



Review

## Adaptability of plants invading North American cropland

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Received 14 July 2003; received in revised form 1 March 2004; accepted 1 March 2004

### Abstract

Invasive species have received considerable attention in recent years, but research has primarily focused on invasive species of natural habitats. Furthermore, cropland weeds have often been viewed as possessing a “general-purpose genotype” and therefore exhibiting relatively static genetics. However, a more current view is that weeds are capable of rapid genetic change, thereby making analysis of their evolutionary ecology a potentially valuable component for the development of sustainable weed management systems. In particular, further analysis of ongoing evolutionary change in cropland weeds is important because (1) most cropland weed species exhibit considerable adaptability, (2) cropland agriculture is continuously changing, and (3) further research on weed adaptability is needed to design cropping systems to address evolutionary change. In this review, we examine the potential of cropland weeds to evolve so as to affect their invasiveness. There is abundant evidence of genetic variation within and among weed populations in traits relevant to invasiveness, including seed germination patterns, life history traits, physiological adaptability and adaptation to disturbance and resource fluctuations. Approximately half of cropland weed species are primarily selfing, and species with a high degree of selfing tend to exhibit homogeneity within populations but divergence among populations. We identified four critical areas for future research: conflicting selection pressures on weeds in agroecosystems, feed-back driven dynamics of human-weed co-evolution, co-evolutionary mechanisms of weed adaptation in conjunction with other weed species or organisms, and the role of weed evolution in the restoration of agroecosystems.

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**Keywords:** Invasive biology; Weeds; Allozyme analysis; Phenotypic plasticity; Evolution

### 1. Introduction

Recently, attention has focused on the ecological effects, global consequences, and management of invasive species (Mack et al., 2000; Pimentel et al., 2000; Pimentel, 2002). That invasive species are the second leading threat to endan-

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gered species after habitat destruction indicates the seriousness of the problem (Wilcove et al., 1998). In the United States, there are approximately 5000 non-native and 17,000 native vascular plants (Morin, 1995; Morse et al., 1995). Thus, a North American flora composed of 23% alien species has developed over four centuries of contact with other parts of the world. The influx of non-native plants has a considerable economic cost. Pimentel et al. (2000) estimated the annual cost of invasive plants to the US economy at about US\$ 40 billion (29% of the total cost from invasive organisms) and of this total, US\$ 26.4 billion was attributed to cropland weeds with the largest cost due to crop losses and damage (US\$ 23.4 billion).

Although the impacts and costs of controlling weeds in cropland production systems are greater than any other category of vegetation management, recent attention on invasive plants has been focused on those invading unmanaged or semi-managed habitats. Richardson et al. (2000) defined an invader as a non-native organism that arrives and spreads to new areas. Because most agricultural weeds have had a relatively long time to interact with and adapt to cropping systems both before and after their introduction to North America, many of them are not considered “invasive” in the strict sense of their dispersal potential into new areas. However, recent examples in which agricultural weeds have rapidly expanded their range by invading new habitat are numerous (Douglas et al., 1990; Warwick, 1990b; Holt and Boose, 2000). In fact, invasion of agricultural landscapes by new species or those expanding their range is an ongoing process and the ecological theory on invasive species applies to weeds of unmanaged and agricultural systems equally well.

Agricultural weeds are confronted with powerful and fluctuating selection pressures that result from changes in cropping systems and agricultural technology. Formerly, the ability of certain plant species to infest a broad range of cropping systems was conceptualized as the result of a “general-purpose genotype”, emphasizing the role of phenotypic plasticity (e.g., Baker, 1965). Recently, it has become clear that rapid evolutionary change (over time scales of years or decades) is a common ecological phenomenon, particularly in ecosystems that are strongly perturbed by human activities (Antonovics, 1992; Thompson, 1999; Palumbi, 2001; Neuhauser et al., 2003). The

close coupling of evolutionary and ecological change suggests that evolutionary mechanisms may be active in biological invasions (Sakai et al., 2001). The evidence suggests that broadly dispersed, abundant, and problematic agricultural weeds may owe this phenotype, at least partially, to rapid and localized evolutionary adaptation.

Our new understanding of how ecological phenomena are conditioned by rapid evolutionary change raises the question of the relative importance of phenotypic plasticity versus local adaptation. This distinction has important implications for weed management. The presumption of a “general-purpose genotype” is that such weedy species are intrinsically dangerous to a broad range of cropping systems, and heightens the importance of limiting weed invasion, e.g., by focusing management efforts on limiting weed dispersal. In contrast, if weediness is regarded as an evolved trait, then management should expand its focus. Logically, such an expanded approach to management would include efforts to reduce the effectiveness of selection for increased weediness, and on other interventions in relevant evolutionary mechanisms such as gene flow. The latter perspective considerably broadens the scope of potential weed management, and also is consistent with a view that weed communities cannot be excluded from agroecosystems and therefore should be managed to reduce problematic effects while increasing the agroecological benefits provided by weeds (Jordan and Vatovec, 2003).

There are three compelling reasons to undertake a detailed assessment of how evolutionary change in weeds may facilitate weed invasions of cropland:

1. Many weed species, particularly those that closely fit the definition of “invasive weeds,” have been shown to adapt genetically to local circumstances. Thus, genetic factors may determine potential for evolutionary adaptation after invasion. Indeed, several workers have already called for increased emphasis on evolutionary aspects in weed management research (Gould, 1991; Jordan and Jannink, 1997; Martínez-Ghersa et al., 2000; Mohler, 2001), and Vermeij (1996) maintains that the evolutionary feature of invasion biology “cannot be ignored.” If potential for genetic change is ignored, managers will continue to be caught

off guard by new invasions of familiar weeds that expand their range through new adaptations.

2. Cropland agriculture is continuously changing, with the introduction of new crop species and genotypes and new types of management regimes. These changes represent a heightened risk of invasion through the potential for evolutionary adaptation within invading plant species. If managers accounted for the action of evolutionary mechanisms a more preventative approach might be developed.
3. Studies of how weeds may adapt to enhance their invasive capabilities are lacking. It is important, therefore, to frame some of the important questions to provide impetus for further research into the evolutionary aspects of cropland weed invasions so that cropping systems can be designed to mitigate adaptation by invaders.

This review first summarizes some of the historical background of weed invasions of North American cropland (Section 2). Second, the population-genetic attributes of weedy plants are reviewed, illustrating the potential for genetic change (Section 3). Third, case studies of weed adaptation are discussed in terms of interactions between various biological traits and agronomic practices (Section 4). Finally (Section 5), we provide potential research approaches for studying evolutionary mechanisms in cropland weeds. This review aims to focus the attention of resource managers, agricultural- and plant invasion-ecologists, on the well-documented history of weed invasion of agro-ecosystems through evolutionary adaptation, and to provide direction for further research into the nature and management of these processes.

## 2. Brief history of cropland weed invasions

Between 1492 and 1600, most plants that crossed the Atlantic to North America were brought inadvertently with cargo (Crosby, 1972). The 17th century saw even greater numbers of weedy plants colonizing North America with the influx of European colonists (Haughton, 1978; Foy et al., 1983). In the 18th century, human immigrants arrived in North America from all parts of Europe, bringing weeds with them (Dewey, 1896). During the 19th century, weeds migrated ex-

tensively across North America as settlers moved westward across the continent. Russian thistle (*Salsola pestifer*), a pest in western regions of North America, made its way west along railway rights-of-way (Dewey, 1896; Evans and Young, 1974). Alien species continued to arrive in North America through the early 1900s, often as crops that later became naturalized as weeds (Foy et al., 1983). Johnsongrass (*Sorghum halepense*) one of the most serious weeds of US cropland was intentionally brought as a forage crop in 1830 (McWhorter, 1971), as was crabgrass (*Digitaria* spp.) in 1849 (Haughton, 1978). Giant foxtail (*Setaria faberii*), a contaminant of millet seed from China was introduced in the early 1930s, becoming a dominant grass weed in the Midwest (Knake, 1977). Mack (1991) chronicled the role of the commercial seed trade in dispersing invasive weeds in the United States. During the 19th century, many exotic species that are now considered noxious were available for purchase through seed catalogues. This practice was responsible for the spread of at least 140 alien plant species into the United States. Novel alien weeds still pose a serious threat to crop production systems, particularly in states such as Florida, California and Hawaii, where environmental conditions and management practices favor the establishment of a broad range of species (Dowell and Krass, 1992; Eldredge and Miller, 1997; Simberloff et al., 1997). The significant increase in the globalization of trade over the last decade is likely to sustain continued introduction and spread of non-indigenous invasive species into North America and other regions of the world (Jenkins, 1996).

Continued introduction of plant species to North America from colonial times to present has resulted in a North American weed flora composed of approximately 50% non-native species, including some of the most troublesome species in agricultural production. Muenscher (1949) found that of 500 weeds in the northern United States 35% were of European origin (Table 1). While McNeil (1976) argued that the influx of new weed species was nearing completion in temperate regions of the world, Forcella and Harvey (1983) reported that the number of US counties infested by alien weeds present before 1910 (i.e. a total of 188 species) increased steadily through 1980, indicating that continued invasion was occurring (Mohler, 2001).

Table 1  
Source of 500 weeds of the northern United States (after Muenscher, 1949)

Origin	Number of species	Percentage of species
Native to North America	196	39
Tropical America	15	3
North America and Europe	13	3
North America and Eurasia	16	3
Europe	177	35
Asia	12	2
Eurasia	66	13
Africa and Eurasia	3	<1
Unknown	2	<1
Native to North America	225	45
Introduced	273	55

Drawing on accounts for individual species detailed in The Biology of Canadian Weeds series, Table 2 provides a sample of 48 North American weed species cropland. Only weeds that were alien to North America and acted as pests in cropland environments were selected. The date of first introduction can be ascertained with some precision for most species, but the degree of continued spread is more difficult to document. Furthermore, the degree to which this continued spread has involved adaptation to previously unexploited climatic zones, new habitats (e.g. new agricultural management techniques) and other adventive niches is not well documented for most species. What is known about these 48 species and others will be expanded on in the next sections, as we examine the various means by which these weeds have adapted to cropland.

### 3. Population-genetic attributes of weedy plants

The “general-purpose genotype” (Baker, 1965), broadly accepted until recently, relegated population-genetic variation—and the evolutionary dynamics of this variation—to a secondary role. However, the “general-purpose genotype” hypothesis is clearly inadequate to explain all examples of historical and current invasion processes and may obscure important management implications. Recent work (e.g. Lee, 2002) continues to highlight the need to consider the evolutionary dynamics of invasive species. Our current understanding of weed population genetics can

be summarized as follows (and explained in more detail below):

1. Weed populations are usually not genetically depauperate (Warwick, 1990a; Eckert et al., 1996).
2. Weedy species frequently have mixed mating systems with high selfing rates (Mulligan and Findlay, 1970).
3. A variety of population and genetic attributes act to restore and restructure genetic variation.

#### 3.1. Weed populations are usually not genetically depauperate

Hamrick et al. (1979) observed that weed species are generally less variable than other groups of plants in terms of allozymes. Hamrick et al. (1979) and Barrett (1982) predicted that agricultural weed populations would exhibit less genetic variation than weeds of non-agricultural habitats, due to apparent homogeneity of agricultural environments relative to other habitats. In fact, some weed populations do contain limited levels of genetic variability. North American populations of *Bromus tectorum* (cheatgrass) exhibit considerably lower variability than Eurasian populations, with existing North American populations likely derived from six separate introductions (Novak and Mack, 1993; Novak et al., 1993). Genetic uniformity reaches extremes in obligately selfing weeds, weeds that reproduce vegetatively, and apomictic species. Common dandelion, *Taraxacum officinale*, is apomictic and each North American genet apparently represents an independent introduction from the Old World (Lyman and Ellstrand, 1984). However, several comparative studies on weeds colonizing both agricultural and non-agricultural habitats have failed to support the prediction of genetic uniformity. Genetic polymorphisms in populations of *Chenopodium album* (lambsquarters) and *Amaranthus retroflexus* (redroot pigweed) were equally prevalent in cropland as in other habitats (Warwick and Black, 1986). Similarly, European populations of *Capsella bursa-pastoris* (shepherd’s purse) exhibited greater genetic heterogeneity in more disturbed, cultivated agricultural sites than populations found growing in lawns and other habitats that were not cultivated (Bosbach and Hurka, 1981). Leiss and Müller-Shärer (2001) showed that agricultural biotypes of *Senecio*

Table 2  
Life history and breeding systems for 48 selected North American crop weeds

Species (life history <sup>a</sup> )	Crops infested	North American Introduction	Breeding system	Reference
<i>Abutilon theophrasti</i> (A)	Field crops	Mid-1700s	Selfing	Cavers, 2000
<i>Acroptilon repens</i> (P)	Field crops, cereals	Early 1900s	Outcrossing	Mulligan, 1984
<i>Agropyron repens</i> (P)	Various	1600s	Outcrossing	Mulligan, 1979
<i>Amaranthus retroflexus</i> (A)	Various	Native	Mostly selfing	Mulligan, 1984
<i>Ambrosia artemisiifolia</i> (A)	Various	Native	Both	Mulligan, 1979
<i>Apera spica-venti</i> (A)	Cereals	Late 1800s	Both	Cavers, 1995
<i>Atriplex patula</i> (A)	Field crops	Late 1800s	Mostly outcrossing	Cavers, 1995
<i>Avena fatua</i> (A)	Cereals	1600s	Mostly selfing	Mulligan, 1979
<i>Barbarea vulgaris</i> (WA/B/P)	Cereals	1800	Mostly outcrossing	Cavers, 2000
<i>Bromus tectorum</i> (A/WA/B)	Cereals	1800s	Mostly selfing	Cavers, 1995
<i>Cardia draba</i> (P)	Cereals	Late 1800s	Outcrossing	Mulligan, 1979
<i>Chenopodium album</i> (A)	Various	Status unknown <sup>b</sup>	Both	Mulligan, 1979
<i>Cirsium arvense</i> (P)	Field crops, cereals	1600s	Outcrossing	Mulligan, 1979
<i>Convolvulus arvensis</i> (P)	Field crops, cereals	1739	Outcrossing	Mulligan, 1984
<i>Cyperus esculentus</i> (P)	Various	Native + non-native	Outcrossing	Mulligan, 1979
<i>Descurainia sophia</i> (A/WA)	Cereals	1700s	Selfing	Mulligan, 1979
<i>Datura stramonium</i> (A)	Field crops	1600s	Mostly selfing	Cavers, 1995
<i>Daucus carota</i> (A/B/P)	Field crops	1700s	Mostly outcrossing	Mulligan, 1979
<i>Erucastrum gallicum</i> (A)	Cereals, oilseeds	1903	Mostly selfing	Warwick and Wall, 1998
<i>Echinochloa crus-galli</i> (A)	Various	Early 1800s	Mostly selfing	Cavers, 1995
<i>Euphorbia esula</i> (P)	Cereals	1827	Mostly selfing	Mulligan, 1979
<i>Fagopyrum tataricum</i> (A)	Cereals, oilseeds	1700s	Mostly selfing	Cavers, 1995
<i>Galeopsis tetrahit</i> (A)	Cereals, oilseeds	1800s	Mostly selfing	Cavers, 1995
<i>Galinsoga quadriradiata</i> (A)	Field crops	1836	Both	Mulligan, 1984
<i>Galium spurium</i> (A)	Cereals, oilseeds	1878 (Canada)	Selfing	Cavers, 2000
<i>Helianthus tuberosus</i> (P)	Field crops, cereals	Native	Outcrossing	Cavers, 2000
<i>Lappula squarrosa</i> (A/WA)	Cereals, oilseeds	1600s	Mostly selfing	Cavers, 1995
<i>Linaria vulgaris</i> (P)	Cereals, oilseeds	Mid-1600s	Outcrossing	Saner et al., 1995
<i>Malva pusilla</i> (A)	Cereals, lentils, flax	1500s	Selfing	Cavers, 2000
<i>Matricaria perforata</i> (A/P)	Cereals	1800s	Outcrossing	Cavers, 2000
<i>Polygonum convolvulus</i> (A)	Field crops, cereals	1860	Selfing	Mulligan, 1984
<i>Portulaca oleracea</i> (A)	Field crops, cereals	Native	Mostly selfing	Mulligan, 1984
<i>Salsola pestifer</i> (A)	Cereals, oilseeds	1870s	Both	Cavers, 1995
<i>Setaria glauca</i> (A)	Field crops, cereals	1862 (Canada)	Selfing	Mulligan, 1984
<i>Setaria viridis</i> (A)	Various	1821 (Canada)	Selfing	Cavers, 1995
<i>Silene alba</i> (A/B/P)	Cereals	1800s	Outcrossing	Mulligan, 1979
<i>Silene noctiflora</i> (A)	Cereals	1820	Mostly outcrossing	Mulligan, 1984
<i>Sinapis arvensis</i> (A)	Various	Mid-1700s	Outcrossing	Mulligan, 1979
<i>Solanum carolinense</i> (P)	Field crops, cereals	Native to S U.S.	Outcrossing	Cavers, 1995
<i>Solanum nigrum</i> (A)	Various	1800s	Mostly outcrossing	Cavers, 1995
<i>Solanum ptycanthum</i> (A)	Various	Native	Mostly outcrossing	Cavers, 1995
<i>Solanum sarrachoides</i> (A)	Various	1800s	Mostly selfing	Cavers, 1995
<i>Sonchus arvensis</i> (P)	Cereals, oilseeds	1814	Outcrossing	Cavers, 2000
<i>Sorghum halepense</i> (P)	Field crops	1840s	Mostly selfing	Mulligan, 1984
<i>Stellaria media</i> (A/WA)	Cereals	1600s	Selfing	Mulligan, 1984
<i>Thlapsi arvense</i> (A)	Cereals, oilseeds	1500s	Mostly selfing	Mulligan, 1979
<i>Viola arvensis</i> (A/WA)	Cereals	1800s	Mostly selfing	Cavers, 2000
<i>Xanthium strumarium</i> (A)	Various	1821 (Canada)	Mostly selfing	Mulligan, 1984

In cases where the reference did not give a general time of introduction for North America (north of Mexico), the Canadian time is given, followed by (Canada).

<sup>a</sup> A: annual, P: perennial, B: biennial, WA: winter annual.

<sup>b</sup> Its introduced status could not be determined.

*vulgaris* (groundsel) were genetically more variable than their ruderal counterparts.

Selfing, in concert with founder effects, tends to reduce within-population variation. Despite reductions in evolutionary potential that may accompany loss of variation, this mating-system modality has been interpreted as adaptive for agricultural weeds, because it is thought to facilitate colonization (Antonovics, 1968; Lloyd, 1992). Among plants in general, weeds have a relatively high capacity for phenotypic plasticity, perhaps resulting from fixed heterozygosity via polyploidy, and this capacity may be an important genetic attribute that provides adaptive flexibility despite loss of variation. For example, Weinig (2000) reported that velvetleaf (*Abutilon theophrasti*) populations in corn and soybeans exhibited adaptive differentiation in terms of their plastic response to light levels.

### 3.2. Implications of mixed mating systems with high selfing rates

Obligate- or predominate-selfing and genetic homogeneity are characteristic of agricultural weeds. Mulligan and Findlay (1970) evaluated self-compatibility in 65 Canadian weeds. All of the 33 annual weeds and 21 of 23 biennials and caespitose perennials set viable seeds in the absence of outcross pollen. The nine rhizomatous or stoloniferous perennial species tested were self-incompatible. Within our inventory of 48 North American cropland weeds, 35 species are capable of self-fertilization, and 8 are exclusively selfing (Table 2). Among the 16 species classified as “mostly selfing,” outcrossing rates are generally less than 10%. Warwick (1990a) reviewed studies of allozyme variation in 24 weeds and found “low levels” of allozyme variation in 17 species. Primarily or totally selfing species were the subject of 15 of 17 studies that reported low levels of allozyme variation, whereas outcrossing species were profiled in six of the seven studies that found high allozyme variation. The one outcrossing species exhibiting low levels of allozyme variation was *Cyperus esculentus* (yellow nutsedge), which reproduces primarily by vegetative means (Horak and Holt, 1986). Thus, genetic variation tends to be reduced in self-fertilizing weedy species. Hamrick et al. (1979) reported an average of 30 and 63% polymorphic loci for weedy species and late-successional species, respectively.

Consaul (1988) compared introduced North American populations of the predominantly selfing species, *Polygonum lapathifolium* (willow weed) to native European populations and showed extremely low allozyme variation for populations from both continents. Selfing grasses were polymorphic at fewer loci per population than outcrossing grasses, and had fewer alleles per locus, lower potential levels of heterozygosity, and were heterozygous at fewer loci; whereas, species with a mixed mating strategy exhibited similar heterozygosity to outcrossers, but had fewer polymorphic loci and alleles (Hamrick et al., 1979).

Lloyd (1992) suggested that mixed mating strategies may allow weeds to follow a best-of-both-worlds strategy. High selfing rates may provide several important advantages to colonizing species; ensuring that reproduction occurs, even if very few (as few as one) propagules are present and that progeny are reasonably similar to highly successful parental genotypes (Antonovics, 1968). Selfing avoids so-called outbreeding depression (via disruption of locally-adapted genotypes, (Lloyd, 1992; Briggs and Walters, 1997), although outcrossers may produce offspring with high fitness under some ecological circumstances (e.g., in co-evolutionary interactions with pathogens, Antonovics, 1992). Furthermore, self-fertilization reduces the amount of biomass required to produce flowers, nectar and other structures involved in attracting pollinators (Briggs and Walters, 1997), allowing greater allocation of resources to seed production.

### 3.3. Population-genetic attributes that restore and restructure genetic variation

Processes that serve to restore and restructure genetic variation among predominantly selfing weed species include occasional outcrossing within populations, the storage of genetic variation in seedbanks, episodes of hybridization between multiple introductions of a single weedy species and evolution of phenotypic plasticity.

Populations of selfing weeds are expected to display genetic uniformity but may be highly differentiated from other conspecific populations (Loveless and Hamrick, 1984; Richards, 1990). Biotypes of witchweed, *Striga asiatica*, diverge widely in height and

flower color. A biotype in Indonesia is only 1 cm tall and produces pink flowers, whereas biotypes in the United States attain heights of 50 cm and possess red or yellow flowers (Musselman, 1982; Werth et al., 1984). With extreme population differentiation, rare migrational events accompanied by outcrossing may potentially lead to explosions of genetic variability (Richards, 1990). When outcrossing among individuals derived from different introductions occurs in predominantly selfing species, the effect on genetic variability will depend on the number of introductions to North America, and the interpopulation variability in their source areas (Cox, 1999). In outcrossing species, mating among individuals from different introductions can mitigate loss of variation via founder effects associated with colonization. The outcrossing weed species, *Apera spica-venti* (wind bentgrass) displayed relatively high levels of allozyme variability in both its native Europe and in Ontario, Canada, where it recently (1975) became established as a weed of winter cereals (Warwick et al., 1985, 1987).

Genetic variability of weed populations, even under selfing, may also be enhanced by the presence of large seed banks. Essentially, the seed bank protects genes from removal from the population by selection. The development of herbicide resistance may be delayed in species having a large proportion of the population in the seed bank (Cavan et al., 2000). Genetic variability may also be substantially enhanced by outcrossing among previously isolated weed populations after invasion or dispersal processes, or interspecific hybridization with related crops or other invasive taxa (Ellstrand and Schierenbeck, 2000; Sakai et al., 2001). Such hybridization may greatly alter the range and structure of genetic variation; large effects on evolutionary potential of weed populations may result. These effects include increases in variability at individual loci, and changes in associations among alleles at multiple loci (Brown et al., 1980).

Interspecific hybridization may also be important in restoring and restructuring variation in weed populations. In some cases, hybridization has resulted in new species, for example, the recent formation of hexaploid *Senecio cambrensis* in Britain by chromosome doubling in hybrids between tetraploid *S. vulgaris* (common groundsel) and the introduced diploid *S. squalidus*, oxford ragwort (Ashton and Abbott, 1992; Harris and Ingram, 1992). Although

many plant taxa are capable of hybridization, invasive weed taxa are particularly prone to reticulate evolutionary patterns involving hybridization because the process of invasion brings species into sympatry that were previously isolated geographically (Abbott, 1992). A striking example of the origin of new weeds through hybridization and subsequent polyploidy within the last 100 years involves the *Tragopogon* complex in western North America. There is evidence of increased vigor and competitive ability in two new allotetraploid hybrid *Tragopogon* species created in the early 20th century in North America, *Tragopogon mirus* and *Tragopogon miscellus* (Brown and Schaack, 1972; Soltis et al., 1995). This hybridization has resulted in increased invasive potential of *Tragopogon* spp. in general (Soltis et al., 1995; Clements et al., 1999). Thus, hybridization allows the development of races and species that have high capacity for invasion due to wide environmental tolerance and high competitive ability conferred by hybrid vigor. Despite these considerations, hybridization is less common in annuals than in perennials (Warburg, 1960), and annuals constitute the majority of most agricultural weed floras.

Hybridization between crops and weeds can create potentially serious problems in the form of weed races of crop species. An early bolting race of *Beta vulgaris* (sugar beet) spread rapidly in the sugar beet growing regions of Europe during the 1970s. Boudry et al. (1993) demonstrated that whereas the cytoplasm of the weed race was derived from the domesticated sugar beet, the gene for annual flowering was nuclear and apparently derived by introgression from wild beet populations (*Beta vulgaris* ssp. *maritima*). Similarly, hybridization with wild or weed species has been documented as the origin of weedy rye, *Secale cereale* (Suneson et al., 1969; Sun and Corke, 1992).

In several cases, weed-crop hybridization has introduced variation of obvious adaptive importance into weed populations. Red rice (weedy *Oryza sativa*) is a substantial weed problem in most of the world's rice growing regions (Holm et al., 1997). When plant breeders in India attempted to facilitate weeding by making the crop more recognizable by introducing genes for purple leaf coloration (Dave, 1943), the weed quickly acquired the purple leaf trait by crossing with the crop (Grist, 1975). Similarly, the transfer of herbicide-resistance genes from crop to related weed

species has been reported in at least two field cases. Glufosinate-resistant canola (*Brassica napus*) outcrosses with birdrape mustard (*Brassica campestris*) to produce glufosinate-resistant hybrids (Brown and Brown, 1996). More recently in the US northwest, imazamox-resistant hybrids of jointed goatgrass (*Aegilops cylindrica*) have been produced when susceptible individuals of this winter annual grass outcrossed with imazamox-resistant wheat (Seefeldt et al., 1998). Once the weedy crop race or crop relative obtains resistance, it becomes a potential threat to many crops in which the broad-spectrum herbicide is used (Boudry et al., 1993).

Plasticity itself is a genetic trait that is determined by natural selection and other evolutionary processes. This concept is distinct from Baker's (1965) static all-purpose phenotype, because within an evolving framework, the degree of plasticity may change with time. As mentioned previously, Weinig (2000) found that the plasticity of the response to light levels varied among velvetleaf populations. Jordan (1986) likewise identified adaptive plasticity among populations of *Diodia teres* (poorjoe) in response to light levels. Hurka (1990) found that populations of the widespread weed, *Capsella bursa-pastoris* (shepherd's purse) exhibited varying degrees of plasticity in the amount of time required to flowering, and concluded that the range of plasticity was likely genetically determined. Marshall and Jain (1968) compared the adaptive strategies of *Avena fatua* (wild oats) and *A. barbata* (slender oat). *Avena fatua* was genetically more variable, whereas *A. barbata* displayed a greater degree of phenotypic plasticity. Brown and Marshall (1981) concluded that environmental variation often leads to polymorphism and plasticity simultaneously and hypothesized that degree of selfing was correlated with phenotypic plasticity.

Polyploidy may be an important basis for phenotypic plasticity in weeds (Warwick, 1990a). Allopolyploidy may enhance the biochemical variability within individuals allowing these species to adapt to a broader array of niches (Roose and Gottlieb, 1976; Warwick, 1990a). The incidence of polyploidy among the most invasive weed species is high. At least 16 of the top 18 species in the Holm et al. (1977) list of the world's worst weeds are polyploid (Brown and Marshall, 1981). Selfing polyploid populations may have heterozygous loci, creating multiple en-

zyme phenotypes. In an analysis of 113 plant species, Hamrick et al. (1979) observed a strong correlation between chromosome number and genic diversity per locus, with polyploids having a mean genic diversity twice that of diploid species. Warwick (1990a) found heterozygous loci occurring at 50% of the duplicated loci in three of four polyploid weed species.

Together, these population-genetic attributes of weeds appear to form an adaptive syndrome, in which trade-offs between colonizing ability, maintenance of locally-adapted genotypes and loss of genetic variation are mitigated by phenotypic plasticity and processes that restore and restructure genetic variation. Indeed, Ellstrand and Schierenbeck (2000) proposed that, in many cases of invasion, these latter processes must act to create sufficient population-genetic variation needed to enable widespread invasion. Many cases suggest that weed populations regain variation sufficient to support local adaptation (Heywood, 1986; Jana and Thai, 1987; Warwick, 1990a) after colonization of isolated areas by only a few individuals. Populations of *Avena fatua* adapted to regional climates developed within 400 years of its introduction to California (Clegg and Allard, 1972). Similarly, Brown and Marshall (1981) found considerable genetic differentiation among populations of *Bromus mollis* (soft brome) in Australia despite limited variation in the genetic starting material.

This conceptual model of weed population genetics—featuring a dynamic tension between processes that reduce and restore genetic variation—allows us to envision the operation of population genetic mechanisms that would support rapid and ongoing evolutionary change in weeds. The following sections describe cases of adaptation in terms of seed germination, life history strategy, physiology and response to disturbance. Taken together, these cases provide strong support for the view that ongoing adaptive evolution of ecologically-relevant traits is an important attribute of agricultural weeds.

#### 4. Observed adaptive variation in cropland weed traits

Many of the cases where adaptive variation has been observed in cropland weed traits involve recent expansion in the geographic ranges of these weed species in

Table 3

Recent range expansions of cropland weeds in North America and associated adaptive traits

Weed species	Description of range expansion	Observed adaptive traits	References
Biennial species, e.g. <i>Conyza canadensis</i> (horseweed)	Invasion of conservation tillage from non-crop environments since the 1980s	Biennial life history	Murphy et al. (unpublished)
<i>Datura stramonium</i> (jimsonweed)	Northward invasion of Canadian and northeastern US cropland in 1950s	Heavier seeds, earlier growth	Weaver et al., 1985; Warwick, 1990b
<i>Echinochloa crus-galli</i> (barnyardgrass)	Northward invasion of Québec from the US in the 19th century	More rapid growth to maturity	Potvin, 1986
<i>Panicum miliaceum</i> (proso millet)	Northward invasion into Canadian cropland by the early 1970s	Seed germination and dispersal characteristics	Warwick, 1990b
<i>Ranunculus repens</i> (creeping buttercup)	Invasion of cropland from non-crop environments	Greater seed dormancy and more rapid growth	Christensen, 1996; Harris et al., 1998
<i>Setaria viridis</i> (green foxtail)	Survival at Churchill, Manitoba, at nearly 60°N latitude (normal range 45–55°)	Leaf production at low temperatures	Douglas et al., 1985; Swanton et al., 1999
<i>Sorghum halepense</i> (Johnsongrass)	Northward expansion by 5° latitude between 1926 and 1979	Northern populations annual (vs. perennial southern populations)	Warwick et al., 1986

North America. Some of these range expansions are illustrated in Table 3, while other adaptive variation has more subtle outcomes; these various cases are discussed in the remainder of Section 4.

#### 4.1. Seed germination patterns

Seed germination characteristics affect the crop-weed relationship critically through differential timing and germination of the weed with respect to the crop. Two species analyzed by Warwick (1990b) illustrate potential changes in germination response that may appear among weed populations expanding their ranges northward to cooler climates. Weedy biotypes of *Panicum miliaceum* (proso millet) had established in Canadian crop fields by the early 1970s (Warwick, 1990b; Table 3). The spread of black seeded biotypes having small, numerous seedheads that shatter easily has been favored by more pronounced seed dormancy and a greater tendency to be spread via combines when harvesting corn (Cavers, 1985; McCanny and Cavers, 1988). *Datura stramonium* (jimsonweed) became established as a weed of field crops in Canada in the late 1950s (Warwick, 1990b; Table 3). This species exhibits an exceptionally high degree of phenotypic plasticity despite its genetic uniformity, with north-

ern populations developing heavier seeds and larger cotyledons within a shorter growing period (Weaver et al., 1985).

One source of cropland weeds is roadside or waste area plants that unexpectedly become invasive and resists control efforts in field or horticultural crops. A species that typifies this latent invader syndrome is creeping buttercup, *Ranunculus repens*, a stoloniferous, seed-producing perennial, naturalized from Europe and spread throughout the northern US and adjacent Canada (Lovett-Doust et al., 1990). An arable-biotype of *R. repens* adapted to field and horticultural crop production conditions arose from the wild-type population commonly found in pastures and wooded areas (Doohan, unpublished data; Table 3). Seed germination of arable- and wild-type populations of *R. repens* in response to incubation temperature and available water were compared in growth chamber experiments. Regardless of treatment, germination of the arable-type seed was consistently lower than germination of the wild-type seed (Harris et al., 1998). As seed viability was undiminished, this variation likely reflected greater seed dormancy in the arable-type. Practices associated with planting strawberries and with intensive weed control soon after planting would favor survival of later germi-

nating, relative to earlier germinating, cohorts. Thus, lower emergence of the arable-type relative to the wild-type reflected a shift to delayed emergence in response to these pressures upon early cohorts. Overall, the arable-type displayed more homogeneity in the seed population with a reduced ability to germinate in response to a wide amplitude in environmental conditions, strongly suggesting adaptation of seed germination characteristics to agricultural practices.

#### 4.2. Life history

Some of the best-documented cases of divergence among populations of agricultural weeds involve changes in weed life-cycle phenology. Between 1926 and 1979, *S. halepense* extended its range in eastern North America northward by 5° latitude (Warwick et al., 1986; Table 3). Throughout most of its range this grass weed is a perennial, but most northern populations are annual. The cold winters of northeastern North America kill the rhizomes of *S. halepense* (Warwick et al., 1986). The annual populations of *S. halepense* contrast with perennial populations in several respects, including increased seed weight and percentage seedling emergence, more rapid seedling growth, earlier flowering, greater allocation to reproduction, and fewer rhizomes (Warwick et al., 1984). These traits allow completion of the life cycle in a single short growing season and provide for maintenance of the population from seed alone. The genetic variation needed for this large shift in the ecology of northward invading *S. halepense* was probably provided by introgression from domesticated *S. bicolor* (Warwick et al., 1984).

Changes in the rate of development have been observed along climatic gradients for other weed species. The recent range extension of *Datura stramonium* northward in the eastern USA and Canada (Table 3) occurred through selection for traits that favor rapid development, including heavier seeds, longer cotyledons and earlier anthesis (Weaver et al., 1985). Given the extreme plasticity observed in temperature responses by certain weed species, it is difficult to predict the range of climatic conditions that a given weedy species will tolerate. Swanton et al. (1999) found that *Setaria viridis* (green foxtail) was able to produce leaves when exposed to temperatures ranging

from 6.5–47°C. Thus, although the distribution of *S. viridis* is mostly between 45–55°N latitude (Douglas et al., 1985), the ability to grow at a greater range of temperatures suggests potential for further range expansion. Although *S. viridis* is typically found in southern areas of Canada, it has been found growing in Churchill, Manitoba, at a latitude of nearly 60°N (Douglas et al., 1985; Table 3).

As predicted by the theory of *r* and *K* selection (Wilson and Bossert, 1971), disturbance and competition can create ecotypic variation in weed populations over relatively short distances and time scales. In a common garden experiment, *Ranunculus repens* (creeping buttercup) biotypes collected from a strawberry field grew more rapidly and colonized bare soil more readily than plants collected from a pasture site (Christensen, 1996). The arable-type displayed twice the growth and colonization potential of the wild-type for each parameter. Jordan (1989a, 1989b) showed that *Diodia teres* (poorjoe) growing in a soybean field had more rapid early growth relative to a dune population, and that conditions in the agricultural habitat were sufficient to select for the observed difference in a few generations. Similarly, *Poa annua* (annual bluegrass) from disturbed environments tend to produce many seeds in their first season of life but suffer high rates of mortality, whereas plants from less disturbed but more competitive environments (e.g., pastures) behave more like biennials (Law et al., 1977; Law, 1979). Frequent intensive weeding has had similar evolutionary effects on plant size and development rate of *Arabidopsis thaliana*, mouseear cress (Jones, 1971) and *Stellaria media*, chickweed (Sobey, 1987; Briggs et al., 1991).

Numerous biotic factors, such as predispersal seed predation (Ohashi and Yahara, 2000), may influence the natural selection of reproductive parameters. Several studies have reported increased post-invasion seed production in invasive plant species, sometimes several orders of magnitude greater than in the native range (Noble, 1989; Fowler et al., 1996). These differences are attributed to better growing conditions and lack of enemies, many of which reduce seed production directly via predation (Blossey and Nötzold, 1995). The absence of natural enemies in newly invaded territories may select for a shift in energy allocation from defensive structures and chemicals to reproduction.

#### 4.3. Physiological adaptability

Physiological adaptability has been characterized for some weed species, particularly species developing herbicide resistance and species expanding into new climatic zones. Adaptations to ecological or cultural control methods may also involve physiological changes. It was long thought that weeds were less likely to develop pesticide resistance than other pests (Gressel and Segel, 1978), but presently, 422 resistant weed biotypes have been found worldwide, 86 of which occur in the United States and 35 in Canada (Heap, 2001). Species likely to develop resistance (e.g. *Lolium rigidum*; Powles and Howat, 1990), are more likely to spread in the face of herbicidal control measures than are less adaptable species.

Several weed species have expanded their ranges to include areas in North America outside their former climatic tolerances (Warwick, 1990b; Table 3). A given plant species may have intrinsic constraints that restrict genetic adaptation to climate. For example, C<sub>4</sub> species may be limited in their ability to colonize northern areas because the C<sub>4</sub> photosystem is more efficient at lower latitudes. An alternative hypothesis offered by Long (1983) is that C<sub>4</sub> plants have not yet fully colonized their potential ranges. Potvin (1986) showed that the C<sub>4</sub> grass, *Echinochloa crus-galli* (barnyardgrass), had adapted to a shorter growing season in Québec than in southern states by evolving a reduced lifecycle (Table 3). *Echinochloa crus-galli* originated in Europe and spread to many parts of North America through the 19th century, including areas of Canada north of 50°N latitude, the boundary delimiting its range in other parts of the world (Holm et al., 1977; Maun and Barrett, 1986). Plants from Québec were able to allocate more resources to reproduction under growing conditions in Québec than plants from North Carolina or Mississippi (Potvin, 1986). Furthermore, an analysis of stage-specific selection coefficients demonstrated that the Québec plants were more successful at every growth stage under Québec conditions. Conversely, conditions in North Carolina selected against the northern plants. Potvin (1986) speculated that although *E. crus-galli* is a C<sub>4</sub> plant, its association with agriculture may have facilitated its northward expansion.

#### 4.4. Adaptation to disturbance and resource fluctuations

In general, invasion results from a disturbance in conjunction with propagule availability (Hobbs, 1991). Sousa (1984) defined disturbance as mortality or damage of existing vegetation creating opportunity for new vegetation to become established. In crop production systems, disturbances consistent with Sousa's (1984) fairly narrow definition are common. Soil disturbance disrupts above-ground vegetation and soil biota. Hobbs and Huenneke (1992) observed that the long-history of soil disturbance in the Mediterranean region has produced a large, successful group of weedy species adapted to this disturbance regime. The other major disturbance in cropping systems is the removal of above-ground biomass annually at harvest. Another key factor facilitating non-crop plant invasions in cropland is nutrient additions; a combination of soil disturbance and nutrient addition may frequently promote the establishment of invasive species (Hobbs and Atkins, 1988). Fluctuations in resource supply, whether through enrichment or through release from soil organic matter promote invasion (Rejmánek, 1989; Davis et al., 2000). The level and frequency of fluctuations experienced in cropping systems is seldom encountered in more natural ecosystems. Having been associated with such systems for a long period of time, invasive agricultural weed species are well-equipped to further adapt to changes in cropping systems.

When farm management techniques become less intensive, habitats more closely resemble "natural areas" in terms of selection pressures. One rationale for lower intensity farming is to mimic natural processes and harness natural enemies for managing weeds (Altieri and Whitcomb, 1979; Andow, 1991). Appropriate design of integrated weed management systems flows from this rationale (Swanton and Weise, 1991). While this may promote natural enemies that reduce weed infestations, it also can allow non-agricultural weed species to become established in farm fields, or permit increased diversity of weeds (Clements et al., 1994). Once adapted to agriculture, these weeds may spread to new areas.

Reduction in tillage may allow many novel species to invade, because the disturbance regime is fun-

damentally altered. Through reduced disturbance, successional trajectories extend weed communities beyond the early successional communities observed when soil is cultivated, thereby permitting invasion by weed species not previously associated with annual crops (Swanton et al., 1993). Predictions of an increased proportion of wind-dispersed species (Froud-Williams et al., 1983) have been borne out in empirical studies (Derksen et al., 1993) and from North American surveys in areas where reduced tillage has been adopted on a large scale (Thomas and Frick, 1993). Although these species patterns have been quantified for a number of systems, little attention has been focused on adaptation by existing and novel weed species to the newly encountered conditions.

Viswanathan and Aarssen (2000) argued that one reason for the dearth of biennials observed within the North American flora is the lack of habitats to facilitate their evolution in pre-Columbian times. The widespread adoption of conservation tillage is now creating such habitats, featuring a suitable intermediate level of disturbance, on a fairly large scale. Evidence for this is the substantial number of obligate or at least facultative biennial species that tend to invade conservation tillage fields such as horseweed (*Conyza canadensis*), bull thistle (*Cirsium vulgare*), and common yarrow (*Achillea millefolium*) (Murphy et al., unpublished data; Table 3). Likewise, existing annual weeds may be selected for lifecycle characteristics that adapt them to reduced tillage practices. Comparisons between no-till and plowed cropping systems indicated a broad range in the germination and emergence behavior of some weed species (Oryokot et al., 1997; Roman et al., 2000). Soil that is not tilled tends to remain cooler longer, and weed species with relatively plastic emergence patterns will have a selective advantage. In addition to the absence of plowing, numerous changes in edaphic and biotic characteristics under conservation tillage (Hendrix et al., 1986; Swanton et al., 1993; Cromar et al., 1999) may also lead to adaptation by weeds. Shallower burial of weed seeds in soil, as observed in reduced tillage (Clements et al., 1996) may result in more rapid evolution of herbicide resistance. Gressel (1991) pointed out that triazine resistance was first observed in *Senecios vulgaris* in untilled environments like orchards and roadsides rather than in tilled fields.

## 5. Evolutionary mechanisms in cropland weeds: prospective issues

As the cases described above make clear, adaptive evolutionary change certainly occurs in cropland weeds. In many cases it is likely that such evolutionary change has been important to the development of widespread, abundant and problematic cropland weeds. For a given species, such adaptation(s) may serve to overcome one or more key barriers to invasiveness. Therefore, there may be many potential pathways of evolutionary change by which a plant species could become a widespread and abundant cropland weed. However, it is unclear whether rapid and ongoing evolutionary change is *typically* important to the development, spread and persistence of important cropland weeds. Additional case studies are needed. We judge that there is sufficient evidence of the intense activity of evolutionary mechanisms in weeds to ask a prospective question. Can an awareness of evolutionary mechanisms and dynamics of these plants be useful in the design of integrated weed management systems? To pursue this question, we recommend research on four issues:

1. Can we develop a better understanding of the positive feedback between weed adaptation and agroecosystem management? (i.e. human-weed coevolution)
2. Are there additional coevolutionary relationships with weeds that need to be considered?
3. Can the design of cropping systems account for tradeoffs among components of weed biology and ecology?
4. How might weed evolution and continued invasion be incorporated into models of agroecosystem restoration or health?

### 5.1. Human-weed coevolution

Evolutionary feedback processes typically link ecological interactions involving humans and invasive organisms in self-reinforcing dynamics (Simberloff and Von Holle, 1999). Such dynamics have probably been important to the evolution of many cropland weeds, via a process of “coevolution” between weeds and humans (Ghersa et al., 1994). This occurs when an agroecosystem modification enables a weed invasion

that further modifies the agroecosystem. This then provokes human managers to make additional changes to the agroecosystem that enable further weed invasions by different weed species.

Evolutionary change in the weed may be necessary to enable initial invasion or subsequent agroecosystem modification; in the absence of such adaptation, feedback effects may not be strong enough to permit invasion. If evolutionary dynamics are implicated in such feedback-driven mechanisms of invasion, then additional perspectives and options for management may become apparent. For example, this model of invasion predicts that when new weeds become established in an agroecosystem, only substantial agroecosystem restructuring will break the feedback cycle. Conversely, this model may explain the “lag phase” observed in many cases of plant invasion whereby invasive plants have been observed to occur at low abundance or restricted distribution for several decades before becoming widely invasive (Ellstrand and Schierenbeck, 2000). Lag phases have been explained by lack of genetic variation after invasion; hybridization between multiple invasive populations may provide sufficient variation to permit invasion. If the significance of this possibility could be better understood, better strategies against invasions could be devised.

### 5.2. Coevolutionary mechanisms and weed invasiveness

Studies of evolutionary mechanisms in weeds have largely focused on selection imposed by abiotic factors associated with human management (e.g., herbicide resistance or agrastral versus ruderal habitat) or on adaptation to climatic or edaphic factors. However, future cropping systems are likely to be more biologically-rich than is presently the case in industrialized field-crop production. Interspecific ecological interactions are likely to comprise more important selective pressures bearing upon cropland weeds. It is also clear that these interactions are evolutionarily fluid on short time scales (Thompson, 1998). Therefore, we should consider the possibility that weed interactions with herbivores, pathogens, pollinators, soil biota and other plants may evolve rapidly in agroecosystems.

The question is whether these evolutionary dynamics can act to reduce the effectiveness of ecologically-

based weed management approaches. No case studies of this possibility exist for cropland weeds. In the case of biocontrol of a rangeland invasive *Chondrilla juncea* (rush skeletonweed) by a pathogenic rust fungus, *C. juncea* genotypes appeared that were much less susceptible to the pathogen, reducing the initial success of this biocontrol effort (Burdon, 1987). Studies of coevolutionary dynamics of interspecific interactions (Neuhauser et al., 2003,) demonstrate that ecological dynamics (affecting distribution and abundance of interacting populations) and evolutionary dynamics (affecting gene frequencies of interacting populations) are closely coupled, and that the outcomes of these interactions cannot be understood without considering both ecological and evolutionary dynamics.

Analysis of these ecological-evolutionary dynamics of interspecific interactions has been termed ‘community genetics’ (Antonovics, 1992), referring to an expansion of the perspective of evolutionary genetics to encompass interspecific interactions, the province of community ecology. Moreover, application of this approach to specific instances has demonstrated that a number of evolutionary mechanisms must be considered in addition to selection. Specifically, gene flow and dispersal in spatially-structured population systems have been found to be very important (Thompson and Nuismer, 2000; Ronce et al., 2000). These models and evidence suggest that efforts to make use of herbivores and pathogens for weed management (Liebman, 2001) may be vitiated by rapid evolutionary dynamics in certain circumstances, and therefore such dynamics should be considered in designing agroecosystems. The general point is that biologically-complex cropping systems that use interspecific interactions to regulate pest populations may be undermined by rapid evolutionary change in these interactions themselves. Weed researchers should collaborate with ecologists interested in rapid evolution of interspecific interactions to elucidate guidelines for agroecosystem design from the rapidly-developing field of community genetics.

### 5.3. Cropping systems design and weed adaptation

Are there some fundamental tradeoffs between components of weed biology and ecology (Sakai et al., 2001) that can be exploited in order to de-

wise cropping systems whose design is intrinsically resistant to weed invasion? For example, there is a correlation between seed size and resistance to certain forms of allelopathy across a wide range of cropland weed species (Liebman and Mohler, 2001). Presumably, presence of these allelopathic agents creates selection for increased weed seed size. However, there is a well-established tradeoff between seed size and seed number (Harper, 1977). If net reproductive rate is strongly affected by seed number, then selection for increased seed size will be opposed by selection for increased seed number. Other identified tradeoffs include resource allocation to anti-herbivore defenses versus vegetative and reproductive growth (Simms, 1992); response to nitrogenous fertilizers versus stress-tolerance (Liebman and Mohler, 2001); seed size versus seed dispersal ability (Ronce et al., 2000); allocation to symbiosis with mutualist soil biota versus direct nutrient uptake or development of aboveground biomass (Schultz et al., 2001), or stress tolerance (e.g. shade, drought or nutrient limitation) versus high growth rates in the absence of stress (Reich et al., 1997).

The genetic basis of tradeoffs in weedy plants has been estimated in only a few instances (Weinig and Delph, 2001; Mercer et al., 2002). The direction and strength of selection on traits involved in tradeoffs is essentially undocumented in cropland weeds, except in the case of herbicide resistance. Triazine-resistant biotypes are usually less fit than susceptibles in the absence of triazines (Jasieniuk et al., 1996), and may show increased sensitivity to unrelated herbicides (Jordan et al., 1999). Such effects have probably slowed the spread of triazine-resistant biotypes despite the widespread use of triazine herbicides. In cases of resistance to some other classes of herbicides, however, evidence of substantial fitness costs has not yet been found (e.g., sulfonyleureas Alcocer-Ruthling et al., 1992; Thompson et al., 1994; picloram Sterling et al., 2001), and biotypes resistant to these herbicides would be expected to spread rapidly through regions where these herbicides are used widely.

The hypothesis that diversified and integrated cropping systems generate conflicting selection pressures on tradeoff traits needs to be tested. Agroecosystems that provide diverse and conflicting selection pressures may be more resistant to weed adaptation, but more explicit assessment of selection pressures and genetic

variation in such systems is needed to test this hypothesis (Jordan and Jannink, 1997).

#### 5.4. Role of weed evolution in agroecosystem health

A final and related issue is the role of weed evolution in ecological restoration of agroecosystems. Weeds represent a component of total plant diversity in an agroecosystem. Although critical studies are few, there is a wide range of suggestive evidence that certain weeds may provide valuable contributions to the agroecological services that are produced by this plant diversity (Jordan and Vatovec, 2003). In particular, certain weeds may be very helpful in efforts to restore agroecological functions that require a certain minimum level of plant species diversity and abundance (Swift and Anderson, 1993) such as efficient nutrient cycling and maintenance of soil quality (Feldmann and Boyle, 1998; Jordan and Vatovec, 2003), promotion of symbiotic bacterial populations (Sturz et al., 2001), and control of arthropod pests by natural enemies (Bugg, 1992). This approach does not mean we should be cavalier about deliberately introducing weeds or ignoring new weed invasions, especially since part of the problem in using weeds to benefit agroecosystem management is predicting which plant species will become troublesome weeds and which species will merely become transients or part of a successional trajectory. Thus, tolerating populations of relatively benign weed species that sometimes occur with alternative practices may be desirable even though general promotion of weeds is not.

These considerations point toward an expanded understanding of weed management that recognizes the potential agroecological value of weeds. Weed ecology should be seen as important part of ecological mechanisms that support sustainable cropping systems (Swanton and Murphy, 1996; Cardina et al., 1999; Gliessman, 2001). Such a notion of weed management emphasizes weed community dynamics; however, it is certainly plausible that evolutionary dynamics may have a considerable effect on the level of agroecological benefits that weed communities provide. Several recent studies have demonstrated that weeds play an important role in maintaining soil biota—in particular arbuscular-mycorrhizal fungi (AMF)—that have strong beneficial effects on crop growth (Jordan et al.,

2000). There is emerging evidence that the nature of plant-AMF relationships is shaped by strong selective forces: AMF impose substantial energetic costs on their hosts, and therefore hosting behavior should be selected for only when benefits outweigh costs (Wilkinson, 1998). Given the occurrence of variation and selection, we can expect that weed relations with AMF will be evolutionarily labile. It seems possible that AMF symbiosis would select for strongly hosting genotypes of weed species. These genotypes may then be more capable of maintaining the diversity and abundance of AMF that are needed for AMF association with crops. Critical studies are needed, but this vignette illustrates how evolutionary dynamics may figure in restoration of agroecosystems. Two important questions can be highlighted: are evolutionary dynamics of weeds important to ecological restoration of agroecosystems, and if so, how can management efforts serve to guide and direct these dynamics?

### 5.5. The larger experiment

In essence, humans are participating in a large series of experiments in evolution, through deliberate and accidental introductions (Brown and Marshall, 1981). In view of problems caused by the strong selection pressure posed on weeds by specific herbicides, Mohler (2001) called for the development of flexible management using multiple ecological weed control tactics within a diverse cropping system. Similarly Martínez-Ghersa et al. (2000) advocated selecting for plasticity in the canopy of crop cultivars to prevent weeds from gaining an evolutionary advantage over crops.

Most ecologists are accustomed to observing adaptation within a community context. Weed scientists, on the other hand, generally focus on one or two species that are problematic in a given crop at a given time, and adaptation is viewed as a response to abiotic factors such as herbicide chemistry. Investigations of weed problems need to consider weed evolution within biotic and community contexts, together with the unique genetic characteristics that weed species bring to these contexts. It is clear from the previous sections that there is ongoing evolutionary adaptation by cropland weeds, although this potential threat is seldom explicitly accounted for in research or management strategies. At the very least, the four prospective research areas identified here should be pursued.

## 6. Conclusions

In this review, we have argued that views of cropland weeds that reflect the assumption that weeds are static entities possessing a “general-purpose genotype” need to be revised. The evidence presented here provides some basis for such revisions, but considerable research is required to assess the full implications of cropland weed evolution. We have identified four critical areas for future research: (1) conflicting selection pressures on weeds in agroecosystems, (2) feed-back driven dynamics of human-weed co-evolution, (3) co-evolutionary mechanisms of weed adaptation in conjunction with other weed species or organisms, and (4) the role of weed evolution in the restoration of agroecosystems. Researching these areas requires study of entire ecological communities, which is contrary to narrower approaches traditionally followed by weed scientists. Similar challenges have been issued to weed scientists in recent years (Radosevich, 1998; Zimdahl, 1999; Mohler, 2001), and the need for weed scientists to respond to the invasive species issue has been made clear (Westbrooks et al., 2001). Thus, studying adaptability of cropland weeds provides a promising avenue for the incorporation of ecological theory into weed science. In turn, this further incorporation of ecological theory will provide important practical information on developing sustainable agroecosystems—sustainable even in the face of the inexorable evolution of weeds.

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