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Competition experiments on alien weeds with crops: lessons for measuring plant invasion impact?

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Abstract

Can we quantify the impact of invasive species? Here we use the per-plant competitiveness of alien weeds on crops as a model of invasive species impact in general. We reviewed 97 weed–crop competition experiments in 32 papers that included 30 alien weed and 14 crop species. The majority (68.92%) were randomised block designs where the alien weed had been either added (additive experiments) or removed (removal experiments). We propose using the relative competition index to estimate the effect of alien species in all systems, specifying in each case the density and proportion of alien and native plants essayed. We found that the impact of the weed cannot be considered independently of the crop and, thus, we should be cautious in ranking weed species according to their competition effect. A similar situation can be postulated for alien plants interfering with native species. Invaded communities are not random assemblages, and researchers tend to study the most competitive alien plants. We also found that the effect of the weed on crop yield depends on the duration of the interference and the life-history stage of the weed–crop system at which the interaction takes place. We were not able to conduct a more rigorous comparative analysis of the impacts, such as a meta-analysis. To do this would require some measure of the variation of the competition effect such as standard deviation or standard error, which we found are almost never reported.

Introduction

Invasions by alien species can have an impact at several levels of ecological complexity from genes to ecosystems (Parker et al. 1999; Mack et al. 2000). However, the ecological impact of ecological invasions is often difficult to measure (Williamson 1999). How do we measure whether the impact of one invasive species is higher than that of another, or that its impact is higher in one ecosystem than in another? Parker et al. (1999) proposed that the impact (I) of an alien plant invader comprised the following three ecological components: size of the new distribution range (R), average abundance per unit area across the new range (A) and effect per individual or per biomass unit on native species (E):

$$I = R \times A \times E.$$

The size of the new range can be obtained by regional grid surveys, networks of permanent plots, museum/herbarium records, and remote sensing; abundance can be interpolated from sampling field studies. Quantification of the effect per individual or per biomass unit of alien plants is not straightforward, but it sometimes can be estimated using competition intensity indices (CI).

Competition intensity indices are the most useful tools for quantifying the size of the competitive effect, and in the last decade they have been widely used in field competition experiments conducted in natural systems (Grace 1995; Goldberg et al. 1999). CI quantify the proportional decrease in plant performance due to competition, and allow the comparison of the competitive effects of different species or the competitive effect of a species in different environmental conditions. Furthermore, CI are consistent indices for comparing differences among independent studies (Gurevitch et al. 1992; Goldberg et al. 1999). In this paper, we explore the use of CI for studying crop–weed systems.

Agroecosystems are systems where alien species have a tangible economic impact due to crop yield loses (Cousens and Mortimer 1995). Pimentel et al. (2000) reported that in USA alien weeds cause an overall reduction of 12% in crop yield, which represents approximately $23.4 billion in lost crop annually. In addition, the total economic impact should include the costs of herbicides applied to control the weeds, the consequences of herbicides for environmental and public health, the effect of crop yield on the crop price and the impact that these alien weeds have on adjacent natural communities. The impact of alien weeds will increase worldwide as developing countries pursue export markets and traditional agroecosystems are increasingly converted to large monocultures (Norgaard 1987).

Imports of grain are a major source of alien weeds (Suominen 1979). As the regional and local rates of introduction of grain gain pace there is an urgent need to predict the identity of the worst alien weeds to prevent and control their spread. Quantitative indicators could provide risk assessment measures to help in deciding which alien weeds have the greatest impact. Predictions should be based not only on the species characteristics (i.e. life-history traits, taxonomy, rate of spread) but also combine information on the interaction with the receiving community, in this case the crop. Competition between crops and weeds has been the subject of much research (Zimdahl 1980; Spitters and van der Bergh 1982; Cousens 1987; Glauninger and Holzner 1982). However, until now there has not been much interaction between researchers working on the interference of alien weeds on crop production and researchers focusing on the impact of alien plants on native species.

In this paper, we review competition experiments between alien weeds and crops in an attempt to investigate the implications of these experimental approaches for understanding plant invasive impact. We synthesise in a quantitative way the per-plant competitiveness of alien weeds on crop yield with the following main objectives: (1) to discuss the outcome of the methodology used to analyse the competitive effect of alien weeds on crops; (2) to consider whether it is feasible to rank alien weeds by their competitive effect on crops, that is, to determine if alien weeds of very high competitive intensity can be distinguished from the rest; and (3) to highlight some of the issues related to weed–crop interaction than can be of interest to study alien–native plant interactions in natural systems.

Methods

Literature search

We searched all published papers on competition between alien weeds and crops in the Life Science Collection from the Current Contents Collection from 1986 to mid-1999. We also checked citations from these papers to older studies, and others published but sometimes not listed in Current Contents. Several of these studies have been published in Symposia or other scientific meetings. However, because Proceedings are often very difficult to procure we could not include them all in the analysis. Our database contains data from published articles selected according to the following criteria:

(1) We selected those publications reporting the effect of alien weeds on crops and not the ones reporting the effect of crops on alien weeds. In most studies we had to check if the weed was alien or native. Studies with native, multiregional, cosmopolitan or cryptogenic weeds were excluded. Studies where several weed species were competing simultaneously were excluded. Similarly, we did not use studies conducted with mixed crops.
(2) The study was an experimental manipulation of the abundance (e.g. density, biomass, and cover) of the alien weed or the crop or both. The competition treatments were compared with an appropriate control performed simultaneously and in the same place. We excluded from our analysis observational studies (i.e. spacing, correlation,

or neighbourhood analysis, changes through time and comparisons between sites with and without alien species) because confounding effects may be present.

(3) Although we are aware that only field experiments can prove that there is competition (Aarsen and Epp 1990), we also surveyed experiments conducted in controlled growth chambers, glasshouses and common gardens because several approaches are required for an adequate evaluation of competition (Roughgarden 1983).
(4) From each study we gathered information on the type of experiment, the alien weed and crop species involved and data on the crop species performance or crop yield at different competition treatments.
(5) In competition studies, several parameters of plant or crop performance are usually measured. We selected only the ones related to yield or any parameter relevant to the produce for which the crop species is cultivated (e.g. number of pods/plant for legumes).
(6) In some studies, the measurements were conducted at several points in time. To overcome problems with the non-independence of data, we only used the measurement taken at the end of the experiment (Gurevitch and Hedges 1999). When several experiments were reported in the same publication that was conducted on the same pair of species, for example at different sites or for different years, we treated the studies as independent.
(7) We did not quantify the effect of interactions with other treatments. When the study was multifactorial (e.g. pesticide application to reduce natural loads of insects), we chose to compare the treatments that were most similar to natural conditions.

Calculation of the size of the effect

A wide set of CI is available for estimating the intensity of the effect size of competition (Reynolds 1999). When plant performance is measured in the presence and in the absence of the competitor, the most commonly used CI is the relative CI (RCI), which measure the proportional decrease in plant performance due to competition (Grace 1995; Goldberg et al. 1999). We calculated RCI as:

$$\mathrm{RCI} = (Y_{\mathrm{no\ weed}} - Y_{\mathrm{weed}})/Y_{\mathrm{no\ weed}}$$

where Y is the measurement of the crop performance or of crop yield, $Y_{\mathrm{no\ weed}}$ for when the crop is free of alien weeds, Y_{weed} when the weed is present. We only calculated RCI for removal and additive experiments at two levels: either with and without weeds or with a low abundance of weeds.

RCI range has no minimum (negative) value but has a maximum value of 1 indicating maximal competition. If $\mathrm{RCI} = 0$ there is no competition. If $\mathrm{RCI} < 0$ the performance of the crop is better with the presence of the alien weed than without the alien weed (facilitation). If $\mathrm{RCI} > 0$ the alien weed has a negative effect on the crop (competition in the broad sense).

In studies comparing monocultures with mixtures but keeping the density constant (replacement series experiments), we estimated the relative importance of interspecific competition relative to intraspecific competition by calculating the relative yield (RY):

$$\mathrm{RY} = (Y_{\mathrm{mixture}}/Y_{\mathrm{monoculture}})$$

where Y_{mixture} is the average yield of a crop plant when grown with the weed and $Y_{\mathrm{monoculture}}$ is the average yield of a crop plant when grown in monoculture (Silvertown and Charlesworth 2001). If $\mathrm{RY} = 1$ weed competition is not significantly different than competition within the crop, if $\mathrm{RY} > 1$, weed competition is lower than competition within the crop and if $\mathrm{RY} < 1$ weed competition is higher than competition within the crop.

Results

Main characteristics of the studies

Only 32 papers met our strict criteria. These reported 97 experiments of the effect of competition of 30 species of alien weeds on 14 crops. Data were mostly recorded at the end of the growing season and only at one site, but a few were repeated in 2, 3, and 4 sites (Figure 1a). Some of the studies were repeated in several consecutive years (2.28 ± 0.23 years) (mean $\pm$ s.e., hereafter) (Figure 1b), and one paper gave averages over the years (Fellows and Roeth 1992).

Only 8 papers out of 32 reported some estimate of the variance in the effect size (e.g. standard error, standard deviation), so it was not possible to use meta-analytical techniques on our database (Gurevitch et al. 1992; Gurevitch and Hedges 1999). We analysed our data by standard parametric tests.

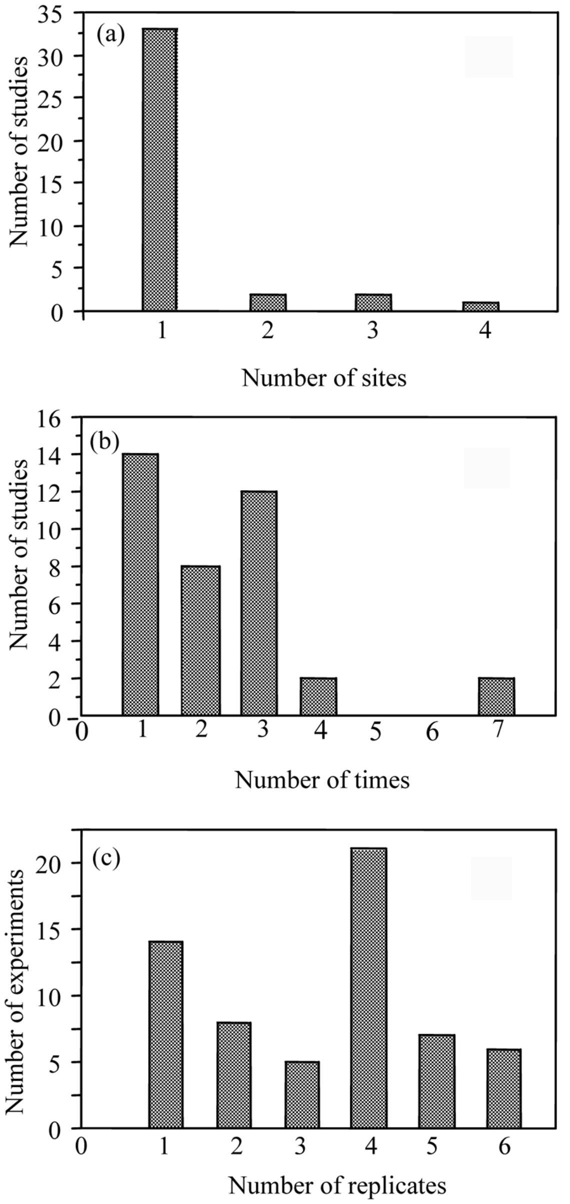

Figure 1. Histogram of the number of studies performed in different sites (a), years (b) and number of replicates used in the experiments (c).

The measurement of the competition effect

Three types of competition experiments have addressed the effect of alien weeds on crops: removal experiments, additive experiments and replacement (substitutive) series experiments.

In removal and additive field experiments, crop yield is compared in plots where the alien weed has been removed or added respectively. Removal experiments are conducted by mechanical and hand weeding or by applying herbicide to the crop. Seeding or planting alien weeds into the crop constitutes additive experiments. In the two types of experiments, the total plant density is not the same in the monoculture as in the mixture.

While removal experiments were only done in the field, additive experiments were also conducted in glasshouses (Fabricius and Nalewaja 1968; Ditommaso and Watson 1995). In the field, the experiments were randomised block designs with a number of replicates ranging from one (no replication) to six replicates. There were 14 studies with no replication. On average (± s.e.) experiments were replicated 3.25 ± 0.22 times (Figure 1c).

These experiments are but a snapshot of the competition effect of the alien weed on the crop at a given weed and crop abundance. From these experiments, it was not possible to integrate the effects of density on competition because the description of the planting densities or plant cover was sometimes obscure. It could not be compared between independent studies.

However, in some additive experiments the crop yield at a fixed population density was related to increasing densities of the alien weed. In such a case, the relation between the yield loss (Yl) of the crop species and the density of the weed (d) is fitted to a rectangular hyperbolic function (Cousens 1985a):

$$\mathrm{Yl} = Id/(I + Id/A)$$

where I is the crop yield loss when weed density approaches zero and A when it is maximum. From this function we can estimate yield loss at all densities. In the papers we reviewed, A ranged from 46.9% to 100% (Table 1).

In replacement (substitutive) series experiments, the total density or abundance of plants is maintained constant but the proportion of alien weed : crop species varies from a crop monoculture to a weed monoculture (de Wit 1960). Across the studies reviewed, we found that on average weed competition is not significantly higher than competition within the crop RY (mean ± s.e.) = 0.85 ± 0.10 (Table 2). For the most part, replacement series experiments have been not carried out in field conditions (but see Bridgemohan and McDavid 1993).

Table 1. Maximum percentage of crop yield loss when alien weed density approaches infinity (A) and when the weed density approaches zero (I).

Reference	Exotic	Native	A	I
Cousens (1985a)	*Kochia scoparia*	*Beta vulgaris*	107.4	269
	Kochia scoparia	*Beta vulgaris*	101.6	375
	Amaranthus hybridus	*Glycine max*	84.7	139.6
	Amaranthus hybridus	*Zea mays*	57.9	25.8
Cousens and Mokhtari (1998)	*Lolium rigidum*	*Triticum aestivum*	92.7	0.008
Cousens et al. (1984)	*Avena fatua*	*Triticum aestivum*	96.7	0.75
	Galium aparine	*Triticum aestivum*	56	2.65
	Bromus sterilis	*Triticum aestivum*	62.7	0.82
Kropff et al. (1984)	*Echinochloa crus-galli*	*Zea mays*	88	
Norris (1992)	*Echinochloa crus-galli*	*Beta vulgaris*	93.1	70.1
	Echinochloa crus-galli	*Beta vulgaris*	86.7	19.4
	Echinochloa crus-galli	*Beta vulgaris*	92.2	127.7
Sattin et al. (1992)	*Abutilon theophrasti*	*Zea mays*	46.9	3.74

A and I are calculated from the rectangular hyperbolic equation $\mathrm{Yl} = Id/(I + Id/A)$ where Yl is the percentage crop yield loss and d is the weed density.

Table 2. Relative yield (RY) of several alien weeds on crops obtained from replacement series experiments.

Reference	Exotic	Native	RY
Bridgemohan and McDavid (1993)	*Rottboellia cochinchinensis*	*Zea mays*	0.6
	Rottboellia cochinchinensis	*Zea mays*	1.1
Norris (1997)	*Portulaca oleracea*	*Beta vulgaris*	0.8
	Portulaca oleracea	*Beta vulgaris*	0.3
Ogg et al. (1993)	*Anthemis cotula*	*Pisum sativum*	1.9
	Anthemis cotula	*Pisum sativum*	1.8
Patterson and Highsmith (1989)	*Anoda cristata*	*Gossypium hirsutum*	0.9
	Abutilon theophrasti	*Gossypium hirsutum*	0.8
Wall (1993)	*Setaria viridis*	*Hordeum vulgare*	0.7
	Avena fatua	*Hordeum vulgare*	0.6

RY = crop yield in the mixture with alien weeds/crop yield in monoculture.

Table 3. Competition indices (mean ± s.e.) for alien weeds according to removal and additional experiments.

Alien weed	RCI	n
Abutilon theophrasti	0.37 ± 0.10	8
Aegilops cylindrica	0.27	1
Amaranthus hybridus	0.40 ± 0.09	6
Amaranthus spinosus	0.23	1
Amsinckia hispida	0.33	1
Avena fatua	0.39 ± 0.03	10
Brassica tournefortii	0.19	1
Cassia obtusifolia	0.38 ± 0.02	4
Cyperus esculentus	0.41	1
Digitaria sanguinalis	0.56 ± 0.15	4
Fumaria parviflora	0.28	1
Kochia scoparia	0.78 ± 0.10	2
Lamium amplexicaule	0.38	1
Lithospermum arvense	0.25	1
Malva pusilla	0.36	1
Medicago littoralis	0.38 ± 0.05	13
Polygonum convolvulus	0.46 ± 0.04	4
Solanum nigrum	0.69 ± 0.13	6
Sorghum bicolor	0.70 ± 0.09	2
Sorghum halepense	0.20 ± 0.02	3

$\mathrm{RCI} = (Y_{\text{no weed}} - Y_{\text{weed}})/Y_{\text{no weed}}$; $Y_{\text{no weed}}$ = crop yield without weed and Y_{weed} = crop yield with weeds present.

Magnitude and variation of yield losses

On average, experiments showed yield losses of 42.52 ± 2.67% (Tables 3 and 4). Removal experiments found marginally larger RCI than additive experiments. However, differences in the RCI between removal and additive experiments were non-significant (RCI: $F_{1,69} = 3.37$, $P = 0.07$).

The RCI distribution was normal (Kolmogorov–Smirnov test: $\chi^2 = 0.68$, $P = 0.99$) and did not show any competitive intensity values that could be distinguished from the rest (Figure 2). Table 5 shows that weed and crop pairing is not independent of their identity. For example, *Kochia scoparia* (kochia) is always paired with *Beta vulgaris* (sugarbeet) and *Digitaria sanguinalis* (large crabgrass) is always paired with *Arachis hypogaea* (peanut). Consequently, ranking weeds according to their effect on crop production should be made with caution.

Only 8 papers out of 32 studied the interaction of competition with manipulation of a soil resource, particularly soil fertilisation with N + P or irrigation with water. These studies found that neither soil fertilisation

Table 4. Competition indices (mean ± s.e.) of alien weeds in crops according to removal and additional experiments.

Crop	RCI	*n*
Arachis hypogaea	0.70 ± 0.05	3
Beta vulgaris	0.78 ± 0.01	2
Daucus carota	0.38 ± 0.05	13
Fragaria spp.	0.36	1
Glycine max	0.39 ± 0.55	20
Gossypium hirsutum	0.69 ± 0.13	6
Hordeum vulgare	0.37 ± 0.06	5
Lactuca sativa	0.23	1
Linum usitatissimum	0.48 ± 0.05	3
Saccharum officinale	0.13	1
Triticum aestivum	0.34 ± 0.03	12
Zea mays	0.36 ± 0.05	4

RCI $= (Y_{\text{no weed}} - Y_{\text{weed}})/Y_{\text{no weed}}$; $Y_{\text{no weed}}$ = crop yield without weed and Y_{weed} = crop yield with weeds present.

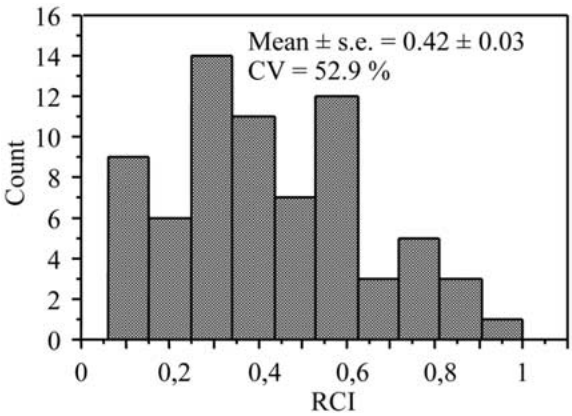

Figure 2. Size distribution of RCI of the effect of weeds on crops for removal and additional experiments.

nor irrigation affected crop yield reduction from the weed.

Discussion

In our review, we have detected some of the problems previously described in reviews on plant competition that limit the data set of studies available for synthesis (Gurevitch et al. 1992; Goldberg et al. 1999). Some of the caveats in primary studies relate to experimental design, such as no replication, and some to data presentation, such as the lack of estimates of error. Without this information meta-analysis is ruled out (Arnquist and Wooster 1995; Hedges et al. 1999). Despite these limitations the survey reveals no difference between removal and additive experiments. Furthermore, crop losses will depend on the density of crop and weed species in the field (Tollenaar 1992 and Table 1) information that is not always reported in published studies.

Manipulation studies have limitations for the interpretation of the results and some approaches do not directly relate to practical ecological or agronomic problems. This is also true for weed–crop competition experiments. Replacement series experiments have been the most criticised because the results depend on the density and spatial arrangement of the plants (Connolly 1986, 1988; Snaydon 1991). Replacement series experiments produce a collective result. Neither do they allow the separation of intraspecific from interspecific competition nor do they disentangle the contribution to interference from each of the constituents of the mixture (Jolliffe 2000). Furthermore, when they are conducted in indoor conditions, pot size or shape influences them.

Additive and removal experiments have also been criticised by Rejmánek et al. (1989) and by Aarsen and Epp (1990) respectively, because the total density is usually lower in monocultures than in the mixtures, and because the manipulation of adding or removing plants can confound the experimental design (i.e. creating soil disturbance, changing the microclimate, adding residues of herbicides, etc.). Moreover, I and A values obtained from additive experiments that test the effect of increasing weed density on crop yield reduction vary with crop density, too (Cousens 1985b). Despite these limitations we believe that when these additive and removal experiments are conducted in the field they give the most realistic estimate of the effect of weeds in crops. Ideally, these experiments should be conducted in 'real' crops where either the pre-existing weeds would be removed or the weeds would be added in abundances matching natural conditions.

Alien plant species are sometimes thought to displace native species by their high competitive ability (Glauninger and Holzner 1982). However, in the alien-crop studies reviewed, values for RY do not show higher competition in weed–crop mixtures than in crop monocultures. This finding implies that probably the effect of alien weeds on crops is not due to higher individual competitive ability of the weed '*per se*' compared to competition within the crop, but rather to the degree of weed infestation and the total plant density. Similarly, in natural systems the high competitive ability attributed to alien plants could be more related to their potential to become abundant in a short period

Table 5. Cross incidence of the crop–weed identity in removal and additional experiments. See 'Appendix' for complete name of the crops.

Alien weed	Crop											
	Arachis	*Beta*	*Daucus*	*Fragaria*	*Glycine*	*Gossypium*	*Hordeum*	*Lactuca*	*Linum*	*Saccharum*	*Triticum*	*Zea*
Abutilon theophrasti					×							
Aegilops cylindrica											×	
Amaranthus hybridus					×							×
Amaranthus spinosus								×				
Amsinckia hispida											×	
Avena fatua							×				×	
Brassica tournefortii											×	
Cassia obtusifolia					×							
Cyperus esculentus												×
Digitaria sanguinalis	×									×		
Fumaria parviflora											×	
Kochia scoparia		×										
Lamium amplexicaule											×	
Lithospermum arvense											×	
Malva pusilla				×								
Medicago littoralis			×									
Polygonum convolvulus									×		×	
Solanum nigrum						×						
Sorghum bicolor					×							
Sorghum halepense					×							

of time than to their per-capita competitive superiority compared with native plants.

Weeds compete for soil resources and light (Glauninger and Holzner 1982; Zimdahl 1993). If competition were for these soil resources, the negative effect of weeds on crop would be different in irrigated or fertilized plots, respectively. This trend was not found probably because the experiments reviewed are overirrigated and overfertilized. However, there are still too few experiments investigating the mechanisms of interference between crop and weed. Such experiments would be necessary to determine how the intensity of competition varies along environmental gradients and agricultural practices.

It is generally stated that variation of the effect of competition is low because all plants require the same type of resources (Goldberg and Werner 1983). Recently, it has been hypothesised that the effect of competition has greater interspecific variability than other types of ecological effects (Parker et al. 1999). Our survey shows that the range of variation of competition is very large and it is not possible to rank weed species according to their competition effect on crops in general for two reasons. First, some experimental designs are poor and the reporting of the data is inadequate to provide all the information needed to perform a correct comparison within weeds and within crops. Second, weed–crop pairs are not random assemblages and the effect of a weed is crop specific. This is also true for alien plants invading natural systems where research mainly focuses on the impact of well established, dominant alien species that anecdotal evidence suggest are highly aggressive. Similarly, the competitive effect of aliens is mostly tested on native species that have low-density populations or are rare. If rarity reflects poor competitive ability then competition between a rare native species and a dominant invader may not represent a random selection of possible native–alien species. In fact, agronomists have diligently been able to compare the extent to which different weeds reduce yields within a specific crop (see Zimdahl 1980 for a review). Ecologists should also bear in mind that any particular alien species cannot invade any ecosystem type. Therefore, ranking alien species by their impact in natural systems should be constructed within specific ecosystem types.

Another issue that can be learned from weed–crop studies is the concept of critical period for weed control (Zimdahl 1980), that is, the time span when weeds present from the beginning of the crop cycle must be removed to prevent yield reduction. Related to this concept is the weed-free period required to prevent crop-yield reduction. These aspects have not been much explored in natural systems. We cannot assume that removing alien species at any time during the growing season controls the invaders and their impacts

(Hobbs and Humphries 1994) or that the competitive effect of an alien species does not depend on its life-history stage. Substantial evidence in weed–crop systems indicate that the time of removal is as important as removal itself and that weed presence cannot automatically be judged damaging and in need of immediate control (Keeley and Thullen 1989a, b; Fellows and Roeth 1992).

Invasions by alien species are increasing and the need for quantitative indicators of their impacts is urgent because too often the costs of aliens are dismissed or under-estimated (Daehler and Gordon 1997). If ecologists are to gain influence in the management and control of alien species, assessment and quantification of their impacts at several levels of ecological complexity are required. We have reviewed the primary effect that an alien has on the species of the same trophic level in the recipient community. It was not our purpose to show the trivial fact that weeds reduce crop yield or to value its reduction, but to focus on the way this agronomic information can fertilise competition studies of alien plants invading well-established natural systems.

From our criteria, we have been able to find and compare only a small number of state-of-the-art competition studies and these are a somewhat unbalanced set. The following considerations emerge from the studies reviewed: (i) the reduction of crops with an increased density of weeds is non-linear; (ii) the crop–weed assemblages are not random; (iii) the effect of weed removal depends on the timing and location characteristics; and finally (iv) a more exhaustive provision of the experimental setting and variability of the effects within the experiment are needed in order to make comparisons between independent studies feasible. We feel that taking into account these same topics for the counterparts' native–alien plant assemblages in natural systems would clarify some important issues in the study of the impact of biological invasions.

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Appendix. Studies of the effect of alien weeds on crops.

Reference	Alien weed	Crop	Study type*
Anderson (1993)	*Aegilops cylindrica* (jointed goatgrass)	*Triticum aestivum* (wheat)	add. exp. (1,1,4)
Bell and Nalewaja (1968a)	*Avena fatua* (wild oat)	*Triticum aestivum*	add. exp. 2 levels (2,3,1)
	Avena fatua	*Hordeum vulgare* (barley)	add. exp. 2 levels (2,3,1)
Bell and Nalewaja (1968b)	*Avena fatua*	*Linum usitatissimum* (flax)	add. exp. (1,3,3)
Bridgemohan and McDavid (1993)	*Rottboellia cochinchinensis* (itchgrass)	*Zea mays* (corn)	green. and field rep. series exp. (1,1,3)
Cousens and Mokhtari (1998)	*Lolium rigidum* (Mediterranean ryegrass)	*Triticum aestivum*	add. exp. (4,4,4)
Cousens et al. (1984)	*Avena fatua*	*Triticum aestivum*	add. exp.
	Galium aparine (cleavers)	*Triticum aestivum*	add. exp.
	Bromus sterilis	*Triticum aestivum*	add. exp.
Ditommaso and Watson (1995)	*Abutilon theophrasti* (velvetleaf)	*Glycine max* (soybean)	greenh. add. exp. (1,1,4)
Ditommaso et al. (1996)	*Abutilon theophrasti*	*Glycine max*	add. exp. (1,3,3-4)
Fabricius and Nalewja (1968)	*Polygonum convolvulus* (wild buckwheat)	*Triticum aestivum*	greenh. add. exp. 2 levels (-,1,2)
Fellows and Roeth (1992)	*Sorghum bicolour* (shatter cane)	*Glycine max*	rem. exp. (1,3,3-4)
Frank et al. (1988)	*Setaria faberi* (giant foxtail)	*Capsicum annuum* (sweet pepper)	rem. exp. (1,2,4)
Gruenhagen and Nalewaja (1969)	*Polygonum convolvulus*	*Linum usitatissimum*	add. exp. (2-3,2,3), c.ch. add. exp (1,1,2)
Helm et al. (1992)	*Abutilon theophrasti*	*Glycine max*	add. exp. 2 levels (1,4,3-4)

Appendix. *Continued.*

Reference	Alien weed	Crop	Study type*
James et al. (1988)	*Cassia obtusifolia* (sicklepod)	*Glycine max*	add. exp. 2 levels (1,1,4)
Keeley and Thullen (1989a)	*Solanum nigrum* (black nightshade)	*Gossypium hirsutum* (cotton)	rem. exp. (1,7,6)
Keeley and Thullen (1989b)	*Sorghum halepense* (johnsongrass)	*Gossypium hirsutum*	rem. exp. (1,2,4)
Kropff et al. (1984)	*Echinochloa crus-galli* (barnyardgrass)	*Zea mays*	add. exp. (1,1,1)
Moolani et al. (1964)	*Amaranthus hybridus* (smooth pigweed)	*Zea mays*	add. exp. (1,3,5)
	Amaranthus hybridus	*Glycine max*	add. exp. (1,3,5)
Mortensen and Makouski (1995)	*Malva pusilla* (round-leaved mallow)	*Fragaria* spp. (strawberry)	rem. exp. (1,1,4)
Murdock et al. (1986)	*Digitaria sanguinalis* (large crabgrass)	*Arachis hypogaea* (peanut)	rem. exp. (1,2,2)
Norris (1992)	*Echinochloa crus-galli*	*Beta vulgaris* (sugarbeet)	add. exp. (1,3,5)
Norris (1997)	*Portulaca oleracea* (common purslane)	*Beta vulgaris*	rep. series exp. (1,1,6)
Ogg et al. (1993)	*Anthemis cotula* (mayweed)	*Pisum sativum* (garden pea)	rep. series exp. (1,2,4)
Patterson and Highsmith (1989)	*Anoda cristata* (spurred anoda)	*Gossypium hirsutum*	c. ch. rep. series exp. (-,1,40)
	Abutilon theophrasti	*Gossypium hirsutum*	c. ch. rep. series exp. (-,1,40)
Rämet (1996)	*Medicago littoralis* (lucerne)	*Daucus carota* (carrot)	add. exp. 2 levels (3,7, ?)
Showler and Reagan (1991)	*Digitaria sanguinalis*	*Saccharum officinarum* (sugarcane)	rem. exp. (1,2,6)
Shrefler et al. (1994)	*Amaranthus spinosus* (spiny amaranth)	*Lactuca sativa* (lettuce)	rem. exp. (1,2,4)
Sims and Oliver (1990)	*Sorghum halepense*	*Glycine max*	add. exp. 2 levels (1,3,4)
	Cassia obtusifolia	*Glycine max*	add. exp. 2 levels (1,3,4)
Stoller et al. (1979)	*Cyperus esculentus* (yellow nutsedge)	*Zea mays*	rem. exp. (1,3,5)
Wall (1993)	*Setaria viridis* (green foxtail)	*Hordeum vulgare*	c. ch. rep. series exp. (-,1,6)
	Avena fatua	*Hordeum vulgare*	c ch. rep. series exp. (-,1,6)
Weatherspoon and Schweiter (1971)	*Kochia scoparia* (kochia)	*Beta vulgaris*	add. exp. 2 levels (1,2,4)
Wells (1979)	*Lithospermum arvense* (white iron weed)	*Triticum aestivum*	rem. exp. (1,1,1)
	Brassica tournefortii (wild turnip)	*Triticum aestivum*	rem. exp. (1,1,1)
	Lamium amplexicaule (deadnettle)	*Triticum aestivum*	rem. exp. (1,1,1)
	Amsinckia hispida (amsinckia)	*Triticum aestivum*	rem. exp. (1,1,1)
	Fumaria parviflora (white fumitory)	*Triticum aestivum*	rem. exp. (1,1,1)

*In parenthesis: number of sites, number of times and number of replicates performed in each publication. All studies are field experiments otherwise noticed.

add. exp. = additional experiment; rem. exp. = removal experiment; green. = green house; rep. series exp. = replacement series experiments; c. ch. = controlled chambers.

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