

Co-evolution of domesticated crops and associated weeds

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ABSTRACT. Crops and weeds co-evolve in particular plant communities that are assembled in agro-ecosystems. In this essay we discuss the mechanisms determining this co-evolution and the processes regulating the success of individual populations within crop-weed communities as a starting point to evaluate and interpret which are the risks of promoting invasive species due to technological changes introduced into cropping activities. We follow a framework considering co-evolutionary mechanisms (namely, genetic variation, breeding system and selective forces) and demographical processes (namely, establishment, competition, dispersion) as a way to predict, not only how weeds will evolve in agricultural land, and thus how new problems for production of food and fibre arise but, also to evaluate the risk of generating species that might affect other semi natural and natural ecosystems.

[Keywords: evolutionary mechanisms, demographical processes, weeds, crops]

RESUMEN. **Coevolución de cultivos domesticados y malezas asociadas:** Cultivos y malezas coevolucionan en las comunidades vegetales que se estructuran en los agroecosistemas. En este ensayo discutimos los mecanismos que determinan esta coevolución y los procesos que regulan el éxito de poblaciones individuales dentro de las comunidades cultivo-malezas. Tomamos esto como punto de partida para evaluar e interpretar cuáles son los riesgos de promover especies invasivas a causa de cambios tecnológicos en las actividades agrícolas. Para ello, seguimos un marco conceptual que integra mecanismos coevolutivos (i.e. variabilidad genética, sistema reproductivo, fuerzas selectivas) y procesos demográficos (i.e. establecimiento, competencia, dispersión) como una forma de predecir no sólo cómo las malezas evolucionan en los campos agrícolas, interfiriendo así con la producción de alimentos y fibras, sino también para evaluar el riesgo de generar especies que puedan afectar otros ecosistemas.

[Palabras clave: mecanismos evolutivos, procesos demográficos, malezas, cultivos]

INTRODUCTION

The humanity is fed by a reduced number of cultivated species, mostly annual species such as wheat, maize, rice and soybean (Evans 1993). Crop production systems based on single annual species were developed in early agriculture and are still widely used to supply human needs. Cropping systems, as they are

presently known, have greatly modified natural ecosystems in order to provide a habitat to domesticated species on which people depend for food and fibre (Cox & Atkins 1979).

Since the expansion of humans over the world, agriculture has contributed to develop a scenario in which the land is periodically disturbed by different means like grazing, burning or tilling. In annual crops production

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systems, land disturbance usually begins with the soil primary tillage that is followed by the sowing of the crop seeds. The crop seeds then germinate and develop into fast growing plants producing a strong demand for resources. After crop maturity the levels of soil resources begin to increase due to biologically controlled transformations of the crop stubble and soil organic matter, and the accumulation of water. Therefore, the land in these production systems undergoes a regular disturbance pattern, with periods in which live plant cover is very high, causing a strong depletion of soil resources followed by periods in which soil cover by live plants is low and resource availability is high. This new ecosystems created by these kind of activities are frequently referred as agro-ecosystems (Odum 1971; Soriano 1971). The cyclic pattern provides assembly conditions for particular plant communities, where immigrating species get established especially during the low cover phase of the cycle when the land is prone to be invaded by any plant species (Salisbury 1961; Ghersa et al. 1994; Ghersa & León 1999). Weed communities are assembled through strong selective forces that occur since the invading species begin to establish, and determine the species that survive and the direction of both, evolutionary patterns and succession (Harlan 1982; Ghersa & León 1999; Booth & Swanton 2002).

In this essay we review existing information on the ways in which crop and weed species coevolved in agro-ecosystems and use this information as a theory framework to discuss the processes determining weed-crop co-evolution and the mechanisms regulating the success of individual populations within crop-weed communities. This may be viewed as a starting point to evaluate and understand which are the technological changes in cropping activities that promote the risks of establishment of invasive species.

THE ORIGIN OF WEED SPECIES

At early stages of agriculture, the new man-made habitats were colonized by pre-adapted species originated in areas with natural cyclic disturbance regimes. For example, many *Amaranthus* spp. that colonized riverbanks be-

came part of the agro-ecosystem structure (Sauer 1988). The agriculturist soon found that some of these plants could be useful as sources for food or fibre, learned how to identify them, and later how to sow and harvest them; thus, recognising them as crops. In the domestication process some wild plants resulted in crops adapted to the simplified and ever changing environments of agro-ecosystems. A parallel process of adaptive trait selection was happening to other species in the agro-ecosystem, which originally were viewed as useless and are now recognised as weeds (Harlan & de Wet 1965). Weeds are defined in various ways but, in a broad sense, weeds are any species interfering with human goals (Radosevich et al. 1997). As a result, in spite of the characteristics enabling the species successful establishment in a particular land area used for human purposes, social values will contribute to determine whether a plant species is a weed or not. For example, when the cropping area was expanded to marginal sites, weeds of many crops became the cropped species, as they were conspicuously better adapted to the new environment than the crop (Tarrant 1978). The social value is the basis of the criteria used to classify problems related to the presence of weeds or weed levels, which in turn determines the kind and magnitude of reaction in the form of human actions that will be used to solve them (Radosevich et al. 1997).

Co-evolution involves reciprocal natural selection between two or more groups of organisms with close relationship, but without exchange of genetic information between the groups, i.e. without interbreeding (Ehrlich & Raven 1965). As proposed by Harlan & de Wet (1965), the process by means of which crops and weeds evolve in agro-ecosystems fits into this co-evolution concept. During crop domestication, selection pressures were directed to improve those traits that contributed to better crop performance, increase yields and adapt species to soil and climate conditions. As these changes were fixed into the cropped plants and the environment is disturbed and manipulated to improve production, individuals of the spontaneous accompanying vegetation reacted to the ecological changes imposed by human activities. The reaction of spontaneous species, when integrated over time at the population

level, resulted also in adaptive changes. Therefore, it is possible to suggest that the primary origins of crops and weeds arose from wild species through selection and adaptation to the recurrent disturbances and concentrated availability of resources released by agro-ecosystems. However, two more origins of weeds are frequently considered; (i) weeds have also arose from cultivated species that escaped or were abandoned from domestication and remained as weeds; and (ii) weeds have appeared due to hybridisation and introgression between crop and wild species (Harlan 1982; Evans 1993; Ghersa et al. 1994). In any case, co-evolution, as described above, may be considered the driving force for the development of most weed species recognised in modern agriculture.

Weed species are present as components of plant communities. A plant community is frequently defined as an assemblage of species that occur in the same space and time (Begon et al. 1996). Plant communities are dynamic and vary in composition and structure over time and space; therefore, there are difficulties in precisely define their components and boundaries (Crawley 1987). Nevertheless, it is possible to accept that, within a particular geographic range and cropping system, weed communities are stable structures that may become quite uniform and predictable from year to year (León & Suero 1962; de la Fuente et al. 1999; Ghersa & León 1999). Then, several authors have argued that the ecological theory on structure and functioning of communities could be applied to weed communities in order to feed practical knowledge of agronomy and weed science with a broader theoretical framework (Soriano 1971; Radosevich et al. 1997; Booth & Swanton 2002).

A THEORETICAL FRAMEWORK: CO-EVOLUTIONARY MECHANISMS IN CROP-WEED COMMUNITIES

Today's weed floras have survived all previous weed control efforts, incorporating demographic traits such as fluctuating temperatures requirements for germination and resistance to herbicides, among others. The frequent and periodical disturbances associated to crop

management have selected weed traits that stabilised floristic composition of weed communities (Martínez Ghersa et al. 2000). Weed phenology, for example, has been finely moulded to fit the patterns of cropping activities along farms and regions.

The process of adaptation that occurs in weed species can be understood considering three basic plant population characteristics; (i) genetic variation, (ii) breeding system and (iii) selective forces imposed on the weeds populations by agricultural practices. Despite any of these characteristics operates at the population level, their effects are also expressed at the community level.

(i) Genetic variation. Widely distributed weeds have maintained genetic variability by particular genetic systems. These genetic characteristics of the population have a strong influence on species ability for range expansion. The response of weeds to selection depends on the heritable variation into their populations. Genetic variation of populations constitutes the basic genetic architecture upon which natural and human selection act, providing weeds with attributes adapted to agricultural systems. Then, we should consider the importance of genetic structure of the species to study evolutionary aspects of weeds. For example, additive genetic variance, epistasis, genomic rearrangement and chromosomal translocation and auto or allopolyploid are significant traits considered the substrate for evolutionary adaptation (Lee 2002). Evolution implies the selection of those phenotypes that express adequately the interaction between genetic and environmental variation. As a consequence of selection, genetic and phenotypic variation is reduced among succeeding individuals possibly affecting the fitness of weed species to invade future scenarios into new cropping systems. This implies that if weeds evolved towards specialised genotypes that fit some particular agro-ecosystems, they would need some way of maintenance of genetic variation into the weed population to avoid future failure or extinction under altering environments.

(ii) Breeding system. Plant evolutionists have speculated about the role of the breeding system of plant species in relation to their ability

to invade and become weeds. In general two fundamental types of systems can be considered: (i) sexual reproduction that increase genetic variability, involving autogamy and allogamy, and hybridisation; (ii) asexual reproduction, which restrict variation, including vegetative propagation and apomixis.

Several hypotheses were proposed conferring some adaptive advantage for weediness linked to uniparental reproduction (i.e. self-fertilization or agamospermy) with occasional genetic recombination (Baker 1974). Species with vegetative reproduction have proved to show more fitness to persist in particular cropping systems (Southerland 2004). According to Baker (1974) many weed species utilize breeding systems adapted for inbreeding or vegetative reproduction to produce stable duplicates of successful genotypes, coupled with occasional out-crossing for recombination to occupy new niches. For example, *Bromus tectorum* (L.) follows this type of strategy when invading *Artemisia* dominated grassland in the west of USA. *B. tectorum* increases its population size following removal of native perennial grasses by overgrazing or fire. After being seriously disturbed, in the *Artemisia-B. tectorum* community a great portion of the competing vegetation dies, excluding some *B. tectorum* seeds. The surviving seeds give raise plants in sites of high resources availability; here phenology of *B. tectorum* changes increasing the probability for cross-pollination. Because each plant is essentially an inbred line, a great heterosis is present in the weed population during the second year after disturbance. Following the hybrid generation recombination that occurs, the wide expression of genetic variation contributes the species to occupy a great number of sites in this habitat. Successful genotypes resume self-pollination duplicating and increasing the frequency of the more adaptive ones. Although, there is no general rule of adaptation, many examples from the literature confirm a greater participation of species with these attributes in the weed flora (reviewed in Radosevich et al. 1997).

In addition, human breeding alters genetic structures of the species modifying their tolerance and behaviour and might facilitate weed successful. Selection of new genotypes for spe-

cific purposes or indirectly, through the breeding of new genotypes of crops to be integrated with specific environmental management (e.g. high doses of fertilization, specific herbicides or pesticides) could act as selective forces.

(iii) Agricultural practices as selective forces.

Many physiological or morphological weed characteristics have arisen from natural selection imposed by biotic, e.g. by competitors or predators; or by abiotic factors, e.g. temperature, photoperiod, herbicides and crop management, enabling the species to produce more seeds or increase the dispersion ability into new habitats (Harlan 1982). However, human selection might act on species traits to confer them some kind of demographical advantage (Palumbi 2001). Present technology has a high transformation power; it aims to correct deficiencies in soil water and nutrients and to disturb enormous areas of land by removing natural or spontaneous vegetation. However, at the same time, once a production system is adopted, no great technological changes occur. When an environment is stabilized by agricultural practices, selection pressures led to changes in the genetic structure of weed populations and selection tends to favours those traits of weeds that converge to fit vacant niches left by cropping systems. Changes in seed dormancy, plant morphology, phenology, herbicide resistance, etc., are well-documented evolutionary processes observed in weed populations as a consequence of cropping practices (Ghersa et al. 1994).

Human intervention acts on species that exhibit different extent of adaptation to local conditions. It means that the rate of change in farming practices within a given geographic area would have exceeded the rate at which weed species could genetically adapt to new habitats. This could determine that, during the last century, co-evolution of crops and associated weeds would have been limited to periods when no important technological changes were adopted (Ghersa et al. 1994; Martínez Ghersa et al. 2000). During this time community dynamics would have been conducted by changes in species composition in a successional way where species composition would have responded to biotic-abiotic interaction at population level.

POPULATION-BASED MECHANISMS AND CROP-WEED CO-EVOLUTION

Although agriculture did not develop linearly neither in space nor in time, some general patterns have been proposed since the introduction of agriculture (Ghersa & León 1999; Martínez Ghersa et al. 2000). Agriculture tended to produce the collapse of the native plant community with a sudden decrease in the number of species from the original grassland or woodland communities. Original communities were impoverished producing a crop-weed community less diverse. Thereafter, the agricultural landscape was continuously invaded by weeds. Exotic and native species increased the species richness of the crop-weed community. Based on historical records, there are many examples in the literature pointing out the effects of cropping systems on associated weed communities (Fryer & Chancellor 1970; Haas & Streibig 1982; Ghersa & León 1999; Martínez Ghersa et al. 2000).

Weeds result from selective forces that are imposed on spontaneous plant species living in habitats in which a significant proportion of the environmental conditions are manipulated by human actions. Ghersa and León (1999) suggested that weed communities of the arable soils were responsive to environmental changes with effects in the short and long term. Short-term effects are related to farming practices, including periodical and seasonal variation; instead, long term effects are imposed by soil deterioration and climate change. Once weed species are available, problems begin as soon as human control on species is no more effective and they spread into productive areas or into other areas-off their limits.

Under this broad perspective weed species invasion process can be described as requiring, three phases: (i) *introduction* of any propagule (seeds or vegetative units) via natural or human transport into a new area that may allow to establish populations of adult plants, (ii) *colonisation*, when the introduced populations increase in number or individual biomass, becoming self perpetuating and (iii) *naturalisation*, when populations undergo

widespread and are incorporated into the local flora (Cousens & Mortimer 1995). Despite these simple and useful ideas to describe weed invasions, improvements in our understanding on adaptation of plant populations to habitats with different levels of human disturbance require a mechanistic approach to the co-evolution of crops and associated weeds. More specifically the weed infestation process may be described mechanistically considering *establishment-competition-dispersion* as three closely interrelated key processes that assure persistence of weed species in agro-ecosystems. This requires the interaction of three phases of weed invasion into a minimalist perspective considering demographic parameters and populations interactions of wild and domesticated species. This view brings the co-evolution of weeds and crops into a completing framework, which may help to consider past changes in the weed flora and to forecast some trends in future weed community composition, predict risks and performance of weed species, due to new crop production technology.

(i) Weed establishment. A minor proportion of the seeds produced by adult plants are exported, die or germinate, but most of them are maintained in the soil to constitute the seed bank of a weed population (Thomson & Grime 1979). The last point responds to a common physiological attribute of weed seeds populations known as dormancy. Dormancy is important in the long term subsistence of species in disturbed habitats. Seed dormancy mechanisms can be released by environmental signals such as particular range of temperatures, light quality or intensity (Benec Arnold et al. 2000). The dispersion of germination (establishment) through time is generally considered to be an adaptative strategy of seeds to avoid hazardous environment during seedlings establishment (Harper 1977). When wild species were domesticated, seed dormancy was eliminated because most cropping systems require germination and establishment of species to occur within a very short time after planting (Simpson 1990). However, when an agricultural cycle begins, the farmer unintentionally operates on the entire system opening niches for other species. Weed species with the same germination requirements than the crop are usually selected by their convenient traits ad-

justed by cropping practices. Crop rotation, tillage, sowing and harvesting time affect the length and opportunity of disturbances, plant and stubble cover, and weed-crop interference throughout the year. All these may influence temperature and soil moisture affecting both the dynamics and intensity of seed dormancy with important effects on both the time and extent of germination-establishment of weed species. Temperature has been identified as the main factor governing the degree of dormancy in temperate zones. There are evidences that soil moisture could also modulate the level of dormancy. Other factors than temperature and water, as alternate temperature, light and nitrates have been indicated as modifiers of seed dormancy release. Fluctuating conditions imposed by repeatedly cropping affects environmental parameters opening and closing opportunities for seed germination and establishment of many weeds (Benech Arnold et al. 2000).

For example, in temperate areas a maize/soybean-weed community at crop harvesting constitutes a very low productivity system with low cover under conventional tillage. Usually some tillage labours are performed during autumn-winter period to prepare the sowing of the next crop. Tillage buries weed seeds of species that may require a burial period of some months to subsequently germinate in the cropping system. As a crop management technique is regularly repeated, those species that succeeded in predicting high resource environments and survive cropping activities sequences are selected. This is the case of *Datura ferox* (L.) an important weed of soybean that possesses seeds with high levels of dormancy when their capsules ripen at crop harvest. There are evidences that *D. ferox* has adjusted the time and rate of germination to the cyclic labours performed under the conventional tillage soybean cropping system. Some studies reported that nearly 17% of the weed seeds completed the germination-establishment of seedlings in the first spring, when the seeds are moved by tillage to the soil surface after being buried, while weed seed loses during winter and early spring fluctuated between 20-50 % (Soriano 1971; Scopel et al. 1994). Most of the weed seedling emergence occurs within one month after crop sowing (Ballaré et al.

1987a). The persistence of a weed seed bank is related to the degree of dormancy after dispersion and to the environmental regime that release dormancy and/or induce secondary dormancy. Such traits of the weed have co-evolved with the crop and were modulated by cultural practices to fit the season with favourable conditions for seedling development and plant growth into the soybean crop. Furthermore, combine harvesting of soybeans favoured the dissemination of the seeds of this weed, thus causing extraordinary representations of *D. ferox* populations in weed communities (see below).

Abrupt changes in the habitat may disrupt the adaptation of species to a crop system; this happened when the no tillage technology was introduced in dryland areas of South America. The no-till system altered the germination-establishment process of the weed population dynamics. A great proportion of seeds remained on the soil surface, becoming more susceptible to predators and reducing their number; at the same time, the physiological condition of the surviving seeds changed, because the new environment reduced the opportunity of releasing seeds from dormancy. The fitness to frequent conditions in previous conventional cropping systems conditions failed in a new scenario and few species had the ability to shift, therefore adapting to new conditions.

Species such as *Tagetes minuta* (L.) have low seed dormancy levels at harvesting. The weed has weakly adjusted its life story to cropping systems and it appears to depend on various processes to persist. Germination-establishment of *T. minuta* varies with tillage system and the depth seeds are buried after dispersion (Cepeda 2002). Under no tillage most of the non-dormant seeds are able to germinate; on the contrary, under conventional tillage seeds are located belowground, diminishing the number of seeds in the upper layers of the soil. In no tillage cropping systems, to persist, the weed populations depend on the crop and the associated scheduling of cultural practices. In no tillage maize, *T. minuta* may germinate immediately at crop harvest forming an autumn weed community, while if it is buried by tillage; seeds remained in the soil until the next

spring-summer sowing (Soriano 1971). The early sowing of maize reduces the germination-establishment of weed plants due to low temperatures, in both tillage systems. This allows to this weed to escape from common pre-sowing control procedures. However, the relative number of individuals emerging under no tillage is higher, due to the high mortality rate of buried seeds under conventional tilled systems. Not only the tillage system affects the weed; *T. minuta* population dynamics is also affected when the crop sequence is altered. In soybean crops most of the established weed plants are killed when herbicides are applied immediately after sowing. As a consequence, *T. minuta* germination-establishment characteristics have evolved according to a complex group of interacting environmental factors associated to crop rotation and management selective pressures. This makes *T. minuta* adaptation to cropping systems in temperate areas more difficult. However, Ghersa and León (1999) proposed that actually *T. minuta* shows adaptation to long-term factors, i.e. processes related to soil deterioration and pest outbreaks in cultivated lands. The authors showed that, under degraded soils, *T. minuta* might be highly successful and better adapted than many other species of the summer-crops weed community. Such mechanisms of long-term adaptation have allowed the species to increase its participation in the weed community and weed infested area of the pampas in Argentina, during the last 30 years. It appeared that the weed ability to produce terpenoids and thiophenes that are active biocides against predators might have had an important role in the performance of *T. minuta* (Gil et al. 2002). Moreover, the production of metabolites has already been related to stress tolerant plant strategies capable of invade these degraded environments (Grime 1979).

(ii) Competition. Competition is a process where two or more proximal individuals interact each other for the capture and use of resources that are not supplied in sufficient quantity to meet their combined demands (Satorre 1988). Competition primarily occurs for water, nutrients and light. Time of crop emergence relative to weed populations is one of the main factors controlling the outcome of plant competition. Hence, the previously dis-

cussed key process is strongly linked with the result of competition. Competition acts at the individual and population levels and takes place during ontogeny of species.

Competition actually performs as a double transformation process, whereby plants and environment in which they exist affect each other. It may be modified through the flux of information and the relationships of dominance among species. Recent studies have demonstrated that plants are capable of modifying the local environment, translating subtle signals produced by neighbours. Some species have evolved to have a sophisticated advisory system that anticipates competition, thus being able to change the structure and function of the community (Ballaré et al. 1987c; Ballaré & Casal 2000; Rajcan & Swanton 2001; Maddonni & Otegui 2004). This mechanism of information would guide species to adapt its morphology and phenology to local habitats and scenarios of plant interaction. In this sense, cropping systems contribute to promote weed populations that follow two strategies: (i) maximising the competitive ability of weeds or (ii) minimising the negative effects of crop competition. In the first case, weeds modify plant architecture (i.e. height, branching ability, leaves angle, etc.) or plant growth rates in order to capture soil or light resources. In the second case, weeds tend to develop strategies that permit them to avoid or tolerate crop competition. For example, *Cynodon dactylon* (L.) Pers. is a perennial species of low growing habit that spreads in the field forming patches constituted by aerial stolons and subterranean rhizomes. This species is highly competitive for soil resources, but it is a poor competitor for light. Its biomass and spatial growth may respond differently to shading when they are under competition from crops. While *C. dactylon* biomass is strongly reduced from 41-50% shading, patch extension rate is only reduced when 74-85% shading levels are reached below the crop canopy. Therefore, weed biomass partitioning is modified by shading; the patch extension rate diminished linearly only when patch biomass growth rate was lower than 1.66 g per day, above this threshold value, the extension rate remained constant (Guglielmini & Satorre 2002). This characteristic let the weed to tolerate light com-

petition from the crop and still grow in empty gaps to sustain the patch green area and colonisation rates under higher shading treatments. The foraging strategy of *C. dactylon* has been also documented in several clonal plants as an adaptive response to both, heterogeneous light and nutrient resources. Foraging strategies were identified in stolon-forming *Glechoma hederacea* L. (Slade & Hutchings 1987), *Hydrocotyle vulgaris* L. and *Lamiastrum galeobdolon* (L.) Ehrend. & Polatschek (Dong 1995) and in the rhizomatous species *Hydrocotyle bonariensis* Comm. (Evans & Cain 1995). Similar effects were reported from plastic responses found in several species, when they are capable of elongating their internodes to concentrate their leaves above the companion crops and rotate their leaves to avoid competition (Ballaré et al. 1987c; Ballaré & Casal 2000; Rajcan & Swanton 2001; Maddonni & Otegui 2004).

(iii) Dispersion. Weed invasion begins with dispersal. Cultivated forms of many species as cereals crops, were selected to have persistent spikelets on the inflorescence at maturity; whereas related weed species, as wild oat (*Avena fatua* L.), has the ability to disperse seeds after an abscission layer is formed between the rachis and the spikelet. Many weed species have seeds with well-adapted appendages to assist them moving to great distances. However, most weed seeds tend to migrate as an advancing front with the greatest concentration of seeds below or only at a short distance from the parent plants. Relative to the total amount produced few seeds may be able to disperse widely. Those, which are dispersed, tend to colonise as isolated individuals and, after density increased locally, they spread as a front. However, weed invasion processes are strongly associated with human activities and weed propagules can travel great distances as contaminants of seeds or transported by machinery or irrigation water (Salisbury 1961; Cousens & Mortimer 1995). Frequent disturbance regimes of agricultural systems offer periods of high resource availability and low plant cover and biomass; in most cases, colonisation of new areas is strongly dependant on the occurrence of such periods and the number of propagules deposited in that area (Auld & Coote 1990; Ghersa & León 1999).

Debate

This determines that in the case of early settlers, the availability of favourable habitats is limited to invasive weeds but, for most weed invasion processes in modern agriculture it is likely that dispersal is often limiting (Cousens & Mortimer 1995). Therefore, the potential rate of dispersal of weeds will depend on the different modes of dispersal that may adjust into particular systems. Some successful invasive weeds have propagules with high ability to disperse. This is, in turn, a property of the propagules by itself (shape, size, etc.), which has evolved in combination with vehicles present in the agro-ecosystem, as wind, water, animals (epizoochory and endozoochory) or human activities (Crawley 1987).

An example of the association between seed dispersal and cropping activity is found in *D. ferox* in soybean crops. Harvesting combines collect more than 90% of ripen capsules and return between 7 and 40% of the captured seeds to the field. This increases seed production per dispersed plant due to a reduction of the intraspecific competition (Ballaré et al. 1987a & b). In a wide area of the Rolling Pampas of Argentina the introduction of soybean increased *D. ferox* population in the weed community. Moreover, the weed population growth was registered under conventional tillage that has been recently curtailed due to the adoption of no tillage in the region (see above).

On periodically disturbed lands, the high dispersion rate of weeds plays a central role in the species success. However, the three commented processes (establishment, competition and dispersion) have to be connected in some way into the species life cycle to overcome the phase of invasion and secure the persistence of the weed.

Linking processes

Various ecophysiological models have been developed to provide insight into single crop-weed processes, such as competition (Spitters & Aerts 1983; Kropff & Spitters 1992; Vitta & Satorre 1999). Most of these models have been biomass centred and did not link the above key processes of weed population dynamics and community structure.

The effect of weed establishment on competition has been explored in various experiments. Among others, Joenje and Kropff (1987) have studied the effect of relative time of weed emergence on competition output. Following germination-establishment, competition between crop and weeds will largely determine the amount of resources captured by each component in mixtures. The main attributes that confer competitive ability to each population are: (i) the relative time of emergence of each competitor; i.e. the earlier a competitor establishes the more competitive it tends to be; and (ii) the capacity to establish a great number of individuals. The density of individual weeds and the dominance relationships among competing species finally determine dispersion of components within a weed-crop community.

The links between competition and dispersion ability of weed has been only scarcely explored through simulation models with annual species (Maxwell & Ghera 1992) and experimentally in a perennial grass (Guglielmini & Satorre 2002). These studies demonstrated that, from the crop perspective, the seed dispersal ability of a weed species might be more important to crop yield than the relative competitive ability of the weed with respect to the crop. This would affect not only the crop benefits, but weed demographic parameters as crop competition on weeds is reducing. On the other hand, some studies have shown that competition is strongly linked to dispersion, as in *C. dactylon* vegetative spread, where this was stated through the effect of competition on biomass partitioning and spatial growth of weed patches (Guglielmini & Satorre 2002).

Establishment and dispersal has been operated as efficient mechanisms for woody weed species (mostly trees) invasion of crop fields, providing another model of linked processes. Woody species invade corridors and cropped fields under no tillage in the Rolling Pampas (Ghera et al. 2001). However, most researchers agree that to perform successfully as new components of weed communities, these species need habitats greatly affected by human activities. In highly productive areas of Argentina, for example, all trees species were introduced by European immigrants who planted

the species in patches near their houses and across the landscape. Therefore, humans efficiently dispersed them following the advance of colonisation and land tenure. At present, no-till agriculture technology is creating new conditions for the establishment and growth of woody species. This environment has allowed trees species such as *Gleditsia triacanthos* (L.), *Melia azedarach* (L.) and *Fraxinus americana* (L.) to invade cropping fields (Ghera & León 1999; Ghera et al. 2001). Moreover, in the middle of these processes, functional characteristics of the community have changed. In some cases, woody species such as *G. triacanthos* emerged into the weed community as dominant contributors to plant biomass (Ghera et al. 2001). Some of these species, as *G. triacanthos*, have been previously reported as invaders to some other habitats (Grime 1979; Facelli & León 1986). This supports the idea that, independently of human role in those processes, some specific genetic characteristics allows it to adjust to various environments. Invasive species, including weeds, have been viewed as having a physiological broad tolerance or plasticity (Williamson 1996) but, recent studies suggest that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on intrinsic physiological characteristics (Lee 2002).

Herbicide resistant weeds provide another example of linked processes. In the last twenty years, various studies have documented evidence that, repeated applications of herbicides with similar mode of action impose a selection pressure leading to resistance, in previously susceptible species (Radosevich et al. 1997). However, although herbicide resistance implies an evolved response to herbicide at physiological level, it also involves a biological cost to the selected populations, which is usually translated to demographic parameters, as well as to the relative competitive ability of plants during their life cycle. In some cases, other ecological processes of surviving phenotypes may be affected, in a way that plant fitness is reduced. Fitness describes the potentially evolutionary success of phenotypes with demographic characteristics adjusted to specific cropping systems. There are numerous reports showing that weed resistance is accompanied

by reduced fitness once the herbicide is not used. Once more, establishment-competition-dispersal processes need to be assessed to define the species fitness. For example, genotypes resistant to triazine herbicide are less fit than susceptible genotypes; when the herbicide is removed natural selection tended to restore susceptibility (Warwick & Black 1994; Jasieniuk et al. 1996).

Several other traits of weeds appeared to evolve under selective forces of agricultural practices. Crop mimics has allowed some weeds to escape control effects and to alleviate weed competition with complementary requirements. For example, *Avena fatua* (L.) matures at a similar time than wheat and, it has morphological characteristics alike the crop, but larger seeds. At harvest, *A. fatua* panicles are collected and threshed with crop spikes. A high proportion (ca. 75%) of weed seeds may be captured by the combine and, hence, widely dispersed from combine cleaning dispositives. Other example, of crop mimics is provided by *Echinochloa crus-galli* (L.) Beauvais. In rice fields, *E. crus-galli* is a mayor weed. Barrett (1983) indicates that mimetic forms have evolved from primitive agricultural systems to modern mechanized rice culture under rice production systems.

Many weed species have evolved as a result of the production activities carried out by humans over centuries, and some of them have spread on invaded vast areas of the world (Salisbury 1961; Harlan 1982). Lifespan is one of the most significant life story traits that distinguish weed condition. Weeds are more likely to be annuals and biennials and less likely to be perennials than non-weeds (Southerland 2004). This is not surprising because weed cycle co-evolved according with the most general cropping cycle.

Undoubtedly crop breeding and cropping activities allowing for seed and gene flows among distant areas and related species, have contributed to exacerbate the generation of species complexes, which are especially important for plant speciation process occurrence (Grant 1989). Weed speciation process has allowed the continuous generation of popula-

tions adapted to disturbed environments such as those well-described cases in the *Amaranthus* spp., *Avena* spp., *Echinochloa* spp., *Lolium* spp. and *Sorghum* spp. (Mc Whorter 1971; Baker 1974; Jauhar 1993a & b; Radosevich et al. 1997; Lee 2002). Surprisingly these species complexes with high adaptive potential were not very successful in generating populations that are able to invade into areas with little or no disturbance and covered with natural or semi natural vegetation, as can be recognized for example in work carried out in the Pampas grasslands (Perelman et al. 2001).

CONCLUSIONS

In the last decades, technological developments have been concentrated in the use of herbicides to kill weeds, reducing the number of weed individuals and their effect on crop yields and quality. However, weed problems still persist in cropping systems, either old or new. Relatively little attention has been paid to the understanding of the process of weed development and of the mechanisms regulating their success in agricultural land. Recently, this has been seen as a starting point to predict the direction of the organisation of weed communities under innovative crop production technologies. New, previously unseen, technologies may strongly affect the structure and functioning of weed communities. Some preliminary models have been proposed to predict weed changes from the adoption of new cropping techniques based on the relative success of weed populations to sort out key phases, establishment, competition and dispersion. However, such efforts are still fragmented. An integrated framework considering co-evolutionary mechanisms and demographical processes is needed to predict, not only how weeds will evolve in agricultural land, and thus how new problems for production of food and fibre arise but, also to evaluate the risk of generating invasive species that might affect other semi natural and natural ecosystems. Such an integrated theoretical framework would undoubtedly contribute to design new concepts of weed management strategies, considering them as components of dynamic complex agro-ecosystems.

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