

University of Warwick institutional repository

This paper is made available online in accordance with publisher policies. Please scroll down to view the document itself. Please refer to the repository record for this item and our policy information available from the repository home page for further information.

To see the final version of this paper please visit the publisher's website. Access to the published version may require a subscription.

Author(s): Neve, Paul; Vila-Aiub, Martin; Roux, Fabrice

Article Title: Evolutionary-thinking in agricultural weed management

Year of publication: 2009

Link to published version :

<http://dx.doi.org/10.1111/j.1469-8137.2009.03034.x>

Publisher statement: The definitive version is available at
www.blackwell-synergy.com

25 **Summary**

26 Agricultural weeds evolve in response to crop cultivation. Nevertheless, the central
27 importance of evolutionary ecology for understanding weed invasion, persistence and
28 management in agroecosystems is not widely acknowledged. We call for more
29 evolutionarily-enlightened weed management, in which management principles are
30 informed by evolutionary biology to prevent or minimise weed adaptation and spread. As
31 a first step, a greater knowledge of the extent, structure and significance of genetic
32 variation within and between weed populations is required to fully assess the potential for
33 weed adaptation. The evolution of resistance to herbicides is a classic example of weed
34 adaptation. Even here, most research focuses on describing the physiological and
35 molecular basis of resistance, rather than conducting studies to better understand the
36 evolutionary dynamics of selection for resistance. We suggest approaches to increase the
37 application of evolutionary-thinking to herbicide resistance research. Weed population
38 dynamics models often ignore intra- and inter-population variability, neglecting the
39 potential for weed adaptation in response to management. We make suggestions for
40 incorporating evolutionary dynamics into these models. Future agricultural weed
41 management can benefit from a greater integration of ecological and evolutionary
42 principles to predict the long term responses of weed populations to changing weed
43 management, agricultural environments and global climate.

44

45 **Keywords:** weed science, evolutionary ecology, herbicide resistance, modelling, climate
46 change

47

48 **Introduction**

49 Agricultural weeds, selected by human crop cultivation, are a relatively recent ecological
50 and evolutionary phenomenon. The life history characteristics that dispose certain plant
51 species to become agricultural weeds are well known (Baker, 1965, 1974; Patterson, 1985;
52 Naylor & Lutman, 2002). The extent and structure of the genetic variation that underlies
53 these weedy traits is less well studied. Baker (1965) suggested the existence of a ‘general-
54 purpose genotype’, whereby a high degree of phenotypic plasticity compensates for low
55 levels of genetic variation in weed populations. More recently, the notion of genetically
56 diverse weed populations, locally adapted to prevailing environmental conditions and
57 crop management practices is gaining favour (Clements *et al.*, 2004). The plasticity
58 versus adaptation viewpoints are not mutually exclusive, though understanding their
59 relative importance may have some important implications for weed management in
60 agroecosystems. That weed populations are able to evolve rapidly in response to intense,
61 human-derived selection pressures supports a wider, recent acknowledgement that
62 evolution is able to occur on ecological timescales (Thompson, 1998; Hairston *et al.*,
63 2005; Carroll *et al.*, 2007)

64 A number of studies have sought to quantify the economic and environmental cost
65 of weeds. Oerke (2006) reported that of all crop pests, weeds have the greatest potential
66 for yield loss (34%), with actual losses in 2001-03 of approximately 10% worldwide. In
67 the USA, the annual cost of agricultural weeds has been estimated to be US\$ 26.4 billion
68 (Pimentel *et al.*, 2000). The percentage crop yield loss attributable to weeds has changed
69 little since the 1960’s (Oerke, 2006), suggesting that crop protection companies, crop
70 breeders, farmers and weed biologists are locked in a ‘weed management arms race’

71 (Figure 1) with clear parallels to the evolutionary arms race in which, for example,
72 pathogens and their hosts are engaged (Van Valen, 1973).

73 It can be difficult to unequivocally demonstrate the genetic basis of adaptation to
74 support this ‘arms race’ hypothesis, though the evolution of resistance to herbicides in
75 weeds has provided an excellent opportunity to do so. Since herbicide resistance was first
76 reported (Ryan, 1970), resistance to a broad range of herbicide modes of action has been
77 confirmed in 189 weed species (Heap, 2009). In some cases, weed populations have
78 evolved multiple resistance whereby resistance to one herbicide mode of action has
79 necessitated a switch to other modes of action to which resistance has subsequently
80 evolved through multiple independent mechanisms (Tardif & Powles, 1994; Cocker *et al.*,
81 1999; Neve *et al.*, 2004). There is even evidence that the arms race is being lost as the
82 rate of discovery of new herbicide modes of action declines (Ruegg *et al.*, 2007) while
83 the evolution of herbicide resistance continues apace. We might expect that as weed
84 control technologies become more advanced, selection for ‘weediness’ will intensify.
85 There is mounting evidence for this in parts of the world that have enthusiastically
86 adopted genetically-modified glyphosate-resistant crops and are now experiencing
87 unprecedented levels of evolved weed resistance to glyphosate (Powles 2008).

88 Agricultural weeds represent the ecological and evolutionary response of the
89 native and introduced flora of a region to the opportunities and challenges presented by
90 human crop cultivation. As such, the discipline of evolutionary ecology should be central
91 to informing concepts and practices in applied crop-weed management. It is our view,
92 that despite some recognition of the importance of weed evolution to weed management
93 (Harper, 1956; Cavers, 1985; Barrett, 1988; Jordan & Jannink, 1997; Mortimer, 1997;

94 Clements *et al.*, 2004), the failure to more widely integrate principles and practices from
95 the field of evolutionary ecology into applied crop-weed research has been (and will be)
96 to the considerable detriment of weed management. In this paper, we call for a greater
97 application of evolutionary-thinking to the ‘weed management arms race’. We do so by
98 drawing on observations from our own work in the evolution and management of
99 herbicide resistance. We believe herbicide resistance research has become overly focused
100 on characterising resistance and has neglected to perform evolutionarily-informed studies
101 to understand the dynamics of selection for resistance. In particular, we consider how
102 models and model organisms may play a role in contributing to a more fundamental
103 understanding of the evolutionary ecology and management of agricultural weeds. We
104 consider the importance of measuring and understanding genetic variation in weed
105 populations, of incorporating evolutionary dynamics into weed population models and of
106 considering the adaptive potential of weeds under future climate change. At each stage,
107 we will make recommendations for ways in which future studies in weed biology and
108 management can incorporate and benefit from a greater degree of evolutionary-thinking.

109

110 **Towards evolutionary-thinking in weed management**

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

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

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

135 Given the economic and environmental importance of weeds and accepting that
136 agricultural weeds are the products of human-driven ‘evolution in action’ it would seem
137 logical to embrace weeds as model organisms to understand plant evolutionary ecology,
138 as has been the case for other crop pests such as insects and pathogens. This approach

139 would contribute fundamental insight to plant ecology and evolution and help to
140 contribute to a greater degree of evolutionary-thinking in agricultural weed management.

141

142 **The evolutionary ecology of agricultural weeds**

143 *Selection for weediness in agricultural landscapes.* Weed adaptation has two
144 prerequisites, genetic variation (see section on *Genetic variation in weed populations*)
145 and selection pressure. Selection pressure may be imposed by (i) local climatic and
146 environmental conditions and (ii) crop and weed management practices, and this
147 selection can result in locally-adapted weed ecotypes. Climatic and/or environmental
148 selection is likely to result in regional or clinal patterns of differentiation between weed
149 populations (Ray & Alexander, 1966; Warwick & Marriage, 1982; Weaver *et al.*, 1985;
150 Warwick *et al.*, 1984; Cavers, 1985; Dunbabin & Cocks, 1999; Michael *et al.*, 2006).
151 From a weed management perspective, this regional variation may be important for
152 determining regional weed problems, for driving range expansions in agricultural weeds
153 (Warwick 1990) and for determining the ability of weed populations to adapt to climate
154 change (Ghersa & León, 1999; Fuhrer 2003).

155 Within a region, agricultural landscapes can potentially vary at a much finer
156 spatial (field to field) and temporal (year to year) scale when diverse crop and weed
157 management is practiced. Theoretical models and experimental evolutionary studies have
158 demonstrated that fine-grained habitats reduce the selection for specialist genotypes
159 (Kassen & Bell, 1998; Sultan & Spencer 2002; Weinig & Schmitt 2004). At a weed
160 population and species level, this environmental heterogeneity should reduce selection for
161 highly adapted, specialist crop mimics (Barrett 1983) and herbicide resistant genotypes.

162 At the weed community level, environmental heterogeneity will prevent communities
163 from becoming dominated by a few, highly adapted, competitive weed species (see next
164 section). Notwithstanding the theoretical benefits of environmental heterogeneity in weed
165 management, many agricultural landscapes are increasingly characterised by low crop
166 diversity with potential impacts for the selection of highly adapted weed genotypes.

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

178 Agricultural weed management that is informed by evolutionary ecology will
179 attempt to diversify selection for other weed adaptations by diversifying weed
180 management in both time and space across the agricultural landscape (Jordan & Jannink,
181 1997; Clements *et al.*, 2004). However, the genetic basis of other weed adaptations has
182 not been demonstrated and there are a number of practical limitations in testing these
183 theories on a field scale in weed populations. In view of this, we believe the most
184 promising approaches to demonstrate the generality of these principles may be simulation

185 modelling and experimental evolution experiments with model organisms (Reboud &
186 Bell, 1997; Kassen & Bell, 1998). The application of both of these approaches to inform
187 agricultural weed management is discussed further in following sections.

188

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

200 Management-induced changes in weed communities (often described as ‘species
201 shifts’) are sometimes discussed in terms of weed evolution, though the actual underlying
202 processes are ecological rather than evolutionary and related to the theories of community
203 assembly (Drake 1990; Booth & Swanton 2002) and ecological succession (Clements
204 1916; Ghera & León, 1999). There are numerous reports of weed ‘species-shifts’ that
205 have occurred in response to tillage systems (Derksen *et al.*, 1993; Buhler, 1995;
206 Swanton *et al.*, 1999), herbicides and genetically-modified herbicide-tolerant crops
207 (Hawes *et al.*, 2003; Owen, 2008), crop sowing date (Hald, 1999) and general changes in

208 cropping systems (Ball & Miller, 1993; Barberi & Mazzoncini, 2001; Fried et al., 2008).
209 Weed management that is more spatially and temporally diverse will reduce the evolution
210 of weed floras that are specifically selected by repeated management practices, resulting
211 in more functionally diverse weed communities. These communities will have less
212 potential for severe crop yield loss, less selection on individual weeds, fewer shifts in
213 community function, and greater value for provision of biodiversity and ecosystem
214 services.

215

216 *Genetic variation in weed populations.* There are widely diverging and largely
217 unresolved views regarding the extent and importance of genetic variation in agricultural
218 weed populations. Clements *et al.* (2004) proposed a conceptual model based on ‘a
219 dynamic tension between processes that reduce and restore genetic variation’ in weed
220 populations. Initial weed colonisation by a few individuals in agricultural habitats will
221 result in a founder effect (Mayr, 1963; Sahli *et al.*, 2008) and subsequent population
222 regulation by highly effective weed control measures will force populations through
223 genetic bottlenecks, further constraining genetic variation in weed populations (Barrett,
224 1988). In opposition to this, multiple introductions of non-native species will bring
225 together diverse genotypes and, in outcrossing species, this will result in novel gene
226 combinations, unleashing a wealth of genetic variation on which selection can act to
227 result in well-adapted weed genotypes (Ellstrand & Schierenbeck, 2000).

228 Genetic variation within and between weed populations has mainly been
229 estimated using neutral genetic markers and contrasting results have emerged from
230 studies on genetic variation in invasive weeds. In *Pennisetum steaceum*, global

231 monoclonality was observed following the invasion of a single super-genotype (Le Roux
232 et al., 2007). By contrast, for some invasive species such as *Ambrosia artemisiifolia*
233 higher levels of genetic variation have been found when compared to native populations
234 (Genton et al., 2005), probably as a result of multiple introductions that buffered the loss
235 of genetic variation associated with bottlenecks (Chapman et al. 2004, Wang et al. 2008).
236 In arable weeds, the expectation for low levels of genetic variation has been confirmed
237 for a few species (Hamrick *et al.*, 1979; Barrett & Richardson, 1985; Novak & Mack,
238 1993). However, as observed for invasive weeds, other studies have demonstrated high
239 levels of genetic variation within and between weed populations (Warwick *et al.*, 1984;
240 Weaver *et al.*, 1985; Leiss & Müller-Schärer, 2001; Ianetta *et al.*, 2007; Menchari *et al.*,
241 2007).

242 The use of estimates of variation at neutral genetic markers as a measure of
243 adaptive potential in weed populations may be ill-founded. Heterogeneous selection has
244 little impact on neutral genetic differentiation especially in highly outcrossing species (Le
245 Corre and Kremer, 2003) and studies have shown that neutral intra-population genetic
246 variation does not always correlate to genetic variation associated with phenotypic traits
247 under selection in plant populations (Merilä and Crnokrak 2001; Reed and Frankham
248 2001). We believe there is an urgent need for more studies in weeds to assess whether
249 genetic variation estimated using neutral genetic markers is an accurate estimate of
250 genetic variation for adaptive traits (Menchari et al., 2007; Sahli et al., 2008).

251 Weed adaptation in response to environmental change may result from selection
252 of new mutations (i.e. spontaneous mutations) or alleles from the standing genetic
253 variation (Orr and Betancourt, 2001). “New mutations” mean that adaptive traits appear

254 in a weed population after the imposition of the selective pressure, while “standing
255 genetic variation” means that adaptive traits segregate in unexposed populations. The
256 source of genetic variation for adaptive traits may be of primary importance for the
257 outcome of a selective process (Hermisson and Pennings, 2005), and may dictate the best
258 weed management strategy to adopt (Neve & Powles, 2005a; Roux *et al.*, 2008). When
259 adaptation originates from standing genetic variation, the fixation probability of an allele
260 depends on its deleterious and beneficial effects before and after the environmental
261 change, respectively. In contrast, the evolutionary trajectories of “new mutations” in a
262 population depend on the net fitness effect associated to the adaptive allele (Orr, 1998;
263 Barton and Keightley, 2002). Striking examples of standing genetic variation comes from
264 the detection of herbicide resistant plants in *Lolium rigidum* populations never previously
265 exposed to any herbicide (Preston and Powles, 2002; Neve & Powles, 2005b). Further
266 studies to determine the extent and structure of genetic variation that underpins that
267 potential for weed adaptation are required.

268

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

270 There can be no clearer demonstration of the evolutionary potential of weeds than the
271 rapid and widespread evolution of resistance to herbicides (Powles & Shaner, 2001). The
272 propensity for evolution of resistance varies, with some species and herbicides being
273 more prone to resistance than others (Heap & LeBaron, 2001). In the most extreme cases,
274 resistance has evolved following exposure of no more than 3 or 4 generations of a weed
275 population to a herbicide (Powles & Holtum, 1994). Herbicide resistance is arguably the
276 single largest global weed management issue and studies concerned with herbicide

277 resistance are at the forefront of current weed science research. Given this, it seems
278 logical that evolutionary biology should play a central role in informing solutions to this
279 escalating problem, yet to the contrary, it is our view that herbicide resistance research
280 most starkly highlights the lack of evolutionary-thinking in weed science.

281 The majority of herbicide resistance research is conducted retrospectively. A
282 suspected resistant population is reported, seed is collected from surviving plants in the
283 field and the dose response curve of the suspected resistant and a known susceptible
284 population are compared under controlled glasshouse or field conditions. Following
285 confirmation of resistance, further physiological, genetic and molecular characterisation
286 is conducted to diagnose the resistance mechanism. These studies are important for
287 characterising new mechanisms of resistance, but endless descriptions of the same
288 mechanism in a different species or from a different cropping system provide rapidly
289 diminishing returns in terms of their ability to better inform resistance management
290 (Cousens, 1999; Neve, 2007). Indeed, it seems that weed researchers have become overly
291 concerned with describing the outcome of resistance evolution to the detriment of studies
292 that seek to better understand the process of selection for resistance. We believe this is a
293 reflection of the alignment of weed science with crop science and physiology, rather than
294 the disciplines of plant ecology and evolution. It also represents a missed opportunity for
295 herbicide resistance research to combine applied management advice with fundamental
296 insight into evolutionary ecology as has been the case in insecticide resistance studies
297 (Lenormand *et al.*, 1999; Tabashnik *et al.*, 2004).

298

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

319 The potential for reduced herbicide application rates to accelerate evolution of
320 resistance has been keenly debated (Gressel, 2002; Beckie & Kirkland, 2003; Neve, 2007)
321 and has practical significance given economic and environmental incentives to reduce

322 herbicide application rates. Low doses of the ACCase-inhibiting herbicide diclofop-
323 methyl have been shown to rapidly select for resistance to very much higher doses via the
324 selection and reassortment of minor genes in *Lolium rigidum*, an outcrossing species
325 (Neve & Powles, 2005a). This phenomenon has also been demonstrated for low dose
326 selection with glyphosate in *L. rigidum*, though the response to selection was less marked
327 (Busi & Powles, 2009). These results suggest a high degree of additive genetic variation
328 for herbicide susceptibility in a weed population never previously exposed to herbicides.
329 High herbicide doses during the initial stages of selection would have prevented selection
330 and reassortment of minor genes into highly resistant phenotypes. Even accepting that the
331 majority of field-evolved herbicide resistance is endowed by single major genes, it is
332 possible that initial selection at low doses is for putative minor genes, resulting in reduced
333 herbicide efficacy, larger population sizes and an ultimately higher probability of
334 subsequent selection for major gene resistance. The ‘low dose’ question also highlights
335 the importance of understanding the process, rather than simply the outcome of selection
336 for resistance.

337 Evolutionary biology, population genetics and physiology all suggest that evolved
338 resistance to novel pesticides will be associated with a fitness cost (Coustau *et al.*, 2000).
339 These costs may be environment-specific (Plowman *et al.*, 1999; Salzman *et al.*, 2008)
340 and they may only be manifest at certain life history stages (Vila-Aiub *et al.*, 2005; Roux
341 *et al.* 2005). Knowledge of the extent of these costs and of their environment- and life
342 history-specific attributes may be crucial for designing ‘biorational management tactics’
343 which could turn the costs and idiosyncrasies associated with resistance into valuable
344 tools in resistance management (Jordan *et al.*, 1999). There have been some excellent

345 studies of herbicide resistance fitness costs. However, in many other cases, the concept of
346 fitness as it relates to herbicide resistance has been poorly understood and many
347 published studies have used wholly inappropriate methods to quantify fitness costs. Many
348 studies have compared resistant (R) and susceptible (S) populations with completely
349 different genetic backgrounds. Numerous studies have also mistakenly made the
350 assumption that comparative growth rate alone is a proxy for fitness. Perhaps more than
351 in any other case, these widespread and repeated faults in fitness studies highlight the
352 application in weed science of methods from crop breeding and physiology rather than
353 from ecology and evolution.

354 Some fitness studies have used isogenic (R) and (S) lines to demonstrate fitness
355 costs associated with triazine resistance in standardised genetic backgrounds (Gressel &
356 Bensinai, 1985; McCloskey & Holt, 1990; Arntz *et al.*, 2000; Salzman *et al.*, 2008).
357 While accepting that isogenic lines are the gold standard for unequivocally demonstrating
358 fitness costs, we suggest that future research should also compare fitness between plants
359 arising from controlled crosses of R and S plants (Menchari *et al.*, 2008) or where plant
360 cloning techniques have enabled the identification and propagation of discrete R and S
361 phenotypes from single populations (Vila-Aiub *et al.*, 2005; Pedersen *et al.*, 2007). In this
362 way, fitness of R alleles can be compared in a broader range of genetic backgrounds,
363 reflecting more closely the situation in natural populations. Wherever possible, fitness
364 studies that have proper control of genetic background should also report the molecular
365 genetic basis of resistance, measure fitness and fitness components at a range of life
366 history stages, under competitive conditions and in a range of environments.

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

377

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

390 Model organisms and mathematical models that simulate evolution of resistance
391 may each have features that overcome some of the difficulties described above, though
392 for some purposes their relevance to the field may be questioned. Simulation models
393 (Maxwell *et al.*, 1990; Diggle *et al.*, 2003; Jacquemin *et al.*, 2008) may be relatively
394 inexpensive to develop and enable rapid comparisons of resistance management
395 strategies over many generations. These models may be used solely to explore the
396 relative importance of parameters that underpin resistance evolution or to address very
397 specific cropping system-related questions (Neve *et al.*, 2003). However, in some cases, a
398 lack of understanding of key model parameters such as the fitness costs associated with R
399 alleles, the extent of standing genetic variation for herbicide resistance and gene flow
400 between metapopulations is hampering further model development and application. As
401 these parameters become available new models incorporating quantitative genetics,
402 demographics and metapopulation dynamics can begin to explore some of the important
403 questions discussed in the preceding sections and relating to the direct or interacting
404 effects of (i) the impact of fitness costs on initial R allele frequency before the first
405 herbicide exposure and resistance trajectories, (ii) the evolution of fitness costs by
406 compensatory evolution, (iii) the relative contribution of major gene and quantitative
407 resistance and the role of herbicide dose and (iv) the impact of environmental
408 heterogeneity, degree of connectedness among patches and cropping systems on the
409 evolution of herbicide resistance.

410 Model organisms may be useful in their own right for developing experimental
411 evolutionary approaches (Elena & Lenski, 2003) to study the dynamics of evolution of
412 herbicide resistance. For example, the unicellular chlorophyte, *Chlamydomonas*

413 *reinhardtii* reproduces rapidly, and millions of individuals can be cultured in a few
414 millilitres of liquid medium. It is also susceptible to many herbicides (Reboud, 2002) and
415 has been used as a model experimental organism in herbicide resistance research (Reboud
416 *et al.*, 2007). Model organisms, such as *Arabidopsis thaliana* may also provide valuable
417 insight for important parameters that drive resistance evolution (Jander *et al.*, 2003). A
418 series of studies examining costs associated with herbicide resistance alleles in *A.*
419 *thaliana* has provided valuable insights for models of herbicide resistance evolution as
420 well as demonstrating the potential for herbicide resistance to provide fundamental
421 insight into the evolutionary genetics of plant adaptation (Roux *et al.*, 2004, 2005; Roux
422 & Reboud, 2005).

423

424 **Modelling weed life histories and population dynamics**

425 Mathematical models have become important tools in weed science to understand weed
426 biology and population dynamics and to predict the long and short term responses of
427 weed populations to management (reviewed in Holst *et al.*, 2007). Most population
428 dynamics models have a simple demographic model as their basis (Cousens & Mortimer,
429 1995). These models are usually parameterised from empirical data gathered for a single
430 population of the species being considered and parameter values generally represent the
431 mean response of the population, so that intra-population variability is not incorporated.
432 As a result, these models have some practical limitations; predictions may be population-
433 specific and the potential for ongoing local adaptation to weed management is not
434 accounted for.

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

450 These challenges will require new modelling approaches that integrate
451 quantitative genetics with demographic and environmental stochasticity. Population
452 dynamics models have been developed which incorporate simple population genetics to
453 simulate the evolution of herbicide resistance (Maxwell *et al.*, 1990; Diggle *et al.*, 2003).
454 However, modelling the response of quantitative traits such as weed seed dormancy and
455 flowering time to environmentally- or management-derived selection may not be so
456 straightforward as it has been for major gene herbicide resistance. These traits are likely
457 polygenically-controlled, subject to complex patterns of genetic co-variation and there

458 will be trade-offs and correlations between traits such as germination timing, flowering
459 time and fecundity (Weiner, 1990; Franks & Weiss, 2008; Wilczek *et al.*, 2009). Jordan
460 (1989) used multivariate selection analysis (Lande & Arnold 1983) to predict the
461 evolutionary response of coastal populations of *Diodea teres* to selection in an
462 agricultural habitat and this method would appear to have some wider application for
463 understanding and modelling weed adaptation. ‘Demo-genetic’ models that incorporate
464 demographic and environmental stochasticity with quantitative genetics at the
465 metapopulation level have been recently developed in the field of conservation genetics
466 to address questions of population persistence and adaptation in small populations of
467 endangered species (Kirchner *et al.*, 2006; Willi & Hoffman 2008). For conservation
468 geneticists these models are used to explore which combinations of demographic and
469 genetic factors will promote population persistence. Conversely, in the case of weed
470 management we are interested in combinations of factors that will reduce persistence and
471 adaptation. Nevertheless, similar ‘demo-genetic models’ may have utility for predicting
472 population level responses of weed species under changing management and climatic
473 conditions.

474

475 **Climate change impacts on weed biology and management**

476 The positive impacts of increased atmospheric CO₂ (Ainsworth & Long, 2005) and the
477 negative effects of elevated ozone levels and higher temperatures (Morgan *et al.*, 2006;
478 Ainsworth, 2008) on crop yield under climate change are well known. The actual crop
479 yields attained in future climates will depend on the effects of climate change on weed,
480 pest and disease populations and on crop interactions with these organisms (Fuhrer, 2003).

481 From a weeds perspective, there are two key questions, i) how will climate change impact
482 crop-weed competition and ii) what is the potential for agricultural weeds to rapidly adapt
483 to changing climates? The presence of weeds in a soybean crop has been shown to reduce
484 the ability of the crop to respond positively to elevated CO₂. When competing with the C₃
485 weed, *Chenopodium album*, relative soybean yield reduction was greatest at higher CO₂
486 levels. Competition with the C₄ weed, *Amaranthus retroflexus* was less intense at
487 elevated CO₂, suggesting that competition from C₃ weeds may increase under climate
488 change (Ziska 2000). Climate change may also result in range expansion through
489 ecotypic differentiation and the ability for rapid colonisation in agricultural weeds,
490 associated with northward range expansion in North America has been shown previously
491 (Warwick *et al.*, 1984; Weaver *et al.*, 1985; Warwick, 1990). There has been no research
492 to specifically examine the potential for agricultural weeds to rapidly adapt to climate
493 change, though elevated CO₂ has been shown to increase the dominance of invasive plant
494 species in natural communities (Smith *et al.*, 2000). Other research has demonstrated how
495 projected climate change may alter the phenology of reproductive and other life history
496 processes in plant populations from natural ecosystems (Cleland *et al.* 2006; Sherry *et al.*,
497 2007). Similar phenological changes in agricultural weeds could significantly alter crop-
498 weed interactions and recent work by Franks & Weis (2007, 2008) has shown the
499 potential for rapid life history evolution in response to climate change in the annual
500 weedy plant, *Brassica rapa*.

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

504

505 **Evolution, Ecology and Agricultural Weeds**

506 Calls for a greater integration of evolutionary-thinking into weed biology and
507 management have been made previously (Jordan & Jannink, 1997; Clements *et al.*, 2004),
508 yet there remains little evidence for this integration in practice. Publications addressing
509 the importance and extent of genetic diversity, intra- and inter-population variability and
510 adaptation in agricultural weeds (Harper, 1956; Cavers, 1985; Warwick, 1986, 1987)
511 have declined since the 1980's. Indeed, there appears to have been a general decline in
512 the number of studies addressing the fundamentals of agricultural weed biology in the last
513 20-30 years. There may be many reasons for this decline, but the rise to prominence of
514 herbicides and the associated simplification of weed management is a likely key factor. In
515 response to this over-reliance on herbicides, evolution of resistance has occurred in
516 agroecosystems worldwide (Powles & Shaner, 2001), yet evolutionary-thinking is even
517 lacking in much herbicide resistance research (Neve, 2007).

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

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

540

541 **References**

542 **Ainsworth EA, Long SP. 2005.** What have we learned from 15 years of free-air CO₂
543 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy
544 properties and plant production to rising CO₂. *New Phytologist* **165**: 251-371.

545 **Ainsworth EA. 2008.** Rice production in a changing climate: a meta-analysis of
546 responses to elevated carbon dioxide and elevated ozone concentration. *Global Change*
547 **14**: 1642-1650.

548 **Andersson DI. 2003.** Persistence of antibiotic resistant bacteria. *Current Opinion in*
549 *Microbiology* **6**: 452-456.

550 **Arntz AM, Delucia EH, Jordan N. 2000.** Fitness effects of a photosynthetic mutation
551 across contrasting environments. *Journal of Evolutionary Biology* **13**: 792-803.

552 **Ashley MV, Willson MF, Pergams ORW, O'Dowd DJ, Gende SM, Brown JS. 2003.**
553 Evolutionarily enlightened management. *Biological Conservation* **111**: 115-123.

554 **Baker HG. 1965.** Characteristics and modes of origins of weeds. In: Baker HG, Stebbins
555 GL, eds. *The Genetics of Colonizing Species*. New York, USA: Academic Press, 147-168.

556 **Baker HG. 1974.** The evolution of weeds. *Annual Review of Ecology and Systematics* **5**:
557 1-24.

558 **Ball DA, Miller SD. 1993.** Cropping history, tillage and herbicide effects on weed flora
559 composition in irrigated corn. *Agronomy Journal* **85**: 817-821.

560 **Barberi P, Mazzoncini M. 2001.** Changes in weed community composition as
561 influenced by cover crop and management system in continuous corn. *Weed Science* **49**:
562 491-499.

563 **Barrett SCH. 1983.** Crop mimicry in weeds. *Economic Botany* **37**: 255-282.

564 **Barrett SCH, Richardson BJ. 1985.** Genetic attributes of invading species. In Groves
565 RH, Burdon JJ, eds. *Ecology of Biological Invasions: An Australian Perspective.*
566 Canberra, Australia: Academy of Science, 21-33.

567 **Barrett SCH. 1988.** Genetics and evolution of agricultural weeds. In: Altieri MA,
568 Liebman M, eds. *Weed Management in Agroecosystems: Ecological Approaches.* Boca
569 Raton, USA, CRC Press, 57-76.

570 **Barton NH, Keightley PD. 2002.** Understanding quantitative genetic variation. *Nature*
571 *Reviews Genetics* **3**: 11-21.

572 **Beckie HJ, Kirkland KJ. 2003.** Implication of reduced herbicide rates on resistance
573 enrichment in wild oat (*Avena fatua*). *Weed Technology* **17**: 138-148.

574 **Beckie HJ, Hall LM, Meers S, Laslo JJ, Stevenson SC. 2004.** Management practices
575 influencing herbicide resistance in wild oats. *Weed Technology* **18**: 853-859.

576 **Booth BD, Swanton CJ. 2002.** Assembly theory applied to weed communities. *Weed*
577 *Science* **50**: 2-13.

578 **Buhler DD. 1995.** Influence of tillage systems on weed population dynamics and
579 management in corn and soybean in the central USA. *Crop Science* **35**: 1247-1258.

580 **Burnside OC. 1993.** Weed Science – the step child. *Weed Technology* **7**: 515-518.

581 **Busi R, Powles SB. 2009.** Evolution of glyphosate resistance in a *Lolium rigidum*
582 population by glyphosate selection at sublethal doses. *Heredity* doi: 10.1038/hdy.2009.64.

583 **Carroll SP, Hendry AP, Reznick DN, Fox CW. 2007.** Evolution on ecological time-
584 scales. *Functional Ecology* **21**: 387-393.

585 **Cavers PB. 1985.** Intractable weeds – intraspecific variation must be considered in
586 formulating control measures. In: *Proceedings of the 1985 British Crop Protection*
587 *Conference – Weeds*, Brighton, UK, 367-376.

588 **Chapman H, Robson B, Pearson ML. 2004.** Population genetic structure of a
589 colonising, triploid weed, *Hieracium lepidulum*. *Heredity* **92**: 182-188.

590 **Cleland EE, Chiarello NR, Loarie SR, Mooney HA, Field CB. 2006.** Diverse
591 responses of phenology to global changes in a grassland ecosystem. *Proceedings of the*
592 *National Academy of Sciences* **103**: 13740-13744.

593 **Clements FE. 1916.** *Plant Succession: An Analysis of the Development of Vegetation*.
594 Washington DC, USA: Carnegie Institute of Washington.

595 **Clements DR, DiTomasso A, Jordan N, Booth BD, Cardina J, Doohan D, Mohler**
596 **CL, Murphy SD, Swanton CJ. 2004.** Adaptability of plants invading North American
597 cropland. *Agriculture, Ecosystems and Environment* **104**: 379-398.

598 **Cocker KM, Moss SR, Coleman JOD. 1999.** Multiple mechanisms of resistance to
599 fenoxaprop-P-ethyl in United Kingdom and other European populations of herbicide-
600 resistant *Alopecurus myosuroides* (Black-grass). *Pesticide Biochemistry & Physiology* **65**:
601 169-180.

602 **Connell JH. 1978.** Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-
603 1310.

604 **Cousens R, Mortimer AM. 1995.** *Dynamics of Weed Populations*. Cambridge, UK:
605 Cambridge University Press.

606 **Cousens R. 1999.** Weed science doesn't have to be a contradiction in terms. In: Bishop
607 AC, Boersma M, Barnes CD, eds. *Proceedings of the Twelfth Australian Weeds*
608 *Conference*. Hobart, Australia. Tasmanian Weed Society, 364-371.

609 **Coustau C, Chevillon C, Ffrench-Constant R. 2000.** Resistance to xenobiotics and
610 parasites : can we count the cost ? *Trends in Ecology and Evolution* **15**: 378-383.

611 **Dauer JT, Luschei EC, Mortensen DA. 2009.** Effects of landscape composition on
612 spread of an herbicide-resistance weed. *Landscape Ecology* **24**: 735-747.

613 **Derksen DA, Lafond GP, Thomas AG, Loepky HA, Swanton CJ. 1993.** Impact of
614 agronomic practices on weed communities: Tillage systems. *Weed Science* **41**: 409-417.

615 **Diggle AD, Neve PB, Smith FP. 2003.** Herbicides used in combination reduce the
616 probability of herbicide resistance in finite weed populations. *Weed Research* **43**: 371-
617 382.

618 **Drake JA. 1990.** The mechanics of community assembly and succession. *Journal of*
619 *Theoretical Biology* **147**: 213-233.

620 **Dunbabin MT, Cocks PS. 1999.** Ecotypic variation for seed dormancy contributes to the
621 success of capeweed (*Arctotheca calendula*) in Western Australia. *Australian Journal of*
622 *Agricultural Research* **50**: 1451-1458.

623 **Elena SF, Lenski RE. 2003.** Evolution experiments with microorganisms: the dynamics
624 and genetic bases of adaptation. *Nature Reviews Genetics* **4**: 457-469.

625 **Ellstrand NC, Schierenbeck KA. 2000.** Hybridization as a stimulus for the evolution of
626 invasiveness in plants. *Proceedings of the National Academy of Sciences* **87**: 7043-7050.

627 **Fernandez-Quintanilla C, Quadranti M, Kudsk P, Bàrberi P. 2008.** Which future for
628 weed science? *Weed Research* **48**: 297-301.

629 **Franks SJ, Weis AE. 2007.** Rapid evolution of flowering time by an annual plant in
630 response to a climate fluctuation. *Proceedings of the National Academy of Sciences* **104**:
631 1278-1282.

632 **Franks SJ, Weis AE. 2008.** A change in climate causes rapid evolution of multiple life-
633 history traits and their interactions in an annual plant. *Journal of Evolutionary Biology* **21**:
634 1321-1334.

635 **Fried G, Norton LR, Reboud X. 2008.** Environmental and management factors
636 determining weed species composition and diversity in France. *Agriculture Ecosystems &*
637 *Environment* **128**: 68-76.

638 **Fuhrer J. 2003.** Agroecosystem responses to combinations of elevated CO₂, ozone and
639 global climate change. *Agriculture Ecosystems and Environment* **97**: 1-20.

640 **Genton BJ, Shykoff JA, Giraud T. 2005.** High genetic diversity in French invasive
641 populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources
642 of introduction. *Molecular Ecology* **14**: 4275-4285.

643 **Ghersa, CM, León RJC. 1999.** Successional changes in the agroecosystems of the
644 rolling Pampas. In: Walker LR, ed. *Ecosystems of the World. Ecosystems of Disturbed*
645 *Ground*. Amsterdam, The Netherlands: Elsevier, 487-502.

646 **Gressel J. 2002.** *Molecular Biology of Weed Control*. London, UK: Taylor & Francis.

647 **Gressel J, Bensinai G. 1985.** Low intraspecific competitive fitness in a triazine-resistant,
648 nearly nuclear-isogenic line of *Brassica napus*. *Plant Science* **38**: 29-32.

649 **Grime JP. 2002.** *Plant Strategies, Vegetation Processes, and Ecosystem Properties*:
650 Wiley.

651 **Hairston Jr NG, Ellner SP, Geber MA, Yoshida T, Fox JA. 2005.** Rapid evolution and
652 the convergece of ecological and evolutionary time. *Ecology Letters* **8**: 1114-1127.

653 **Hald AB. 1999.** The impact of changing the season in which cereals are sown on the
654 diversity of the weed flora in rotational fields in Denmark. *Journal of Applied Ecology* **36**:
655 24-32.

656 **Hamrick JL, Linhart YB, Mitton JB. 1979.** Relationships between life history
657 characteristics and electrophoretically detectable genetic variation in plants. *Annual*
658 *Review of Ecology and Systematics* **10**: 173-200.

659 **Harper JL. 1956.** The evolution of weeds in relation to resistance to herbicides. In:
660 *Proceedings of the 1956 British Weed Control Conference*, Brighton, UK, 179-188.

661 **Hawes C, Haughton AJ, Osborne JL, Roy DB, Clark SJ, Perry JN, Rothery P,**
662 **Bohan DA, Brooks DR, Champion GT et al. 2003.** Response of plants and invertebrate
663 trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of
664 genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal*
665 *Society of London Series B – Biological Sciences* **358**: 1899-1913.

666 **Heap I. 2009.** The International Survey of Herbicide Resistant Weeds. Available at:
667 www.weedscience.com.

668 **Heap I, LeBaron H. 2001.** Introduction and overview of resistance. In: Powles SB,
669 Shaner DL, eds. *Herbicide Resistance and World Grains*. Boca Raton, USA: CRC Press,
670 1-22.

671 **Hermisson J, Pennings PS. 2005.** Soft sweeps: molecular population genetics of
672 adaptation from standing genetic variation. *Genetics* **169**: 2335-2352.

673 **Holst N, Rasmussen IA, Bastiaans L. 2007.** Field weed population dynamics: a review
674 of model approaches and applications. *Weed Research* **47**: 1-14.

675 **Ianetta PPM, Begg G, Hawes C, Young M, Russell J, Squire GR. 2007.** Variation in
676 *Capsella* (shepherd's purse): an example on intraspecific functional diversity.
677 *Physiologia Plantarum* **129**: 542-554.

678 **Jacquemin B, Gasquez J, Reboud X. 2008.** Modelling binary mixtures of herbicides in
679 populations resistant to one of the components: evaluation for resistance management.
680 *Pest Management Science* **65**: 113-121.

681 **Jander G, Baerson SR, Hudak JA, Gonzalez KA, Gruys KJ, Last RL. 2003.**
682 Ethylmethanesulfonate saturation mutagenesis in *Arabidopsis* to determine frequency of
683 herbicide resistance. *Plant Physiology* **131**: 139-146.

684 **Jordan N. 1989.** Predicted evolutionary response to selection for tolerance of Soybean
685 (*Glycine max*) and intraspecific competition in a nonweed population of poorjoe (*Diodia*
686 *teres*). *Weed Science* **37**: 451-457.

687 **Jordan NR, Jannink JL. 1997.** Assessing the practical importance of weed evolution: a
688 research agenda. *Weed Research* **37**: 237-246.

689 **Jordan N, Kelrick M, Brooks J, Kinerk W. 1999.** Biorational management tactics to
690 select against triazine-resistant *Amaranthus hybridus*: a field study. *Journal of Applied*
691 *Ecology* **36**: 123-132.

692 **Kassen R, Bell G. 1998.** Experimental evolution in *Chlamydomonas*. IV. Selection in
693 environments that vary through times at different scales. *Heredity* **80**: 732-741.

694 **Kirchner F, Robert A, Colas B. 2006.** Modelling the dynamics of introduced
695 populations in the narrow-endemic *Centaurea corymbosa*: a demo-genetic integration.
696 *Journal of Applied Ecology* **43**: 1011-1021.

697 **Lande R. 1983.** The response to selection on major and minor mutations affecting a
698 metrical trait. *Heredity* **50**: 47-65.

699 **Lande R & Arnold SJ. 1983.** The measurement of selection on correlated characters.
700 *Evolution* **37**: 1210-1226.

701 **Leiss KA, Müller-Schärer H. 2001.** Adaptation of *Senecio vulgaris* (Asteraceae) to
702 ruderal and agricultural habitats. *American Journal of Botany* **88**: 1593-1599.

703 **Lenormand T, Bourguet D, Guillemaud T, Raymond M. 1999.** Tracking the evolution
704 of insecticide resistance in the mosquito *Culex pipiens*. *Nature* **400**: 861-864.

705 **Le Corre V, Kremer A. 2003.** Genetic variability at neutral markers, Quantitative Trait
706 Loci and trait in a subdivided population under selection. *Genetics* **164**: 1205-1219.

707 **Le Roux JJ, Wiczorek AM, Wright MG, Tran CT. 2007.** Super-genotype: global
708 monoclonality defies the odds of nature. *PLoS One* **2(7)**: e590.

709 **Maxwell BD, Roush ML, Radosevich SR. 1990.** Predicting the evolution and dynamics
710 of herbicide resistance in weed populations. *Weed Technology* **4**: 2-13.

711 **Mayr E. 1963.** *Animal Species and Evolution*. Cambridge, USA: Harvard University
712 Press.

713 **McCloskey WB, Holt JS. 1990.** Triazine resistance in *Senecio vulgaris* parental and
714 nearly isonuclear backcrossed biotypes is correlated with reduced productivity. *Plant*
715 *Physiology* **92**: 954-962.

716 **Menchari Y, Délye C, Le Corre V. 2007.** Genetic variation and population structure in
717 black-grass (*Alopecurus myosuroides* Huds.), a successful, herbicide resistant, annual
718 grass weed of winter cereal fields. *Molecular Ecology* **16**: 3161-3172.

719 **Menchari Y, Chauvel B, Darmency H, Délye C. 2008.** Fitness costs associated with
720 three mutant acetyl coenzyme A carboxylase alleles endowing herbicide resistance in
721 black-grass *Alopecurus myosuroides*. *Journal of Applied Ecology* **45**: 939-947.

722 **Merilä J, Crnokrak P. 2001.** Comparison of genetic differentiation at marker loci and
723 quantitative traits. *Journal of Evolutionary Biology* **14**: 892–903.

724 **Michael PJ, Steadman KJ, Plummer JA. 2006.** Climatic regulation of seed dormancy
725 and emergence of diverse *Malva parviflora* populations from a Mediterranean-type
726 environment. *Seed Science Research* **16**: 273-281.

727 **Morgan PB, Mies TA, Bollero GA, Nelson RL, Long SP. 2006.** Season-long elevation
728 of ozone concentration to projected 2050 levels under fully open-air conditions
729 substantially decreases the growth and production of soybean. *New Phytologist* **170**: 333-
730 343.

731 **Mortensen DA, Bastiaans L, Sattin M. 2000.** The role of ecology in the development of
732 weed management systems: an outlook. *Weed Research* **40**: 49-62.

733 **Mortimer AM. 1997.** Phenological adaptation in weeds – an evolutionary response to
734 the use of herbicides? *Pesticide Science* **51**: 299-304.

735 **Moss SR, Perryman SAM, Tatnell LV. 2007.** Managing herbicide-resistant blackgrass
736 (*Alopecurus myosuroides*): Theory and Practice. *Weed Technology* **21**: 300-309.

737 **Naylor REL, Lutman PJ. 2002.** What is a weed? In: Naylor REL, ed. *Weed*
738 *Management Handbook, ninth edition*. Oxford, UK: Blackwell Publishing, 1-16.

739 **Neve P, Diggle AD, Smith FP, Powles SB. 2003.** Simulating evolution of glyphosate
740 resistance in *Lolium rigidum* II: past, present and future glyphosate use in Australian
741 cropping. *Weed Research* **43**: 418-427.

742 **Neve P, Sadler J, Powles SB. 2004.** Multiple resistance to selective herbicides in a
743 glyphosate resistant *Lolium rigidum* population from the Western Australian wheatbelt.
744 *Weed Science* **52**: 231-239.

745 **Neve P, Powles SB. 2005a.** Recurrent selection with reduced herbicide rates results in
746 the rapid evolution of herbicide resistance in *Lolium rigidum*. *Theoretical and Applied*
747 *Genetics* **110**: 1154-1166.

748 **Neve P, Powles SB. 2005b.** High survival frequencies at low herbicide use rates in
749 populations of *Lolium rigidum* result in rapid evolution of herbicide resistance. *Heredity*,
750 **95**: 485-492.

751 **Neve P. 2007.** Challenges for herbicide resistance evolution and management: 50 years
752 after Harper. *Weed Research* **47**: 365-369.

753 **Novak SJ, Mack RN. 1993.** Genetic variation in *Bromus tectorum* (Poaceae):
754 Comparison between native and introduced populations. *Heredity* **71**: 167-176.

755 **Oerke EC. 2006.** Crop losses to pests. *Journal of Agricultural Science* **144**: 31-43.

756 **Orr HA. 1998.** The population genetics of adaptation: the distribution of factors fixed
757 during adaptive evolution. *Evolution* **52**: 935-949.

758 **Orr HA, Betancourt AJ. 2001.** Haldane's sieve and adaptation from standing genetic
759 variation. *Genetics* **157**: 875-884.

760 **Owen MDK. 2008.** Weed species shifts in glyphosate-resistant crops. *Pest Management*
761 *Science* **64**: 377-387.

762 **Patterson DT. 1985.** Comparative ecophysiology of weeds and crops. In: Duke SO, ed.
763 *Weed Ecophysiology Volume 1. Reproduction and Ecophysiology*. Boca Raton, USA: CRC
764 Press, 101-130.

765 **Pedersen BP, Neve P, Andreasen C, Powles SB. 2007.** Ecological fitness of a
766 glyphosate-resistant *Lolium rigidum* population: growth and seed production along a
767 competition gradient. *Basic and Applied Ecology* **8**: 258-268.

768 **Pimentel D, Lach L, Zuniga R, Morrison D. 2000.** Environmental and economic costs
769 of nonindigenous species in the United States. *BioScience* **50**: 53-65.

770 **Plowman AB, Richards AJ, Tremayne MA. 1999.** Environmental effects on the fitness
771 of triazine-resistant and triazine-susceptible *Brassica rapa* and *Chenopodium album* in
772 the absence of herbicide. *New Phytologist* **141**: 471-485.

773 **Powles SB, Holtum JAM. 1994.** *Herbicide Resistance in Plants: Biology and*
774 *Biochemistry*. Boca Raton, USA: CRC Press.

775 **Powles SB, Shaner DL. 2001.** *Herbicide Resistance and World Grains*. Boca Raton,
776 USA: CRC Press.

777 **Powles SB. 2008.** Evolved glyphosate-resistant weeds around the world: lessons to be
778 learnt. *Pest Management Science* **64**: 360-365.

779 **Preston C, Powles SB. 2002.** Evolution of herbicide resistance in weeds: initial
780 frequency of target-site based resistance to acetolactate synthase-inhibiting herbicides in
781 *Lolium rigidum*. *Heredity* **88**: 8-13.

782 **Ray PM, Alexander WE. 1966.** Photoperiodic adaptation to latitude in *Xanthium*
783 *strumarium*. *American Journal of Botany* **53**: 709-709.

784 **Reboud X. 2002.** Response of *Chlamydomonas reinhardtii* to herbicides: Negative
785 relationship between toxicity and water solubility across several herbicide families.
786 *Bulletin of Environmental Contamination and Toxicology* **69**: 554-561.

787 **Reboud X, Bell G. 1997.** Experimental evolution in *Chlamydomonas* III. Evolution of
788 specialist and generalist types in environments that vary in time and space. *Heredity* **78**:
789 507-514.

790 **Reboud X, Majerus N, Gasquez J, Powles SB. 2007.** *Chlamydomonas reinhardtii* as a
791 model system for pro-active herbicide resistance evolution research. *Biological Journal*
792 *of the Linnean Society* **91**: 257-266.

793 **Reed DH, Frankham R. 2001.** How closely related are molecular and quantitative
794 measures of genetic variation? A meta-analysis. *Evolution* **55**: 1095–1103.

795 **Roux F, Gasquez J, Reboud X. 2004.** The dominance of the herbicide resistance cost in
796 several *Arabidopsis thaliana* mutant lines. *Genetics* **166**: 449-460.

797 **Roux F, Camilleri C, Giancola S, Brunel D, Reboud X. 2005.** Epistatic interactions
798 among herbicide resistances in *Arabidopsis thaliana*: The fitness cost of multiresistance.
799 *Genetics* **171**: 1277-1288.

800 **Roux F, Reboud X. 2005.** Is the cost of herbicide resistance expressed in the breakdown
801 in the relationships between characters? A cast study using synthetic auxin-resistant
802 *Arabidopsis thaliana* mutants. *Genetical Research* **85**: 101-110.

803 **Roux F, Giancola S, Durand S, Reboud X. 2006.** Building an experimental cline with
804 *Arabidopsis thaliana* to estimate herbicide fitness cost. *Genetics* **173**: 1023-1031.

805 **Roux F, Paris M, Reboud X. 2008.** Delaying weed adaptation to herbicide by
806 environmental heterogeneity: A simulation approach. *Pest Management Science* **64**(1):
807 16-29.

808 **Ruegg WT, Quadranti M, Zoschke A. 2007.** Herbicide research and development:
809 Challenges and opportunities. *Weed Research* **47**: 271-275.

810 **Ryan GF. 1970.** Resistance of common groundsel to simazine and atrazine. *Weed*
811 *Science* **18**; 614-616.

812 **Sahli HF, Conner JK, Shaw FH, Howe S, Lale A. 2008.** Adaptive differentiation of
813 quantitative traits in the globally distributed weed, wild radish (*Raphanus raphanistrum*).
814 *Genetics* **180**: 945-955.

815 **Salzmann D, Handley RJ, Mueller-Scharer H. 2008.** Functional significance of
816 triazine-herbicide resistance in defence of *Senecio vulgaris* against a rust fungus. *Basic*
817 *and Applied Ecology* **9**: 577-587.

818 **Sherry RA, Zhou X, Gu S, Arnone III JA, Schimel DS, Verburg PS, Wallace LL,**
819 **Luo Y. 2007.** Divergence of reproductive phenology under climate warming.
820 *Proceedings of the National Academy of Sciences* **104**: 198-202.

821 **Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS,**
822 **Fenstermaker LK, Seemann JR, Nowak RS. 2000.** Elevated CO₂ increases
823 productivity and invasive species success in an arid ecosystem. *Nature* **408**: 79-82.

824 **Sultan SE, Spencer HG, 2002.** Metapopulation structure favours plasticity over local
825 adaptation. *American Naturalist* **160**: 271-283.

826 **Swanton CJ, Shrestha A, Roy RC, Call-Coelho BR, Knezevic SZ. 1999.** Effect of
827 tillage systems, N, and cover crop on the composition of weed flora. *Weed Science* **47**:
828 454-461.

829 **Tabashnik BE, Gould F, Carriere Y. 2004.** Delaying evolution of insect resistance to
830 transgenic crops by decreasing dominance and heritability. *Journal of Evolutionary*
831 *Biology* **17**: 904-912.

832 **Tardif FJ & Powles SB. 1994.** Herbicide multiple-resistance in a *Lolium rigidum*
833 biotype is endowed by multiple mechanisms: isolation of a subset with resistant acetyl-
834 CoA carboxylase. *Physiologia Plantarum* **91**: 488-494.

835 **Thompson JN. 1998.** Rapid evolution as an ecological process. *Trends in Ecology and*
836 *Evolution* **13**: 329-332.

837 **Van Acker RC. 2009.** Weed biology serves practical weed management. *Weed Research*
838 **49**: 1-5.

839 **Van Valen L. 1973.** A new evolutionary law. *Evolutionary Theory* **1**: 1-30.

840 **Vila-Aiub MM, Neve P, Powles SB. 2005.** Resistance cost of a cytochrome P450
841 herbicide metabolism mechanism but not an ACCase target site mutation in a multiple
842 resistant *Lolium rigidum* population. *New Phytologist* **167**: 787-796.

843 **Wang T, Su Y, Chen G. 2008.** Population genetic variation and structure of the invasive
844 weed *Mikania micrantha* in southern China : consequences of rapid range expansion.
845 *Journal of Heredity* **99**: 22-33.

846 **Warwick SI, Marriage PB. 1982.** Geographical variation in populations of
847 *Chenopodium album* resistant and susceptible to Atrazine II. Photoperiod and reciprocal
848 transplant studies. *Canadian Journal of Botany* **60**: 494-504.

849 **Warwick SI, Thompson BK, Black LD. 1984.** Population variation in *Sorghum*
850 *halepense*, Johnson grass, at the northern limit of its range. *Canadian Journal of Botany*
851 **62**: 1781-1789.

852 **Warwick SI. 1986.** Isozyme variation in proso millet (*Panicum miliaceum* L.). *Journal*
853 *of Heredity* **78**: 210-212.

854 **Warwick SI. 1987.** Genetic variation in Canadian and European populations of the
855 colonizing weed species, *Apera spica-venti*. *New Phytologist* **106**: 301-317.

856 **Warwick SI. 1990.** Allozyme and life history variation in five northwardly colonizing
857 North American weed species. *Plant Systematics and Evolution* **169**: 41-54.

858 **Weaver SE, Dirks VA, Warwick SI. 1985.** Variation and climatic adaptation in
859 northern populations of *Datura stramonium*. *Canadian Journal of Botany* **63**: 1303-1308.

860 **Weiner J. 1990.** Asymmetric competition in plant-populations. *Trends in Ecology &*
861 *Evolution*, **5**, 360-364.

862 **Weinig C, Schmitt J. 2004.** Environmental effects on the expression of quantitative trait
863 loci and implications for phenotypic evolution. *Bioscience* **54**: 627-635.

864 **Westra P, Wilson RG, Miller SD, Stahlman PW, Wicks GW, Chapman PL,**
865 **Withrow J, Legg D, Alford C, Gaines TA. 2008.** Weed population dynamics after six
866 years under glyphosate- and conventional herbicide-based weed control strategies. *Crop*
867 *Science* **48**: 1170-1177.

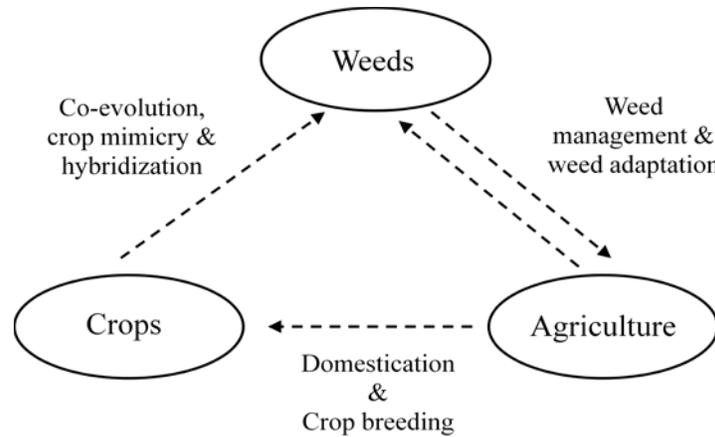
868 **Wijngaarden PJ, van den Bosch F, Jeger MJ, Hoekstra RF. 2005.** Adaptation to the
869 cost of resistance: a model of compensation, recombination, and selection in a haploid
870 organism. *Proceedings of the Royal Society of London Series B-Biological Sciences* **272**:
871 85-89.

872 **Wilczek AM, Roe JL, Knapp MC, Cooper MD, Lopez-Gallego C, Martin LJ, Muir**
873 **CD, Sim S, Walker A, Anderson J et al. 2009.** Effects of genetic perturbation on
874 seasonal life history plasticity. *Science* **323**: 930-934.

875 **Willi Y, Hoffmann AA. 2008.** Demographic factors and genetic variation influence
876 population persistence under environmental change. *Journal of Evolutionary Biology* **22**:
877 124-133.

878 **Ziska LH. 2000.** The impact of elevated CO₂ on yield loss from a C₃ and C₄ weed in
879 field-grown soybean. *Global Change Biology* **6**: 899-905.

880



881
 882
 883
 884
 885
 886
 887
 888
 889
 890
 891
 892
 893
 894
 895
 896
 897
 898
 899
 900
 901
 902

Figure 1. A schematic representation of the *Weed Management Arms Race* showing the co-evolutionary dynamics of interactions between humans, crops and weed populations. Unconscious and conscious human selection during domestication and subsequent breeding has produced modern, specialised 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 co-evolution 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.

903
904