ecological niche optimum temperatures.

Underground morphology can also be critical for weed herbicide sensitivity, for instance in the case of herbicides such as thiocarbamates. Their physiological site of action is located at the coleoptile node of Poaceae. After treatment, these herbicides remain in the superficial layer of the soil. In susceptible species such as *A. myosuroides*, *A. fatua* and *Lolium spp.*, the mesocotyl growth brings the coleoptile node near the surface that is in the soil layer of high herbicide concentration. By contrast, mesocotyl growth is virtually nil in barley and wheat, which are not susceptible to these herbicides, because their coleoptile node remains near the seed, below the soil layer rich in herbicide (Parker, 1963). Uptake of herbicide, for example for 2,4-D, can also depend on the weed phenological stage and leaf age (Peterson *et al.*, 2016).

Reproduction mode: the mating systems

As most of arable weeds are therophytes, reproductive success is a crucial determinant of population persistence. Timing of flowering and flowering duration are important for weeds to respond to disturbance events,

such as harvest, induced by agricultural practices (e.g. in *Capsella* sp. (Iannetta 2007) or at the weed community level (Fried *et al.*, 2012). Traits related to mating systems of weed species have been shown to play a key role in the evolutionary and ecological responses of weeds to environmental and agronomical changes, such as changes in the diversity of crops (i.e. increasing areas of winter wheat), which impact the duration of cropping season (Barrett, 2011). Many traits reflect mating strategy, including (i) the floral design, that is the characteristics of the flower (its size and shape, colour, odour), (ii) the spatio-temporal presence of male (stamen) and female (pistil) function (herkogamy, dichogamy) and (iii) the floral display, that is the number and disposition of opened flowers. Mating systems in weeds range from obligate outcrossing (allogamy), through various mixtures of mixed mating, to predominant selfing (autogamy). Species with heteromorphic flowers (e.g. self-incompatibility, monoecy, dioecy or heterostyly) must outcross, whereas monomorphic flowers, that is hermaphroditic species, can have mixed mating system and can produce both self and outcrossed progeny (Winn *et al.*, 2001). The evolutionary and ecological consequences of variations in plant mating systems was thoroughly analysed in a large number of angiosperms (Barrett, 2014), including a number of arable weeds. However, the frequency of polymorphic sexual systems with obligatory outcrossing is expected to be rare in annual life forms. A long-standing hypothesis, in the philosophy of ‘Baker’s rule’, is that plant weediness could be facilitated by self-compatibility because these species colonise highly disturbed habitats where pollinators may be rare or plant population size may be small during the primary invasive phase. A strong association between self-pollination (in particular predominant and autonomous selfing) and the annual life form have been documented, suggesting that most annual species are self-compatible (Aarssen, 2000). Moreover, Barrett (1988) has suggested that the environmental homogeneity of cropping systems should select for higher selfing and lower genetic diversity in arable weeds compared with ruderals more generally. Therefore, weed floras are often assumed to be dominated by preferential selfing mating (Clements *et al.*, 2004), although there are many exceptions such as *Cyanus segetum* Hill (Bellanger *et al.*, 2015).

The shift towards higher selfing rates is generally associated with a selfing syndrome, that is the modification of flower traits that facilitates autonomous self-pollination while (concomitantly) decreasing the costs attached to pollinator attractiveness (see section ‘Weed interaction with pollinators’ for more details on weed traits related to pollination). Predominantly selfing plants generally show a reduction of herkogamy

(anther–stigma separation) and dichogamy (i.e. lower differences in timing of anther–stigma maturation), positioning the anthers close to the stigma. Moreover, in autonomous selfing species, the floral traits involved in pollinator attraction are less apparent than those of insect pollinated species and flowers are frequently white. The rate of autogamy can also be estimated by the pollen–ovule ratio, that is the mean number of pollen grains by ovule produced by a flower. In autonomous selfing species, the pollen–ovule ratio is very low. A similar pattern is observed in annual species compared with perennial ones (see Scalone *et al.*, 2013 for an example in *Veronica* spp.). Another interesting trait is the nuclear DNA amount per chromosome, known as the C-value. The C-value is positively correlated with cell size and negatively correlated with the duration of mitosis (Bennett, 1985). Life forms also differ in their C-value and annual selfing species tend to have smaller C-values compared with others plant species (Knight *et al.*, 2005). Species (and individuals) with smaller genomes have smaller cells and a faster cell division rate that allow a faster growth than bigger genomes. Bennett *et al.* (1998) found that the nuclear DNA amount and DNA amount per genome in weeds was smaller than in other herbaceous species. However, there were more polyploids in weeds suggesting that polyploidy may have been selected to fix beneficial genetic variation and that antagonistic selective forces may shape genome size and chromosome number evolution in weeds.

Functional effect traits related to biotic interactions

Crop–weed competition

Competition is known to play a key role in weed community assembly, mainly due to a resource depletion mechanism (Zimdahl, 2004; Navas, 2012). A plant suppresses the growth of its neighbours through resource depletion, while the ability of a plant to grow and survive in response to resource depletion due to competition by neighbouring plants is described by its competitive response. As the level of resources during the cropping season is difficult to assess through synthetic descriptors (Gaba *et al.*, 2014a), the effect traits of crop plants may be used as proxies, being directly related to resource use according to the trait-based framework proposed by Navas and Violle (2009) and Violle *et al.* (2009). As part of this framework, the competition process is described by the relationships among plant traits, resource depletion and competitive outcome. The effect trait values of the dominant species, usually the crop, are indicative of the amount of resources which is unavailable for the other

subordinate plants in the community, such as weeds, that respond to limited resources on the basis of their response traits. Such a framework can be applied when investigating the effects of crop–weed competition in arable fields, including cover crop–weed competition. However, numerous traits can be considered both as competitive effect and response traits for weeds and crops when studying weed–crop competition (Wang *et al.*, 2010; Andrews *et al.*, 2015). Therefore, a substantial overlap exists between competitive effect and response traits, because underlying biological and ecological processes affect the vertical and horizontal growth, the light interception, water and nutrient uptake abilities for both dominant competitors and subordinate or rare species.

Competitive effect traits are linked to resource capture. These traits reflect the amount of depleted resources, for instance due to light interception that is considered as the main limiting factor for weed growth, especially in conventional cropping systems (Holt, 1995), and soil resource uptake by plants (Smith *et al.*, 2009). Regarding the competition for below-ground resources, a large depletion is related either (i) to large plant size, that is size symmetric competition for which resources can be divided in proportion to the biomass of individuals, thus plants with larger and deeper root systems deplete soil resources on a larger soil volume; or (ii) to higher plant activity due to high resource acquisition rate. For instance, plants with a high nitrogen uptake rate per unit of root locally induce a strong depletion of soil resources at the local scale. Among others, root biomass, root area (or root length), rooting depth and width, and root mass per soil volume are classically considered to characterise root system structures, whereas traits such as specific root length, which is considered as a good proxy of root absorption rate for nutrients, or root affinity for specific substrates (e.g. preference for nitrate vs. ammonium) can be used to characterise root activity (Maire *et al.*, 2009; Wang *et al.*, 2010). Regarding competition for light, due to early establishment and a high sowing density, crops usually have a preferential access to light. In addition, given the unidirectional nature of this resource, asymmetric competition is commonly observed in arable fields; that is the tallest plant competitors get more than their proportional biomass share (Weiner *et al.*, 2010). Canopy height has often been considered as a reliable proxy to assess competitive ability for light resource, especially for cereal crops (Seavers & Wright, 1999) because competitive outcomes are strongly influenced by resource capture hierarchy between crop and weeds at crop canopy closure (Cudney *et al.*, 1991). However, other traits are directly connected to the potential for light capture

and should be considered for a detailed understanding of competition.

As competition is a dynamic process, the early stages of plant growth determine the subsequent plant–plant interactions. Early seedling vigour might be associated with both (i) the initial green area just after seedling emergence, a trait directly related to seed mass, and (ii) the early relative growth rate (RGR) of leaf area, a variable related with the specific leaf area (SLA) at the seedling stage (Saverimuttu & Westoby, 1996; Storkey, 2004). Later in the plant life cycle, other traits related to plant morphology influence the ability for light capture, including the distribution of leaf area with plant height (McLachlan *et al.*, 1993), the shape of leaves and the leaf angle, the leaf mass fraction (Brainard *et al.*, 2005) and the SLA, which is an indicator of the efficiency of the leaf biomass allocated to the production of leaf area (Cavero *et al.*, 1999; Brainard *et al.*, 2005; Storkey, 2005; Munier-Jolain *et al.*, 2013). In cropping systems including multi-annual forage crops and regular hay cuttings, the presence of low axillary buds and of below-ground carbohydrates reserves are traits determining the ability of post-cutting regrowth speed and therefore the fate of subsequent competition for light (Meiss *et al.*, 2008).

Competitive response traits are closely associated with changes in plant performance due to resource depletion. These traits reflect the ability of an individual to avoid suppression by dominant neighbouring plants because of different strategies of resource acquisition from those of dominant competitors. For instance, early emergence may allow a more efficient use of resources by lower competitors, resulting in their persistence in the presence of dominant competitors. Plant height, leaf morphology and SLA are relevant traits to study weed response in response to competition for light (Cavero *et al.*, 1999). Two strategies have been observed in weeds: a shade-tolerance syndrome that characterises small weeds species with high SLA values and a shade-avoidance syndrome, which is the most visible response in the context of competitive hierarchies among plants (Storkey, 2005). Competitive response traits are also related to tolerance to low levels of resources; shoot to root biomass ratio decreases in response to low soil resource availability (Poorter & Nagel, 2000; Smith *et al.*, 2009), leaf thickness decreases in response to low light availability (Regnier *et al.*, 1998) and leaf mass fraction increases in response to low red:far red ratio (Brainard *et al.*, 2005). Although vegetative shoot and root traits are good proxies to assess competition, phenological traits can also be classified as competitive response traits in arable fields. The period of emergence of many weed species can range from a few weeks to several months

(see section ‘Germination and emergence onset and season’). Species emerging early in the crop season, with early flowering onset and a short life cycle, can escape competition and produce seeds before crop canopy closure, avoiding intense competition for light (Meiss *et al.*, 2010). Temporal niche partitioning via a storage effect (Chesson, 2000) is another strategy for species to co-exist. Such a strategy has recently been experimentally revealed in communities dominated by weeds (Garcia de Leon *et al.*, 2014).

Seed traits and seed-eating species

The use and manipulation of the guild of seed-eating species may be a promising way to contribute to weed control, because these organisms can potentially affect both the densities and growth rates of weeds (Westerman *et al.*, 2003; Bohan *et al.*, 2011; De Vega *et al.*, 2011; Eraud *et al.*, 2015), although the actual effect of seed predation on weed dynamics remains to be demonstrated and quantified. The manipulation of granivorous species to optimise weed management strategies is a challenge that needs an understanding of the complex relationship between weed seed traits and feeding behaviour of seed predators (Moles *et al.*, 2003; Wang & Chen, 2009). Seed selection by granivorous species is influenced by seed morphology (in particular seed mass) and the nature of stored reserves (see Gaba *et al.*, 2014c for an example in *Alopecurus arvensis*). Indeed, seed predators tend to eat energy-rich seeds while minimising searching and handling times. Many studies exploring optimal foraging strategy have shown that seed mass (size) is a key characteristic for seed selection by insects, mammals and birds, due to ease of handling and higher encounter rate (Thompson *et al.*, 1987; Barrette & Giraldeau, 2008). Seed predators, such as arthropods or most farmland birds, show preferences for small seeds, but with sufficient nutritive value to limit mechanical handling constraints in agreement with optimal foraging theory (Krebs, 1980). Seed predators can distinguish the structural strength of seeds as well as their size (Lundgren & Rosentrater, 2007). Moreover, seed coat thickness may play a crucial role in seed foraging by rodent or arthropods. Indeed, under the crypsis hypothesis, hard seeds are more cryptic from an olfactory point of view than smallest ones for foraging granivores; hence, the primary function of hard seed coat could be the diminution of predation rate (Paulsen *et al.*, 2013). To our knowledge, neither a standardised methodology nor a database have been so far designed to report on released seed volatiles in different weed species. Seed coat thickness can also be a derived trait promoting seed survival after ingestion by

birds, mammals or worms (Clause *et al.*, 2011; Hogan & Phillips, 2011), the transfer via the digestive system ensuring most of the seed dispersal phase.

Weed interaction with pollinators

Weed flowers supply arthropods with pollen and nectar, improve their reproductive success and thus exert a bottom-up control on the assemblage and the functioning of several guilds of pollinators and phytophagous insects (Heimpel & Jervis, 2005). Interactions between flowers and arthropods depend on three groups of traits (Ricou *et al.*, 2014): (i) attractiveness of the flower, (ii) accessibility of the trophic resource and (iii) the amount and quality of floral rewards. Attractiveness of the flower (or of the inflorescence) depends on its dimensions, odour, colour and UV reflection (Mulligan & Kevan, 1973). Flower morphology, symmetry and corolla shape, which may also be visual signals affecting flower attractiveness (Sivinski *et al.*, 2011), determine the accessibility of the nectar and pollen (Heimpel & Jervis, 2005). The insect head size can physically restrict access to flower sources when it is larger than the corolla diameter (Wäckers *et al.*, 1996). In such a situation, the length of the proboscis (mouthparts) plays a crucial role. A relationship between the nectar depth within the corolla and the proboscis length of the visitor has been established for several insect groups. For instance, hoverflies (*Syrphidae*) are favoured by short corolla flowers, while bumblebees prefer long corolla ones (Campbell *et al.*, 2012). As a result, size constraints (corolla shape and dimensions) seem important in determining the abundance and diversity of nectar foraging visitors on plants (Stang *et al.*, 2006). Accessibility also depends on the onset and duration of the flowering period; synchrony between the flowering period and insect activity is crucial (Welch & Harwood, 2014). The presence and the amount of nectar and pollen provided by the flowers are the rewards searched by arthropods on the flowers, and they thus influence the frequency of visits and abundance of foraging arthropods (Carvell *et al.*, 2006; Pywell *et al.*, 2006). In addition to resource quantity, their quality (e.g. sugar composition or viscosity of the nectar) is taken into account by arthropods depending on their preferences (Géneau *et al.*, 2012). Among these traits, the role of flower morphology has been largely explored, especially structuring trophic and mutualistic plant–insect networks (Stang *et al.*, 2009). At community level, the structure of weed communities (e.g. functional trait diversity) should also be taken into account, because it shapes the interactions between insect species (e.g. between bees and hoverflies, Hogg *et al.*, 2011).

Do parasitic weeds harbour specific traits?

Among arable weeds, some species use a plant-parasitic strategy to obtain competitive advantage from neighbouring host plants (Heide-Jørgensen, 2013). Instead of competing for resource capture at field scale, they invade the crop to rob it of nutritive resources and water. During parasitic plant evolution, competitive effect traits involved in light interception and root acquisition of resources were minimised and in return a new feature, the haustorium. This unique organ in parasitic plants among the plant kingdom was developed allowing host invasion and direct withdrawal of nutrients and water from crop vascular system (Westwood *et al.*, 2012), which increases disproportionately resource acquisition rate relative to biomass of acquisition organs. Orobanchaceae is the largest family of parasitic plants and includes 34 weed species, 12 of them in the *Orobanche*, *Phelipanche*, *Striga* and *Alectra* genera devastating millions of hectares of major crops worldwide (Parker, 2013). Root parasitic weeds of the Orobanchaceae comprise a broad spectrum of host dependence, ranging from facultative hemiparasites to obligate holoparasites (Westwood *et al.*, 2012). Facultative hemiparasitic weeds have both parasitic and autotrophic growth capabilities, but parasitism is their optimal trophic mode. In the absence of host plants, they grow more poorly, although independently. Therefore, during susceptible crop cultivation, the population of facultative parasitic weeds infesting the field would be composed by a mixture of plants that germinate close enough to be able to infect the crop and extract their nutrients and plants growing autotrophically due to lack of crop invasion. By contrast, in obligate root parasitic weeds, the lack of functional roots means seedlings must withdraw nutritive resources and water from the crop shortly after germination, otherwise they quickly die. In facultative parasites, weed emergence precedes infection, while in obligate root parasites, infection occurs before weed emergence and the timing of emergence relative to parasitic sink activity has implications for the selection of control strategies. Parasitic weeds show high variability in photosynthetic capability. Broadly, obligate parasitic weeds are classified as hemiparasites and holoparasites, depending on the presence or absence of photosynthetic machinery, although different levels of photosynthetic efficiency exist among hemiparasitic species, and in consequence sink strength (i.e. the ability of the parasite to withdraw resources from its host) for host-derived photoassimilates. Despite their photosynthetic capability, root hemiparasites do not photosynthesise before emergence and therefore, their sink strength extends beyond inorganic resources during

underground shoot development. Few trait-based approaches have been yet applied to understand the response of these parasitic weeds to agricultural practices. In the following section, we present some examples of functional traits that are common to non-parasitic and parasitic weed species, and some of the new traits emerged during the evolution of parasitism in angiosperms usually related to their degree of host dependence. Traits can be used to classify parasitic weed species into groups with similar survival rates in response to management strategies.

As for non-parasitic weeds, seed traits play a key role in the persistence of parasitic weeds. Seed longevity is usually related to the degree of host dependence, being longer in obligate than in facultative parasites (Bekker & Kwak, 2005). In obligate parasitic weeds, microspermy, that is the strategy of production of numerous long-living seeds with little resource investment per seed unit (tiny seed of about 0.2–0.3 mm long), ensures their persistence in agricultural landscapes by maximising their probability of encountering a compatible host (Joel *et al.*, 2013). This is of special importance given their inability to develop autotrophy and the short length of their infective organ. Similar to non-parasitic weeds, germination in facultative parasitic weeds is triggered by environmental cues. However, obligate root parasites use a seed trait of host chemodetection. This trait consists of a germination-triggering mechanism sensitive to molecules exuded by crop roots and is important for the design of parasitic weed-specific strategies of control (Fernández-Aparicio *et al.*, 2011). For example, crop rotations including false hosts (e.g. weed species, trap crops) can stimulate suicidal germination in obligate parasites without allowing penetration and consequent nutritive supply. However, a broad spectrum of specificity of germination responses is found among obligate parasitic weeds, ranging from highly specialist species that only germinate in response to their specific hosts, to generalist species in which seed receptors are sensitive to root exudates from a large number of crop species and families regardless their host or non-host nature (Fernández-Aparicio *et al.*, 2011). A different set of *KAI2d* receptor genes has been found to characterise each parasitic weed species, enabling host recognition through diversified germination responses (Conn *et al.*, 2015). This seed trait influences the success of weed management strategies based on suicidal germination. In addition, this trait influences the chances of changing host specificities in the event of non-host-induced germination. Species that germinate easily in the presence of non-hosts are subjected to a life or death pressure once they have germinated that could lead to changes in host specificities by genetic reprogramming.

Underground morphological features can affect survival rates in response to management strategies. Shortly after vascular connection, the broomrape seedling develops a storage organ called a tubercle just above the surface of the host root. The tubercle size varies with the nutritive quality of the host, but is mainly dependent on the parasitic species, varying from a few millimetres to several centimetres. The tubercle accumulates starch that is later used by the parasitic weed during reproductive stages (Joel *et al.*, 2013). Therefore, plants with bigger tubercles could gain a fitness advantage. In addition, when parasitic weeds are hand-weeded or harvested along with the crop before maturity, they can complete seed maturation and dispersal using stored reserves. Obligate parasites also differ from facultative parasites and non-parasitic weeds regarding their root system. Facultative parasites develop both a functional root system and lateral haustoria in the event of host contact. In contrast, obligate parasitic weeds only develop terminal haustoria, which are the main organs for resource acquisition. It is complemented in some species with an adventitious root system called crown roots with functions of soil stability and establishment of lateral haustorial connections in neighbouring roots for additional nutritive transfer (Joel *et al.*, 2013). The length of crown roots differs across parasitic species. For example, *Orobancha crenata* and *Phelipanche aegyptiaca* can develop adventitious roots of up to 10 cm with abundant lateral haustoria, while the adventitious roots in *O. cumana* are very short and lack lateral haustoria (Joel *et al.*, 2013). It remains unknown if the immune system of resistant crop plants equally recognises signals from either terminal haustorium in the seedling or lateral haustoria in the crown root.

Phenological traits and synchrony of life cycle between parasite and hosts are paramount to parasitic weed competitive success in agricultural ecosystems (Manschadi *et al.*, 1996). The life cycle of the plant parasite is crop species dependent. The phenology of each parasite is successfully adapted to that of its host to maximise competition for resource allocation against host reproductive sinks. For a given parasitic weed–crop species association, phenology is highly dependent on temperature (Eizenberg *et al.*, 2005). Lastly timing of parasite flowering relative to that of the host could influence either attraction or competition for pollinators between the crop and the parasite.

Perspectives

Trait-based approaches have been extensively used during the last two decades and have provided general insights into weed community response to agricultural

practices, but the traits linking weeds to agro-ecosystem functioning have been seldom documented so far. In the previous sections, we have provided a synthesis of the current knowledge on weed response and effect traits and others important plant characteristics (Fig. 5; Table 1). To date, the functional trait-based approach remains largely limited to the analysis of weed response to management practices using trait data retrieved from databases. In contrast, limited attention has been paid to the effects of weeds on agro-ecosystem functioning and on the provisioning of ecosystem services. This lack of studies contributes to the lack of knowledge that can help to pave the way towards more sustainable weed management. In the next section, we suggest several major research avenues that may significantly advance trait-based research in weed science.

Consolidating trait value data to improve trait-based research in weed science

So far, most of the values of weed traits are retrieved in databases such as TRY (Küttge *et al.*, 2011), LEDA

Traitbase (Kleyer *et al.*, 2008) or Bioflor (Klotz *et al.*, 2002). These sources are not restricted to weeds, but rather consider the full European or World flora. WTDB (Storkey *et al.*, 2015) or Weed-Data (Gaba *et al.*, 2014b) are databases restricted to weeds. These databases provide data on vegetative and reproductive traits and potentially whole-plant performance traits. However, these data have some limitations. First, while trait values for the most frequent weed species are relatively well documented, they are generally lacking for rarer weeds. However, current changes in weed management (e.g. no-till, organic systems) or climate may select for these currently less frequent species. Second, the trait values available are frequently averaged over multiple populations and habitats. These data are of interest insofar as trait values vary far more between than within species (e.g. Keddy, 1992), and can therefore be useful when analysing weed distribution along wide gradients such as biogeographic ones (Violle *et al.*, 2014). These averaged trait values may, however, be limited in their power to predict weed response to management practices. Indeed, there is some evidence that intraspecific variability constitutes

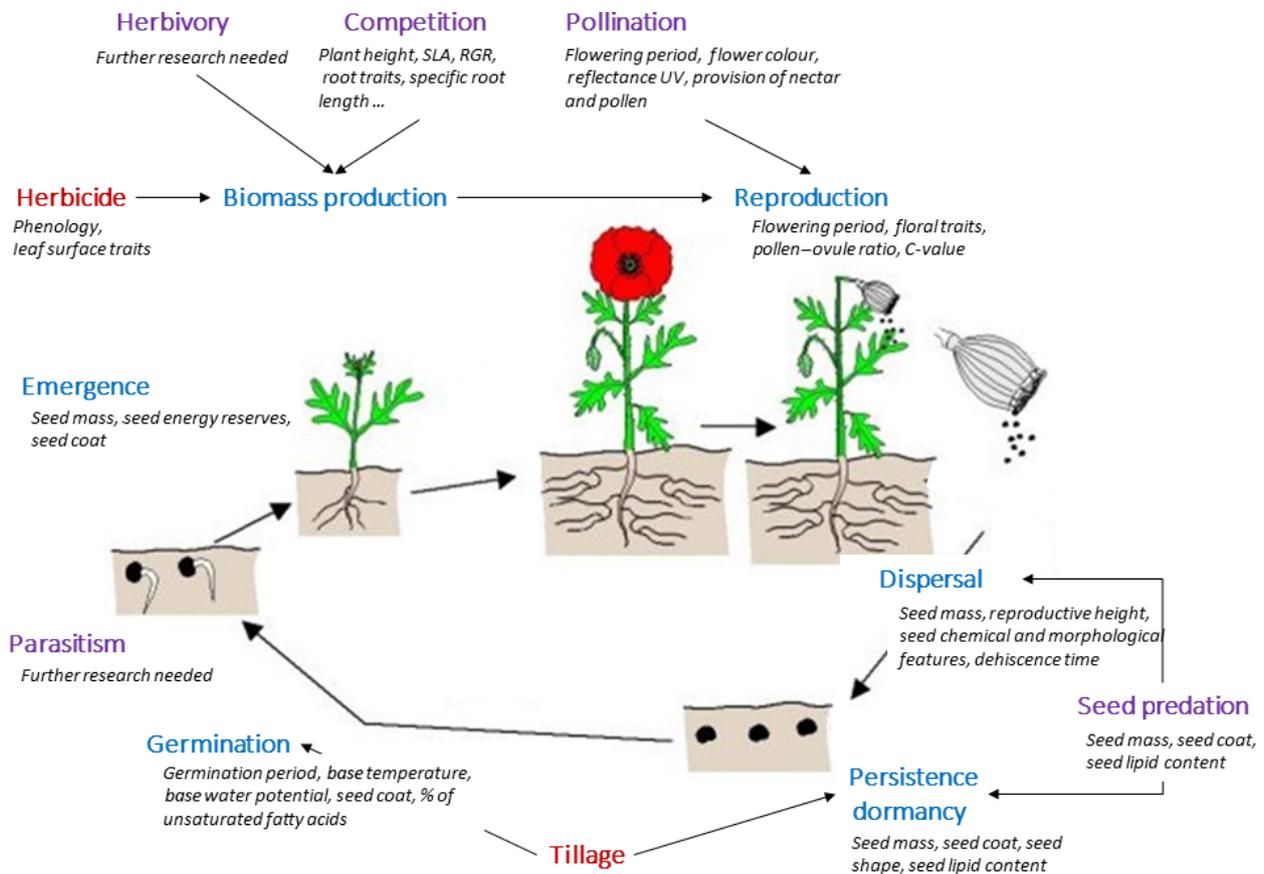


Fig. 5 Synthesis of the most significant weed functional traits over a plant life cycle. This life cycle is represented by main life stages from the germination and emergence, the development of a standing plant, a flowering plant to the production of seeds. Biotic interactions affecting the development the plant are presented in purple, whereas the two main management practices affecting the plant performance are presented in red.

Table 1 Summary of the weed traits related to functional response and effect. Traits are categorised by life cycle stage. A grey box indicates that the trait is relevant for the related function. Details on the traits are provided in the main text

List of traits	Functional responses traits										Functional effects					
	Landscape characteristics	Pedoclimatic conditions	Crop sowing Timing	Crop harvest Timing	Crop type	Tillage Timing	Tillage Intensity	Herbicide regimes Timing	Herbicide regimes Intensity	Nitrogen input	Plant-plant competition Light	Plant-plant competition Nutrient	Harvest quality	Seed predation	Insect Pollination	Biological control by natural enemies
At landscape scale																
Traits related to spatial dispersal																
Seed mass																
Reproductive height																
Seed chemical																
Seed morphological features																
Dehiscence time																
At field scale																
Traits related to seed persistence and dormancy																
Seed mass																
Seed shape																
Seed coat																
Seed characteristics																
Seed chemical composition																
Traits related to germination																
Germination period																
Base temperature																
Base water potential																
Seed coat characteristics																
% of unsaturated fatty acids in seeds																
Traits related to emergence																
Seed mass																
Seed energy reserves																
Seedling shoot morphology																
Traits related to biomass production																
Vegetative plant height																
Specific leaf area (SLA)																
Relative growth rate																
Root growth (root area, depth, width)																
Specific root length																
Phenology																
Leaf dry matter content																
Leaf nitrogen content																

Table 1 (Continued)

List of traits	Functional responses traits					Functional effects										
	Landscape characteristics	Pedoclimatic conditions	Crop sowing Timing	Crop harvest Timing	Crop type	Tillage Timing	Intensity	Herbicide regimes Timing	Intensity	Nitrogen input	Plant-plant competition Light	Nutrient	Harvest quality	Seed predation	Insect Pollination	Biological control by natural enemies
Traits related to reproduction																
Flowering period																
Floral traits																
Pollen-ovule ratio																
Number of seeds produced																
C-value																
Flower colour																
Reflectance UV																
Nectar quantity																
Nectar sugar composition																
Nectar viscosity																
Reproductive plant height																

an essential component of the functional response of weed species to management, climate and crop-weed competition at the field scale but also within a field (e.g. Borgy *et al.*, 2016). Furthermore, data on trait values must be related to metadata on (i) sampling location and main meteorological data during the growing period preceding trait measurements, that is rainfall, mean air temperature and photosynthetic active radiation; (ii) environmental conditions at field scale, by characterising, for instance, the crop light interception or soil mineral nitrogen availability; (iii) cropping systems by means of farm surveys, including detailed information in terms of dates and options on cultural practices (e.g. tillage, sowing, harvest, herbicides, fertiliser); and (iv) crop plant information by measuring similar traits on crop plants at the same time and in the same sampling area than for weed traits to better understand competition outcome and the relative efficiency of resource use. Acquiring these metadata will certainly be challenging, and perhaps unrealistic due to the cost (time and money) for data collection. However, achieving even a subset of these characteristics will greatly improve the interpretation of weed functional diversity patterns. Overall, we believe that there is a broad interest to reinforce weed trait measurement in arable fields when studying the effects of cropping systems.

Specialised functional traits in weeds

Trait-based approaches were originally developed to study plant communities in semi-natural habitats such as permanent grasslands (Garnier *et al.*, 2007). Arable fields differ from these habitats as they are more nutrient-rich and highly disturbed environments. As a consequence, the selection of response traits should reflect these specificities.

Phenological traits have been shown to be powerful response traits, in particular to identify opportunities for germination and seed production by accounting for the timing of disturbances defined by the crop sowing and harvesting dates. Less frequently, seed coat and leaf surface traits have also been suggested to investigate weed response to tillage and herbicides, being the most important disturbances in arable fields. The use of these traits is however currently limited by the availability of functional trait data measured under a wide range of environmental conditions (e.g. different levels of shading for leaf surface traits) or cropping systems (e.g. for phenology). In such a case, *in situ* trait measurement appear particularly important because weeds show high intraspecific variability for phenological traits and SLA (Bagavathiannan & Norsworthy, 2012; Perronne *et al.*, 2014; Borgy *et al.*, 2016).

New research avenues for understanding the response to agricultural practices are also offered by further investigating weed mating system and DNA content, that is the C-value and ploidy level. In particular, it could be fruitful to compare these traits between arable and non-arable weed communities, but also to quantify the possible intraspecific variation across contrasted environmental situations (such as altitudinal and latitudinal gradients).

Combining phylogenetic and trait diversity in trait-based analysis

To date, few trait-based studies on weeds have analysed the links between functional trait values of weeds and their evolutionary history. The combined use of phylogenetic and functional diversity in trait-based analysis can provide insights into the mechanisms that drive functional diversity by determining the amount of phylogenetic differences among species that explain the observed trait differences, that is the degree of phylogenetic signal (Losos, 2008). Variation in trait values may be partitioned into components related to pedoclimatic environment, management, phylogeny and all second-order interactions of the weeds (modified from Desdevises *et al.*, 2003). Studying phylogenetic structure of weed assemblages may also be particularly relevant when investigating how competition or herbicides (Fig. 5) affect weed assembly. It has been hypothesised that competition should be stronger between close relatives (but see Vellend *et al.* 2011 for further details). The traits involved in weed response to herbicides are indeed mainly of physiological nature and difficult to measure; phylogenetic information could have a more explanative power than a trait-based one. From a practical point of view, phylogenetic distances between crops and weed community composition could even be considered as key elements for designing crop succession for a given field, when attempting to avoid the impacts of the most competitive species.

Investigating weed effects on agro-ecosystem functioning

One of the main challenges in weed science is to quantify the role of weed communities in agro-ecosystem functioning, including crop production but also other ecosystem services. Most recent studies focused on identifying seed traits related to seed predator preferences, mostly carabids. Such traits are relevant when efficient biocontrol by seed predators is demonstrated. We would encourage more research on functional effect traits related to pollination, herbivores and also to crop pest persistence. Indeed, weeds have been

revealed as crucial in agro-ecosystem for the maintenance of honeybees and wild bees (Rollin *et al.*, 2013; Requier *et al.*, 2015), hence with potential return benefit for the production of oilseed rape and sunflowers. Design of weed management strategies that can support the maintenance of pollinators suffers from major gaps of knowledge.

Leaves and stems of weeds also provide an important food supply for phytophagous insects or molluscs. In some families of Coleoptera (*Curculionidae*, *Alticinae*) and Diptera (*Agromyzidae*), a large number of species have a specialist diet; that is, their larvae are feeding on a restricted number of closely related species (often in the same genera or family), so that their diversity would strongly depend on weed community diversity (Marshall *et al.*, 2003). Weeds may therefore play a crucial role for the persistence of these species. In the same way, some studies have pointed out the potential impact of weeds on the dynamics of several parasites or pests of crops (but see section 'Do parasitic weeds harbour specific traits?'). Determining which traits are related to the ability of a weed plant to decrease or increase an infection would be an opportunity for the management of multiple crop pests. Future research therefore needs to be conducted to fill these gaps.

Among the traits presented above, several key traits are related to both weed response to environmental factors and weed effect on community structure and ecosystem functioning (e.g. stem elongation, crop canopy or seed mass). This can offer an opportunity to link weed biodiversity to ecosystem functions and services (e.g. crop production, pollination or pest regulation) in various cropping systems, as these traits may constitute relevant agro-ecological indicators. For instance, plant height can be a good indicator of weed competitive ability. Seed chemical composition and nectar quantity may be relevant proxies of trophic resources for granivorous species and insect pollinators respectively (Table 1). The use of aggregated values of these traits may contribute to quantify the potential supply of ecosystem services according to management and landscape in various farmlands. Indeed, analyses of ecosystem services using plant functional variation across landscapes have been shown to be a powerful approach to understand the fundamental ecological mechanisms underlying ecosystem services provision, and trade-offs or synergies among these services (see, for example, Lavorel *et al.*, 2011).

Conclusions

In this article, we review the most significant plant traits in weed ecology. Based on literature and recent

work in weed science, we have identified and explained weed functional response traits associated with the response to disturbances induced by most management practices and resource gradients. So far, research has focussed on understanding weed responses to cropping systems, confirming the relevance of fundamental links between weed functional traits and management practices. The remaining challenges not only concern further understanding of the significance of particular traits, or fundamental trade-offs among them, but also how weeds will respond to global changes, as well as how weed functional diversity will affect agro-ecosystem functioning as a whole. First, understanding the multiple mechanisms that underpin weed assembly and weed functional diversity is a priority requiring theoretical, experimental and modelling approaches conducted at different spatial (from the plot to the biogeographic gradient) and temporal scales (from the physical effect of a particular management practice to the influence of a crop sequence during a decade). Second, our understanding of how weeds affect agro-ecosystems functioning remains very preliminary. Significant challenges to be addressed include effects of weed functional diversity on multiple ecosystem functions (e.g. pollination, bio-control, soil erosion) in contrasting pedoclimatic and agricultural contexts. Progress in this area will call upon multifactorial experiments, long-term monitoring of arable flora in multiple sites and the further development of agro-ecosystem models that directly use those weed traits that can be easily measured for large numbers of species. Trait-based approaches are therefore a promising way to address the challenge of designing sustainable and environmentally sustainable weed management strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary References.