Research review

Evolutionary-thinking in agricultural weed management

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Summary

Agricultural weeds evolve in response to crop cultivation. Nevertheless, the central importance of evolutionary ecology for understanding weed invasion, persistence and management in agroecosystems is not widely acknowledged. This paper calls for more evolutionarily-enlightened weed management, in which management principles are informed by evolutionary biology to prevent or minimize weed adaptation and spread. As a first step, a greater knowledge of the extent, structure and significance of genetic variation within and between weed populations is required to fully assess the potential for weed adaptation. The evolution of resistance to herbicides is a classic example of weed adaptation. Even here, most research focuses on describing the physiological and molecular basis of resistance, rather than conducting studies to better understand the evolutionary dynamics of selection for resistance. We suggest approaches to increase the application of evolutionary-thinking to herbicide resistance research. Weed population dynamics models are increasingly important tools in weed management, yet these models often ignore intrapopulation and interpopulation variability, neglecting the potential for weed adaptation in response to management. Future agricultural weed management can benefit from greater integration of ecological and evolutionary principles to predict the long-term responses of weed populations to changing weed management, agricultural environments and global climate.

Introduction

Agricultural weeds, selected by human crop cultivation, are a relatively recent ecological and evolutionary phenomenon. The life-history characteristics that dispose certain plant species to become agricultural weeds are well known (Baker, 1965, 1974; Patterson, 1985; Naylor & Lutman, 2002). The extent and structure of the genetic variation that underlies these weedy traits is less well studied. Baker (1965) suggested the existence of a 'general-purpose genotype', whereby a high degree of phenotypic plasticity compensates for low levels of genetic variation in weed populations.

More recently, the notion of genetically diverse weed populations, locally adapted to prevailing environmental conditions and crop management practices is gaining favour (Clements *et al.*, 2004). The plasticity vs adaptation viewpoints are not mutually exclusive, although understanding their relative importance may have some important implications for weed management in agroecosystems. That weed populations are able to evolve rapidly in response to intense, human-derived selection pressures supports a wider, recent acknowledgement that evolution is able to occur on ecological timescales (Thompson, 1998; Hairston *et al.*, 2005; Carroll *et al.*, 2007)

A number of studies have sought to quantify the economic and environmental cost of weeds. Oerke (2006) reported that of all crop pests, weeds have the greatest potential for yield loss (34%), with actual losses in 2001–2003 of *c.* 10% worldwide. In the USA, the annual cost of agricultural weeds has been estimated to be US$ 26.4 billion (Pimentel *et al.*, 2000). The percentage crop yield loss attributable to weeds has changed little since the 1960s (Oerke, 2006), suggesting that crop protection companies, crop breeders, farmers and weed biologists are locked in a 'weed management arms race' (Fig. 1) with clear parallels to the 'evolutionary arms race' in which, for example, pathogens and their hosts are engaged (Van Valen, 1973).

It can be difficult to unequivocally demonstrate the genetic basis of adaptation to support this 'arms race' hypothesis, although the evolution of resistance to herbicides in weeds has provided an excellent opportunity to do so. Since herbicide resistance was first reported (Ryan, 1970), resistance to a broad range of herbicide modes of action has been confirmed in 189 weed species (Heap, 2009). In some cases, weed populations have evolved multiple resistance whereby resistance to one herbicide mode of action has necessitated a switch to other modes of action to which resistance has subsequently evolved through multiple independent mechanisms (Tardif & Powles, 1994; Cocker *et al.*, 1999; Neve *et al.*, 2004). There is evidence that the arms race is being lost as the rate of discovery of new herbicide modes of action declines (Ruegg *et al.*, 2007) while the evolution of herbicide resistance continues apace. We might expect that as weed control technologies become more advanced, selection for 'weediness' will intensify. There is mounting evidence for this in parts of the world that have enthusiastically adopted genetically modified glyphosate-resistant crops and are now experiencing unprecedented levels of evolved weed resistance to glyphosate (Powles, 2008).

Agricultural weeds represent the ecological and evolutionary response of the native and introduced flora of a region to the opportunities and challenges presented by human crop cultivation. As such, the discipline of evolutionary ecology should be central to informing concepts and practices in applied crop-weed management. It is our view, that despite some recognition of the importance of weed evolution to weed management (Harper, 1956; Cavers, 1985; Barrett, 1988; Jordan & Jannink, 1997; Mortimer, 1997; Clements *et al.*, 2004), the failure to more widely integrate principles and practices from the field of evolutionary ecology into applied crop-weed research has been (and will be) to the considerable detriment of weed management. In this paper we call for a greater application of evolutionary-thinking to the 'weed management arms race'. We do so by drawing on observations from our own work in the evolution and management of herbicide resistance. We believe herbicide resistance research has become overly focused on characterizing resist-
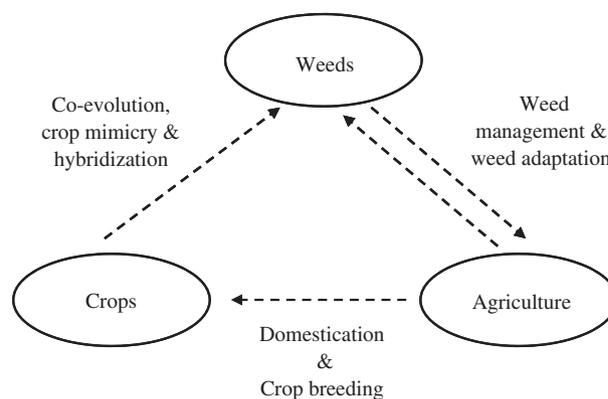

Fig. 1 A schematic representation of the 'Weed Management Arms Race' showing the coevolutionary dynamics of interactions between humans, crops and weed populations. Unconscious and conscious human selection during domestication and subsequent breeding has produced modern, specialized crop species and varieties. Widespread cultivation of these crops has created 'opportunity space' for the invasion of agricultural land by ruderal plant species and subsequent crop–weed coevolution has resulted in the evolution of highly adapted weed ecotypes that mimic the crop lifecycle and morphological characteristics. This evolution of highly adapted weeds has stimulated the development of sophisticated weed control tools and these highly effective tools (for example, herbicides) have exerted extreme selection pressure for weed adaptation. The continuing and ongoing development of crop varieties, weed control tools and weed management systems in response to weed adaptation requires a greater acknowledgement of the key role of evolutionary dynamics in management of agricultural weeds.

ance and has neglected to perform evolutionarily informed studies to understand the dynamics of selection for resistance. In particular, we consider how models and model organisms may play a role in contributing to a more fundamental understanding of the evolutionary ecology and management of agricultural weeds. We consider the importance of measuring and understanding genetic variation in weed populations, of incorporating evolutionary dynamics into weed population models and of considering the adaptive potential of weeds under future climate change. At each stage, we will make recommendations for ways in which future studies in weed biology and management can incorporate and benefit from a greater degree of evolutionary-thinking.

Towards evolutionary-thinking in weed management

Weed science is a relatively new academic discipline. This fact, it has been argued, has diminished its impact and perceived academic stature (Burnside, 1993) and caused weed science to suffer the 'new kid in town syndrome' (Fernandez-Quintanilla *et al.*, 2008). Most departments of entomology or plant pathology include researchers concerned with basic pest and disease biology as well as those concerned with the application of this knowledge to management. Conversely,

weed science has become divorced from, or is rarely associated with, botany and plant ecology departments and is more closely aligned with crop science. This close association between crop and weed scientists has, in our view, led weed science to focus primarily on physiology and agronomy, viewing weeds in a similar manner to genetically uniform crops and ignoring the importance of plant ecology and evolution for understanding weed biology and management.

Over 50 yr ago, Harper (1956) talked of weed species 'selected by the very cultural practices which were originally designed to suppress them' and his observations remind us that the idea of evolutionary-thinking in weed management is not new, though it may have been lost in a weed science driven more by technology than by biology. The development and rise to prominence of herbicides following the discovery of 2,4-dichlorophenoxyacetic acid (2,4-D) in the 1950s played a significant role in a more general decline in weed biology research, as highly effective chemical weed control reduced the impetus for more biologically informed weed management approaches. More recently, mounting concerns with herbicide resistance and the agronomic and environmental sustainability of herbicide-dominated weed control have seen a resurgence in interest in integrated weed management that is underpinned by knowledge of weed biology and ecology (Mortensen *et al.*, 2000; Van Acker, 2009). We would contend, however, that within this new weed biology, there remains too little consideration of weed evolution and local adaptation.

Given the economic and environmental importance of weeds, and accepting that agricultural weeds are the products of human-driven 'evolution in action' it would seem logical to embrace weeds as model organisms to understand plant evolutionary ecology, as has been the case for other crop pests such as insects and pathogens. This approach would contribute fundamental insight to plant ecology and evolution and help to contribute to a greater degree of evolutionary thinking in agricultural weed management.

The evolutionary ecology of agricultural weeds

Selection for weediness in agricultural landscapes

Weed adaptation has two prerequisites, genetic variation (see section Genetic variation in weed populations) and selection pressure. Selection pressure may be imposed by local climatic and environmental conditions, and crop and weed management practices, and this selection can result in locally adapted weed ecotypes. Climatic and/or environmental selection is likely to result in regional or clinal patterns of differentiation between weed populations (Ray & Alexander, 1966; Warwick & Marriage, 1982; Warwick *et al.*, 1984; Cavers, 1985; Weaver *et al.*, 1985; Dunbabin & Cocks, 1999; Michael *et al.*, 2006). From a weed management perspective, this regional variation may be

important for determining regional weed problems, for driving range expansions in agricultural weeds (Warwick, 1990) and for determining the ability of weed populations to adapt to climate change (Ghersa & León, 1999; Fuhrer, 2003).

Within a region, agricultural landscapes can potentially vary at a much finer spatial (field to field) and temporal (year to year) scale when diverse crop and weed management is practised. Theoretical models and experimental evolutionary studies have demonstrated that fine-grained habitats reduce the selection for specialist genotypes (Kassen & Bell, 1998; Sultan & Spencer, 2002; Weinig & Schmitt, 2004). At a weed population and species level, this environmental heterogeneity should reduce selection for highly adapted, specialist crop mimics (Barrett, 1983) and herbicide-resistant genotypes. At the weed community level, environmental heterogeneity will prevent communities from becoming dominated by a few, highly adapted, competitive weed species (see 'Evolution of weed communities'). Notwithstanding the theoretical benefits of environmental heterogeneity in weed management, many agricultural landscapes are increasingly characterized by low crop diversity with potential impacts for the selection of highly adapted weed genotypes.

The evolution of herbicide resistance provides an interesting, although unproven, test for the effects of environmental heterogeneity on weed adaptation. In countries such as Australia and the USA, where there is relatively little diversity in crop production and herbicide application over vast areas, the scale of the herbicide resistance problem is far greater than in Europe (Powles & Shaner, 2001) where agriculture is more spatially and temporally diversified. In Canada, Beckie *et al.* (2004) demonstrated a clear negative correlation between cropping system diversity and the occurrence of resistance to acetohydroxy acid synthase (AHAS)inhibiting herbicides in *Avena fatua*. These general observations are supported by simulation studies that show that the evolution of herbicide resistance can be slowed by increased spatial (Roux *et al.*, 2008; Dauer *et al.*, 2009) and temporal (Diggle *et al.*, 2003) heterogeneity in herbicide application.

Agricultural weed management that is informed by evolutionary ecology will attempt to diversify selection for other weed adaptations by diversifying weed management in both time and space across the agricultural landscape (Jordan & Jannink, 1997; Clements *et al.*, 2004). However, the genetic basis of other weed adaptations has not been demonstrated and there are a number of practical limitations in testing these theories on a field scale in weed populations. In view of this, we believe the most promising approaches to demonstrate the generality of these principles may be simulation modelling and experimental evolution experiments with model organisms (Reboud & Bell, 1997; Kassen & Bell, 1998). The application of both of these

approaches to inform agricultural weed management is discussed further in following sections.

Evolution of weed communities

Temporal and spatial variation in agricultural habitats also affects weed community composition and diversity. As the predictability (homogeneity) of agricultural environments increases at both field and regional scales, the intensity and importance of plant competition increases (Connell, 1978). In homogeneous environments, resource partitioning between species is reduced, interspecific competition increases and competitive exclusion results (Grime, 2002). In this way, over successional time it is expected that weed community diversity is reduced and communities become dominated by a few highly competitive weed species. In a sort of positive feedback, populations of these dominant species become larger, making them more likely to evolve novel weedy adaptations as the rate of generation of novel genetic variation through adaptive mutation and recombination is increased.

Management-induced changes in weed communities (often described as 'species shifts') are sometimes discussed in terms of weed evolution, although the actual underlying processes are ecological rather than evolutionary and related to the theories of community assembly (Drake, 1990; Booth & Swanton, 2002) and ecological succession (Clements, 1916; Ghersa & León, 1999). There are numerous reports of weed 'species-shifts' that have occurred in response to tillage systems (Derksen *et al.*, 1993; Buhler, 1995; Swanton *et al.*, 1999), herbicides and genetically modified herbicide-tolerant crops (Hawes *et al.*, 2003; Owen, 2008), crop sowing date (Hald, 1999) and general changes in cropping systems (Ball & Miller, 1993; Barberi & Mazzoncini, 2001; Fried *et al.*, 2008). Weed management that is more spatially and temporally diverse will reduce the evolution of weed floras that are specifically selected by repeated management practices, resulting in more functionally diverse weed communities. These communities will have less potential for severe crop yield loss, less selection on individual weeds, fewer shifts in community function and greater value for provision of biodiversity and ecosystem services.

Genetic variation in weed populations

There are widely diverging and largely unresolved views on the extent and importance of genetic variation in agricultural weed populations. Clements *et al.* (2004) proposed a conceptual model based on 'a dynamic tension between processes that reduce and restore genetic variation' in weed populations. Initial weed colonization by a few individuals in agricultural habitats will result in a founder effect (Mayr, 1963; Sahli *et al.*, 2008) and subsequent population regulation by highly effective weed

control measures will force populations through genetic bottlenecks, further constraining genetic variation in weed populations (Barrett, 1988). In opposition to this, multiple introductions of non-native species will bring together diverse genotypes and, in outcrossing species, this will result in novel gene combinations, unleashing a wealth of genetic variation on which selection can act to result in well-adapted weed genotypes (Ellstrand & Schierenbeck, 2000).

Genetic variation within and between weed populations has mainly been estimated using neutral genetic markers and contrasting results have emerged from studies on genetic variation in invasive weeds. In *Pennisetum steaceum*, global monoclonality was observed following the invasion of a single super-genotype (Le Roux *et al.*, 2007). By contrast, for some invasive species such as *Ambrosia artemisiifolia* higher levels of genetic variation have been found when compared with native populations (Genton *et al.*, 2005), probably as a result of multiple introductions that buffered the loss of genetic variation associated with bottlenecks (Chapman *et al.*, 2004; Wang *et al.*, 2008). In arable weeds, the expectation for low levels of genetic variation has been confirmed for a few species (Hamrick *et al.*, 1979; Barrett & Richardson, 1985; Novak & Mack, 1993). However, as observed for invasive weeds, other studies have demonstrated high levels of genetic variation within and between weed populations (Warwick *et al.*, 1984; Weaver *et al.*, 1985; Leiss & Müller-Schärer, 2001; Ianetta *et al.*, 2007; Menchari *et al.*, 2007).

The use of estimates of variation at neutral genetic markers as a measure of adaptive potential in weed populations may be ill-founded. Heterogeneous selection has little effect on neutral genetic differentiation, especially in highly outcrossing species (Le Corre & Kremer, 2003), and studies have shown that neutral intrapopulation genetic variation does not always correlate with genetic variation associated with phenotypic traits under selection in plant populations (Merilä & Crnokrak, 2001; Reed & Frankham, 2001). We believe there is an urgent need for more studies in weeds to assess whether genetic variation estimated using neutral genetic markers is an accurate estimate of genetic variation for adaptive traits (Menchari *et al.*, 2007; Sahli *et al.*, 2008).

Weed adaptation in response to environmental change may result from selection of new mutations (i.e. spontaneous mutations) or alleles from the standing genetic variation (Orr & Betancourt, 2001). 'New mutations' mean that adaptive traits appear in a weed population after the imposition of the selective pressure, while 'standing genetic variation' means that adaptive traits segregate in unexposed populations. The source of genetic variation for adaptive traits may be of primary importance for the outcome of a selective process (Hermisson & Pennings, 2005) and may dictate the best weed management strategy to adopt (Neve

& Powles, 2005a; Roux *et al.*, 2008). When adaptation originates from standing genetic variation, the fixation probability of an allele depends on its deleterious and beneficial effects before and after the environmental change, respectively. By contrast, the evolutionary trajectories of 'new mutations' in a population depend on the net fitness effect associated to the adaptive allele (Orr, 1998; Barton & Keightley, 2002). Striking examples of standing genetic variation comes from the detection of herbicide resistant plants in *Lolium rigidum* populations never previously exposed to any herbicide (Preston & Powles, 2002; Neve & Powles, 2005b). Further studies to determine the extent and structure of genetic variation that underpins the potential for weed adaptation are required.

The evolution of resistance to herbicides: a classic tale of weed adaptation

There can be no clearer demonstration of the evolutionary potential of weeds than the rapid and widespread evolution of resistance to herbicides (Powles & Shaner, 2001). The propensity for evolution of resistance varies, with some species and herbicides being more prone to resistance than others (Heap & LeBaron, 2001). In the most extreme cases, resistance has evolved following exposure of no more than three or four generations of a weed population to a herbicide (Powles & Holtum, 1994). Herbicide resistance is arguably the single largest global weed management issue and studies concerned with herbicide resistance are at the forefront of current weed science research. Given this, it seems logical that evolutionary biology should play a central role in informing solutions to this escalating problem, yet, conversely, it is our view that herbicide resistance research most starkly highlights the lack of evolutionary thinking in weed science.

The majority of herbicide resistance research is conducted retrospectively. A suspected resistant population is reported, seed is collected from surviving plants in the field and the dose–response curve of the suspected resistant and a known susceptible population are compared under controlled glasshouse or field conditions. Following confirmation of resistance, further physiological, genetic and molecular characterization is conducted to diagnose the resistance mechanism. These studies are important for characterizing new mechanisms of resistance, but endless descriptions of the same mechanism in a different species or from a different cropping system provide rapidly diminishing returns in terms of their ability to better inform resistance management (Cousens, 1999; Neve, 2007). Indeed, it seems that weed researchers have become overly concerned with describing the outcome of resistance evolution to the detriment of studies that seek to better understand the process of selection for resistance. We believe this is a reflection of the alignment of weed science with

crop science and physiology rather than the disciplines of plant ecology and evolution. It also represents a missed opportunity for herbicide resistance research to combine applied management advice with fundamental insight into evolutionary ecology as has been the case in insecticide resistance studies (Lenormand *et al.*, 1999; Tabashnik *et al.*, 2004).

The evolutionary dynamics of selection for herbicide resistance

Studies that focus solely on characterizing the outcome of resistance evolution may prejudice assumptions about the process of selection. For example, the ultimate fixation of a single major resistance allele with no fitness cost (Coustau *et al.*, 2000), does not preclude the possibility that many other minor alleles were also initially selected or that an initial cost of resistance was compensated during the course of selection (Andersson, 2003; Wijngaarden *et al.*, 2005). Evolution of herbicide resistance is a stochastic process and resistance management strategies attempt to 'load the dice' in favour of herbicide susceptibility. It is likely that the key steps towards evolution of resistance occur during the early stages of selection, long before field resistance is apparent, and that following this initial selection, resistance becomes an inevitable or deterministic consequence of further exposure to herbicides. Greater knowledge and understanding of genetic variation for herbicide susceptibility in weed populations, of fitness costs and trade-offs associated with this variation and of population genetic processes during the early stages of selection for resistance should be incorporated into simulation models, and will, we argue, greatly improve resistance management. Key to this understanding will be a greater appreciation of the relative contributions of spontaneous mutation and standing genetic variation to the evolution of resistance (Lande, 1983; Orr, 1998; Hermisson & Pennings, 2005). In the following text, we consider this question in relation to the impact of herbicide dose on potential for evolution of resistance.

The potential for reduced herbicide application rates to accelerate evolution of resistance has been keenly debated (Gressel, 2002; Beckie & Kirkland, 2003; Neve, 2007) and has practical significance given economic and environmental incentives to reduce herbicide application rates. Low doses of the acetyl-coenzyme A carboxylase (ACCase) inhibiting herbicide diclofop-methyl have been shown to rapidly select for resistance to very much higher doses via the selection and reassortment of minor genes in *L. rigidum*, an outcrossing species (Neve & Powles, 2005a). This phenomenon has also been demonstrated for low-dose selection with glyphosate in *L. rigidum*, though the response to selection was less marked (Busi & Powles, 2009). These results suggest a high degree of additive genetic variation for herbicide susceptibility in a weed population never prev-

iously exposed to herbicides. High herbicide doses during the initial stages of selection would have prevented selection and reassortment of minor genes into highly resistant phenotypes. Even accepting that the majority of field-evolved herbicide resistance is endowed by single major genes, it is possible that initial selection at low doses is for putative minor genes, resulting in reduced herbicide efficacy, larger population sizes and an ultimately higher probability of subsequent selection for major gene resistance. The 'low dose' question also highlights the importance of understanding the process, rather than simply the outcome of selection for resistance.

Evolutionary biology, population genetics and physiology all suggest that evolved resistance to novel pesticides will be associated with a fitness cost (Coustau *et al.*, 2000). These costs may be environment-specific (Plowman *et al.*, 1999; Salzmann *et al.*, 2008) and they may only be manifest at certain life-history stages (Roux *et al.*, 2005; Vila-Aiub *et al.*, 2005). Knowledge of the extent of these costs and of their environment-specific and life-history-specific attributes may be crucial for designing 'biorational management tactics' which could turn the costs and idiosyncrasies associated with resistance into valuable tools in resistance management (Jordan *et al.*, 1999). There have been some excellent studies of herbicide resistance fitness costs. However, in many other cases, the concept of fitness as it relates to herbicide resistance has been poorly understood and many published studies have used wholly inappropriate methods to quantify fitness costs. Many studies have compared resistant (R) and susceptible (S) populations with completely different genetic backgrounds. Numerous studies have also mistakenly made the assumption that comparative growth rate alone is a proxy for fitness. Perhaps more than in any other case, these widespread and repeated faults in fitness studies highlight the application in weed science of methods from crop breeding and physiology rather than from ecology and evolution.

Some fitness studies have used isogenic (R) and (S) lines to demonstrate fitness costs associated with triazine resistance in standardized genetic backgrounds (Gressel & Bensinai, 1985; McCloskey & Holt, 1990; Arntz *et al.*, 2000; Salzmann *et al.*, 2008). While accepting that isogenic lines are the gold standard for unequivocally demonstrating fitness costs, we suggest that future research should also compare fitness between plants arising from controlled crosses of R and S plants (Menchari *et al.*, 2008) or where plant cloning techniques have enabled the identification and propagation of discrete R and S phenotypes from single populations (Vila-Aiub *et al.*, 2005; Pedersen *et al.*, 2007). In this way, fitness of R alleles can be compared in a broader range of genetic backgrounds, reflecting more closely the situation in natural populations. Wherever possible, fitness studies that have proper control of genetic background should also report the molecular genetic basis of resistance,

measure fitness and fitness components at a range of life-history stages, under competitive conditions and in a range of environments.

As fitness is directly related to the average contribution of an allele or genotype to future generations, the evolution of R allele frequency in pesticide-treated and untreated populations may provide a better estimate of fitness cost than those based on direct measures of fitness-related traits. Using migration-selection models developed to estimate migration rates and selection coefficients in clines, Lenormand *et al.* (1999) and Roux *et al.* (2006) empirically showed that studying R allele frequency along a transect of pesticide treated and untreated areas gave more precise, and sometimes contrasting estimates of fitness costs than estimates based solely on fitness-related traits. We argue that in future, the most accurate estimates of fitness costs will be obtained by measuring changes in R allele frequencies in studies such as those described earlier.

Models and model organisms in herbicide resistance research

It is inherently difficult to design and perform experiments that study the dynamics of herbicide resistance evolution in weed populations. To be informative, these experiments must select for resistance at realistic spatial and temporal scales, so that herbicides are applied to millions of individuals over multiple generations. Some studies have sought to explore the efficacy of weed and resistance management strategies on small field plots (Westra *et al.*, 2008), but weed populations are too small to represent the full range of genetic variation on which selection acts at the agronomic scale. Other studies have attempted to overcome this constraint by sowing weed populations with a low frequency of herbicide resistance into small field plots (Beckie & Kirkland, 2003; Moss *et al.*, 2007). However, this approach has limited application as it examines the effectiveness of proactive resistance management strategies against populations that are already resistant.

Model organisms and mathematical models that simulate evolution of resistance may each have features that overcome some of the difficulties described above, although for some purposes their relevance to the field may be questioned. Simulation models (Maxwell *et al.*, 1990; Diggle *et al.*, 2003; Jacquemin *et al.*, 2008) may be relatively inexpensive to develop and enable rapid comparisons of resistance management strategies over many generations. These models may be used solely to explore the relative importance of parameters that underpin resistance evolution or to address very specific cropping system-related questions (Neve *et al.*, 2003). However, in some cases, a lack of understanding of key model parameters such as the fitness costs associated with R alleles, the extent of standing genetic variation for herbicide resistance and gene flow between

metapopulations is hampering further model development and application. As these parameters become available, new models incorporating quantitative genetics, demographics and metapopulation dynamics can begin to explore some of the important questions discussed in the preceding sections and relating to the direct or interacting effects of: the impact of fitness costs on initial R allele frequency before the first herbicide exposure and resistance trajectories; the evolution of fitness costs by compensatory evolution; the relative contribution of major gene and quantitative resistance, and the role of herbicide dose; and the impact of environmental heterogeneity, degree of connectedness among patches and cropping systems on the evolution of herbicide resistance.

Model organisms may be useful in their own right for developing experimental evolutionary approaches (Elena & Lenski, 2003) to study the dynamics of evolution of herbicide resistance. For example, the unicellular chlorophyte, *Chlamydomonas reinhardtii* reproduces rapidly, and millions of individuals can be cultured in a few millilitres of liquid medium. It is also susceptible to many herbicides (Reboud, 2002) and has been used as a model experimental organism in herbicide resistance research (Reboud *et al.*, 2007). Model organisms, such as *Arabidopsis thaliana* may also provide valuable insight for important parameters that drive resistance evolution (Jander *et al.*, 2003). A series of studies examining costs associated with herbicide resistance alleles in *A. thaliana* has provided valuable insights for models of herbicide resistance evolution as well as demonstrating the potential for herbicide resistance to provide fundamental insight into the evolutionary genetics of plant adaptation (Roux *et al.*, 2004, 2005; Roux & Reboud, 2005).

Modelling weed life histories and population dynamics

Mathematical models have become important tools in weed science to understand weed biology and population dynamics and to predict the long- and short-term responses of weed populations to management (reviewed in Holst *et al.*, 2007). Most population dynamics models have a simple demographic model as their basis (Cousens & Mortimer, 1995). These models are usually parameterized from empirical data gathered for a single population of the species being considered and parameter values generally represent the mean response of the population, so that intrapopulation variability is not incorporated. As a result, these models have some practical limitations; predictions may be population-specific and the potential for ongoing local adaptation to weed management is not accounted for.

These limitations reduce the capability of models to realistically predict long-term weed population dynamics, particularly where it is likely that adaptation to changing management and environment will be important. The fitness of agricultural weed populations depends on their ability to synchronize their life cycle with key stages in crop development and management (crop establishment, weed control, crop harvest). Cultural weed management aims to reduce the establishment, impact and fecundity (fitness) of weeds in crops by uncoupling crop and weed life cycles by, for example, encouraging precocious weed germination, rotating crops with quite different sowing and harvesting dates or minimizing weed seed production. As resistance and increased regulation continue to compromise herbicide-dominated weed control in some parts of the world, there is an increased need for more cultural weed management as part of integrated weed management strategies. These new strategies rely on an ability to predict and influence the timing of key life history processes and transitions such as seed dormancy cycling, germination timing and the timing and duration of flowering. There is likely to be life-history evolution in the face of these new management challenges.

These challenges will require new modelling approaches that integrate quantitative genetics with demographic and environmental stochasticity. Population dynamics models have been developed which incorporate simple population genetics to simulate the evolution of herbicide resistance (Maxwell *et al.*, 1990; Diggle *et al.*, 2003). However, modelling the response of quantitative traits such as weed seed dormancy and flowering time to environmentally derived or management-derived selection may not be so straightforward as it has been for major gene herbicide resistance. These traits are likely polygenically controlled, subject to complex patterns of genetic covariation and there will be trade-offs and correlations between traits such as germination timing, flowering time and fecundity (Weiner, 1990; Franks & Weis, 2008; Wilczek *et al.*, 2009). Jordan (1989) used multivariate selection analysis (Lande & Arnold, 1983) to predict the evolutionary response of coastal populations of *Diodea teres* to selection in an agricultural habitat and this method would appear to have some wider application for understanding and modelling weed adaptation. Demo-genetic models that incorporate demographic and environmental stochasticity with quantitative genetics at the metapopulation level have been developed recently in the field of conservation genetics to address questions of population persistence and adaptation in small populations of endangered species (Kirchner *et al.*, 2006; Willi & Hoffmann, 2008). For conservation geneticists these models are used to explore which combinations of demographic and genetic factors will promote population persistence. Conversely, in the case of weed management we are interested in combinations of factors that will reduce persistence and adaptation. Nevertheless, similar demo-genetic models may have utility for predicting population level responses of weed species under changing management and climatic conditions.

Climate change effects on weed biology and management

The positive effects of increased atmospheric CO_2 (Ainsworth & Long, 2005) and the negative effects of elevated ozone levels and higher temperatures (Morgan *et al.*, 2006; Ainsworth, 2008) on crop yield under climate change are well known. The actual crop yields attained in future climates will depend on the effects of climate change on weed, pest and disease populations and on crop interactions with these organisms (Fuhrer, 2003). From a weeds perspective, there are two key questions: How will climate change affect crop-weed competition; What is the potential for agricultural weeds to rapidly adapt to changing climates? The presence of weeds in a soybean crop has been shown to reduce the ability of the crop to respond positively to elevated CO_2. When competing with the C_3 weed, *Chenopodium album*, relative soybean yield reduction was greatest at higher CO_2 levels. Competition with the C_4 weed, *Amaranthus retroflexus* was less intense at elevated CO_2, suggesting that competition from C_3 weeds may increase under climate change (Ziska, 2000). Climate change may also result in range expansion through ecotypic differentiation and the ability for rapid colonization in agricultural weeds, associated with northward range expansion in North America has been shown previously (Warwick *et al.*, 1984; Weaver *et al.*, 1985; Warwick, 1990). There has been no research to specifically examine the potential for agricultural weeds to rapidly adapt to climate change, although elevated CO_2 has been shown to increase the dominance of invasive plant species in natural communities (Smith *et al.*, 2000). Other research has demonstrated how projected climate change may alter the phenology of reproductive and other life-history processes in plant populations from natural ecosystems (Cleland *et al.*, 2006; Sherry *et al.*, 2007). Similar phenological changes in agricultural weeds could significantly alter crop–weed interactions and recent work by Franks & Weis (2007, 2008) has shown the potential for rapid life-history evolution in response to climate change in the annual weedy plant, *Brassica rapa*.

Future climate change is one of the greatest challenges to global food production and understanding the potential for, and rate of, weed adaptation to climate change should be a research priority in weed science.

Evolution, ecology and agricultural weeds

Calls for a greater integration of evolutionary thinking into weed biology and management have been made previously (Jordan & Jannink, 1997; Clements *et al.*, 2004), yet there remains little evidence for this integration in practice. Publications addressing the importance and extent of genetic diversity, intrapopulation and interpopulation variability and adaptation in agricultural weeds (Harper, 1956; Cavers,

1985; Warwick, 1986, 1987) have declined since the 1980s. Indeed, there appears to have been a general decline in the number of studies addressing the fundamentals of agricultural weed biology in the last 20–30 yr. There may be many reasons for this decline, but the rise to prominence of herbicides and the associated simplification of weed management is a likely key factor. In response to this over-reliance on herbicides, evolution of resistance has occurred in agroecosystems worldwide (Powles & Shaner, 2001), yet evolutionary thinking is even lacking in much herbicide resistance research (Neve, 2007).

We believe that future weed management will rely more heavily on an underpinning knowledge of weed biology, ecology and evolution. The continuing evolution of herbicide resistance, a reduction in the discovery of new herbicide modes of action and increased pesticide regulation will reduce reliance on herbicides. This will precipitate a move towards more integrated weed management, organic production may increase and, in some areas, weeds will be more widely recognized for the biodiversity and ecosystem services benefits they provide. All of these changes will take place in the face of global climate and environmental change.

An 'evolutionarily enlightened' (Ashley *et al.*, 2003) weed management will move away from the typological straitjacket that considers weed species as fixed entities with static demographic and life-history characteristics. New studies are required to quantify the extent and functional significance of genetic diversity within and between weed populations. Increasing access to high-throughput molecular and genomic tools and a greater degree of collaboration between weed scientists, molecular ecologists and evolutionary biologists will help in this regard. Armed with this better understanding of weed population biology, selection experiments can begin to determine the response of key weed traits under selection from changing management and environmental pressures. In turn, this knowledge should be incorporated in weed population dynamics models to better understand the likely long-term consequences of weed management and environmental change with the ultimate aim of designing and implementing better integrated weed management strategies and reducing selection for weedy traits in agricultural weed populations.

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