

Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments

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Vilà, M. and Weiner, J. 2004. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. – *Oikos* 105: 229–238.

Invasive plants often appear to be more competitive than native species, but there have been few tests of this hypothesis. We reviewed published pair-wise experiments between invading and native plant species. Although the designs that have been used allow only limited inferences, the available data suggest that the effect of invasive species on native species is usually stronger than vice versa. Furthermore, mixtures of invasive and native species are generally less productive than monocultures of the native species, but not less than monocultures of the invasive species. However, the selection of invaders and natives for study has not been random, and the data could be biased towards highly competitive invaders and natives that are weaker than average competitors. We attempt to clarify confusion surrounding the concept of competitive superiority in the context of plant invasions, and we discuss the limitations of the methods that have been used to investigate competition between invasive and native species. To rigorously test the generality of the hypothesis that invaders are better competitors than natives we need to compare the effects of closely related native and invasive species on each other. We suggest that the influence of an invading species on total plant community biomass is an important clue in understanding the role of competition in a plant invasion. The role of competition in the establishment and naturalization stages of the invasion process may be very different from its role in the “outbreak” stage.

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Biological invasions are recognized as major environmental problems and one of the major threats to biodiversity (Drake et al. 1989, Di Castri et al. 1990, Williamson 1996). The success and impacts of alien species depends on their biological attributes, the environmental characteristics of the invaded ecosystem and the biotic interactions with the receptive community. The role of natural enemies in controlling invasion success has received much attention (Maron and Vilà 2001, Keane and Crawley 2002), but when an alien plant species is introduced, competition for limiting resources is probably the first interaction the species has with the recipient community. Interspecific competition is considered one of the most important processes determining

the likelihood of plant invasion (Crawley 1990), as suggested by the important role of disturbance, which decreases competition and increases the probability of invasion. High competitive ability of alien species has been mentioned as a key factor promoting successful invasive potential (Baker 1965, Roy 1990), and competitive exclusion by native plant species seems to be a major force resisting exotic invasions (Keane and Crawley 2002). Studies on the control of invasive species suggest that competition can reduce invasive plant growth more than herbivory (Lonsdale and Farrell 1998, Willis et al. 1998, Müller-Schärer 1991).

An understanding of the role of competition in plant invasions requires the study of both the ability of the

Accepted 8 September 2003

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ISSN 0030-1299

invader to grow and increase in population size in the recipient community, and the recipient community's tolerance of the invading species. Field observations and experiments have confirmed that the presence of alien species can threaten the persistence of native species (Parker and Reichard 1998), presumably because of the negative effects of competition from the invasive alien on native species populations. On the other hand, disturbance, which results in reduced competition and an increase of resources at the individual level, often appears to be necessary for many alien species to establish (Hobbs and Huenneke 1992). Thus, release from competitors is another mechanism that can contribute to the success of invasion of a community (Crawley 1986).

How can one go about asking if invasive species are better competitors than native species? Per-amount or per-individual effects of an alien species on native species and vice versa can be estimated with competition intensity indexes (Goldberg and Werner 1983). Despite their limitations, competition indexes are useful tools for quantifying the effect of competition between pairs of species (Grace 1995, Goldberg et al. 1999). Competition indexes can quantify the proportional decrease in plant performance due to competition, and compare effects of competition on different species or under different environmental conditions. Furthermore, competition indexes meet the criteria necessary to compare differences among independent studies (Gurevitch et al. 1992, Goldberg et al. 1999).

Here we review and discuss pair-wise competition experiments between alien and native plant species in a first attempt to address the following questions: (1) What is the overall magnitude and variation of the effects of natives on aliens and the effects of aliens on natives? (2) Is there evidence to support the hypothesis that invaders are generally better competitors than natives?

A meta-analysis of available data

We searched for publications listed in the Life Science Collection for the period 1986–2001 that reported the effect of alien plant species on individual native species and vice versa. We selected articles according to the following criteria:

1) We restricted our review to experiments on pairs of species, not other taxonomic or functional groups. Studies where several plant species were competing simultaneously were excluded. Although in natural conditions competition is diffuse and exotic species invading a new community compete with an array of neighbourhood species, pair-wise experiments are a suitable starting point for assessing and comparing traits that may determine competitive ability among species

since there are no indirect effects of the larger plant community that make the results difficult to interpret (Goldberg and Scheiner 1993). We did not include weed-crop experiments because crop species or varieties are usually selected for high productivity, because agricultural systems are not natural plant communities in any sense, and because crop-weed studies usually focus primarily on yield loss. A review of alien weed-crop competition experiments has recently been published (Vilà et al., in press).

2) We considered only experimental manipulations of the abundance (e.g. density, biomass and cover) of the alien or native species or both in which the competition treatments were compared to an appropriate control performed simultaneously and in the same place. We excluded from our analysis purely 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) We include experiments conducted in controlled growth chambers, glasshouses, common gardens, and under field conditions.

4) From each study we gathered information on the type of experiment, the alien and native species involved. In competition studies, several parameters of plant performance are usually measured. We selected measurements of biomass or other measures of plant size or growth.

5) When different competition regimes or treatments (e.g. separation of shoot and root competition) were performed, we selected the data from the full competition treatment and the control treatment. Similarly, several studies focus on the interaction between competition and other ecological factors (e.g. herbivory, nutrient addition) but we looked at data from the treatments that most closely reflected the situation in the field.

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 conducted on the same pair of species under different conditions (e.g. different sites or different years), we treated the studies as independent.

Calculation of effect sizes

A wide set of competition intensity indexes (CI) are 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 CIs are (1) the relative CI (RCI) which measures the proportional

decrease in plant performance due to competition,

$$RCI = (Y_{\text{no neigh}} - Y_{\text{neigh}}) / Y_{\text{no neigh}}$$

and (2) the log response ratio (ln RR; Grace 1995, Goldberg et al. 1999),

$$\ln RR = \ln (Y_{\text{no neigh}} / Y_{\text{neigh}})$$

where Y is the measurement of the plant performance, $Y_{\text{no neigh}}$ when the target plant is free of neighbours, Y_{neigh} when the neighbours are present. We only calculated RCI and ln RR for removal and additive experiments at two levels: either with or without the alien or native species, or at a low or high abundance of neighbours (Aarssen and Epp 1990).

RCI has no minimum (negative) value but has a maximum value of 1 indicating maximal competition. If $RCI = 0$ there is no competition. If $RCI < 0$ the performance of the target plant is higher in the presence of the neighbour (facilitation). If $RCI > 0$ neighbours have a negative effect on the target plant (competition in the broad sense). Values for ln RR do not have a ceiling and thus variation of ln RR is usually higher than for RCI (Goldberg et al. 1999).

We performed a meta-analysis to test for the homogeneity of effect sizes on standard parameters and between types of experiments (additional versus removal). Meta-analysis was conducted using the software package MetaWin 2.0 (Rosenberg et al. 1997).

In substitutive studies comparing monocultures with mixtures at a constant density (replacement series experiments) we evaluated the relative importance of interspecific to intraspecific competition by the relative yield (RY):

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

where Y_{mixture} is the average biomass of an individual of one species when grown with the other and $Y_{\text{monoculture}}$ is the average biomass of an individual of the species when grown in monoculture (Silvertown and Charlesworth 2001). If $RY = 1$ interspecific competition is not significantly different than intraspecific competition, if $RY > 1$, interspecific competition is lower than intraspecific competition and if $RY < 1$ interspecific competition is higher than intraspecific competition. Despite the limits of replacement series experiments for predicting population dynamics in the field (Connolly 1986), they can still provide some indication of a potential competitive advantage and are commonly used.

Results

Only 36 papers met our criteria. These papers reported experiments of the effect of 26 alien species on 48 native species, and of the effect of 26 native species on 17 alien species (Table 1).

Three types of experiments addressed the effect of alien plants on native plants: additive experiments ($n = 20$), removal experiments ($n = 19$) and replacement series experiments ($n = 34$). In contrast, only additive experiments ($n = 24$) and replacement series experiments ($n = 31$) addressed the effect of natives on aliens. While removal experiments were only conducted in the field, additive experiments have also been conducted in greenhouses. Few replacement series experiments have been carried out under field conditions.

On average (\pm SE) experiments were replicated 5.93 ± 0.50 times and there were not significant differences between the three experiment types (ANOVA, $F_{2, 97} = 2.74$, $p = 0.069$). Removal experiments were always longer (30.52 ± 1.4 months) than additive (5.47 ± 0.59 months) and replacement series experiments (7.65 ± 0.86 months, ANOVA, $F_{2, 99} = 194.02$, $p < 0.0001$).

Some experiments did not present information on the variance in the effect size (e.g. standard error or standard deviation). Therefore, the sample size for the meta-analysis is reduced somewhat.

Experiments reported average (\pm SE) losses on native plant biomass or size of $46.60 \pm 0.68\%$ due to the presence of the alien species. The weighted mean log response ratio (ln RR) was 0.03 with 95% confidence interval corrected for bias ranging from -0.05 to 0.51. The heterogeneity test showed that there was a high variability among studies ($Q_t = 1905.32$, $df = 38$, $p < 0.0001$). The experimental method used, removal or additive experiment, did not have a significant effect on native plant performance ($Q_b = 66.19$, $p = 0.82$). There was no significant difference between the losses on native plant biomass or size for experiments conducted in glasshouses and those performed under field conditions ($Q_b = 57.26$, $p = 0.83$).

Experiments reported average (\pm SE) losses on alien plant biomass or size of $17.6 \pm 1.24\%$ due to the presence of native species. The effects of natives on aliens were thus lower than vice versa ($t = 2.24$, $df = 66$, $p = 0.029$; Fig. 1). Similarly, in replacement series experiments, the relative yield for natives was smaller than for alien species ($RY_{\text{native}} = 0.65 \pm 0.09$, $RY_{\text{alien}} = 1.17 \pm 0.18$, $t_{\text{paired}} = 2.66$, $p = 0.012$). Therefore, interspecific competition between native and alien plants was stronger than intraspecific competition between native plants but weaker than intraspecific competition between alien plants (Fig. 2).

Overall, our review on pair-wise experiments between invader and native plant species supports the general perception that invaders are good competitors (Baker 1965, Newsome and Noble 1986), and that the resistance to invaders imposed by single native species is weak. Both resource competition and non-resource mediated effects (e.g. allelopathy) may be involved in giving invaders an advantage. For example, in Australian forests, allelopathy appears to play a role in the invasion

Table 1. Summary of experimental studies of competition between native and alien plant species.

Reference	Alien sp	Life form, stage	Native sp	Life form, stage	Study type	Effect	System	Region
Aplet and Laven 1993	<i>Tagetes minuta</i>	shrubby herb	<i>Tetramolopium arenarium</i>	shrub, seedl	AE greenhouse	A, N	shrubland	Hawaii
Aplet and Laven 1993	<i>Tagetes minuta</i>	shrubby herb	<i>Tetramolopium consanguinarium</i>	shrub, seedl	AE greenhouse	A, N	shrubland	Hawaii
Aplet and Laven 1993	<i>Tagetes minuta</i>	shrubby herb	<i>Bidens menziesii</i>	shrub, seedl	AE greenhouse	A, N	shrubland	Hawaii
Ashton et al. 1998	<i>Pinus caribaea</i>	tree, seedl	<i>Caryota urens</i>	tree, seedl	RE	A	oldfield	Sri Lanka
Ashton et al. 1998	<i>Pinus caribaea</i>	tree, seedl	<i>Dipterocarpus zeylanicus</i>	tree, seedl	RE	A	oldfield	Sri Lanka
Ashton et al. 1998	<i>Pinus caribaea</i>	tree, seedl	<i>Pericopsis mooniana</i>	tree, seedl	RE	A	oldfield	Sri Lanka
Ashton et al. 1998	<i>Pinus caribaea</i>	tree, seedl	<i>Shorea stipularis</i>	tree, seedl	RE	A	oldfield	Sri Lanka
Brown et al. 1998	<i>Cryptostegia grandiflora</i>	woody vine	<i>Heteropogon contortus</i>	tussock grass	AE greenhouse	N	woodland	Queensland
Brown et al. 1998	<i>Acacia nilotica</i>	tree	<i>Heteropogon contortus</i>	tussock grass	AE greenhouse	N	woodland	Queensland
Buman et al. 1988	<i>Bromus tectorum</i>	ann grass	<i>Agropyron cristatum</i> x <i>desertorum</i>	per grass	RSE	A, N	grassland	USA
Buman et al. 1988	<i>Bromus tectorum</i>	ann grass	<i>Secale montanum</i>	per grass	RSE	A, N	grassland	USA
Callaway et al. 1999	<i>Centaurea maculosa</i>	ann forb	<i>Festuca idahoensis</i>	bunchgrass	AE	A	grassland	Montana
Callaway and Aschehoug 2000	<i>Centaurea diffusa</i>	ann forb	<i>Festuca idahoensis</i>	bunchgrass	AE greenhouse	A, N	grassland	Montana
Callaway and Aschehoug 2000	<i>Centaurea diffusa</i>	ann forb	<i>Koeleria laersserii</i>	bunchgrass	AE greenhouse	A, N	grassland	Montana
Callaway and Aschehoug 2000	<i>Centaurea diffusa</i>	ann forb	<i>Pseudoroegneria spicatum</i>	bunchgrass	AE greenhouse	A, N	grassland	Montana
Callaway et al. 2001	<i>Centaurea maculosa</i>	ann forb	<i>Nassella pulchra</i>	bunchgrass	AE greenhouse	A, N	grassland	Montana
Cohn et al. 1989	<i>Cynodon dactylon</i>	ann forb	<i>Acacia smallii</i>	tree seedl	RSE	A, N	grassland	Texas
D'Antonio and Mahall 1991	<i>Carpobrotus edulis</i>	succulent per	<i>Haplopappus ericoides</i>	shrub	RE	A	coastal scrub	California
D'Antonio and Mahall 1991	<i>Carpobrotus edulis</i>	succulent per	<i>Haplopappus venetus</i> var <i>sedoides</i>	shrub	RE	A	coastal scrub	California
D'Antonio et al. 1998	<i>Schizachyrium condensatum</i>	per grass	<i>Dodonea viscosa</i>	shrub	RE	A	tropical forest	Hawaii
D'Antonio et al. 1998	<i>Schizachyrium condensatum</i>	per grass	<i>Metrosideros polymorpha</i>	tree	RE	A	tropical forest	Hawaii
D'Antonio et al. 1998	<i>Schizachyrium condensatum</i>	per grass	<i>Osteomeles anthylidifolia</i>	shrub	RE	A	tropical forest	Hawaii
D'Antonio et al. 1998	<i>Schizachyrium condensatum</i>	per grass	<i>Styphelia tameiamea</i>	shrub	RE	A	tropical forest	Hawaii
Da Silva and Bartolome 1984	<i>Bromus mollis</i>	ann grass	<i>Baccharis pilularis</i>	shrub, seedl	AE	A	coastal scrub	California
Dillenburg et al. 1993	<i>Lonicera japonica</i>	climber	<i>Liquidambar styraciflua</i>	tree, seedl	RE	A	coastal plain	Washington
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Plantago erecta</i>	ann forb	AE microcosm	N	prairie	California
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Lasthenia californica</i>	ann forb	AE microcosm	N	prairie	California
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Hemizonia congesta</i>	ann forb	AE microcosm	N	prairie	California
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Lessingia hololeuca</i>	ann forb	AE microcosm	N	prairie	California
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Nassella pulchra</i>	ann forb	AE microcosm	N	prairie	California
Dukes 2001	<i>Centaurea solstitialis</i>	ann forb	<i>Elymus glaucus</i>	per grass	AE microcosm	N	prairie	California
Facelli and Pickett 1991	<i>Ailanthus altissima</i>	tree seedl	<i>Setaria faberii</i>	per grass	AE	N	old field	New Jersey
Gentle and Duggin 1997	<i>Lantana camara</i>	shrub	<i>Cryptocarya rigida</i>	tree, seedl	RE and AE	A	temperate forest	Australia
Gentle and Duggin 1997	<i>Lantana camara</i>	shrub	<i>Alectryon subcinereus</i>	tree, seedl	RE and AE	A	rainforest	Australia
Gentle and Duggin 1997	<i>Lantana camara</i>	shrub	<i>Cryptocarya rigida</i>	tree, seedl	RSE	A	temperate forest	Australia
Gerry and Wilson 1995	<i>Bromus inermis</i>	ann grass	<i>Bouteloua gracilis</i>	per grass	AE in pots	A	oldfield	Canada
Gerry and Wilson 1995	<i>Bromus inermis</i>	ann grass	<i>Elaeagnus commutata</i>	tree, seedl	AE in pots	A	oldfield	Canada
Gerry and Wilson 1995	<i>Bromus inermis</i>	ann grass	<i>Fraxinus pennsylvanica</i>	tree, seedl	AE in pots	A	oldfield	Canada
Gerry and Wilson 1995	<i>Bromus inermis</i>	ann grass	<i>Potentilla pennsylvanica</i>	per forb	AE in pots	A	oldfield	Canada
Gillespie et al. 1994	<i>Dactylis glomerata</i>	per grass	<i>Fraxinus pennsylvanica</i>	tree	RE	A	grassland	Indiana
Gillespie et al. 1994	<i>Dactylis glomerata</i>	per grass	<i>Juglans nigra</i>	tree	RE	A	grassland	Indiana
Gillespie et al. 1994	<i>Dactylis glomerata</i>	per grass	<i>Quercus rubra</i>	tree	RE	A	grassland	Indiana
Gillespie et al. 1994	<i>Trifolium repens</i>	per forb	<i>Fraxinus pennsylvanica</i>	tree	RE	A	grassland	Indiana

Table 1 (Continued)

Reference	Alien sp	Life form, stage	Native sp	Life form, stage	Study type	Effect	System	Region
Gillespie et al. 1994	<i>Trifolium repens</i>	per forb	<i>Juglans nigra</i>	tree	RE	A	grassland	Indiana
Gillespie et al. 1994	<i>Trifolium repens</i>	per forb	<i>Quercus rubra</i>	tree	RE	A	grassland	Indiana
Gordon et al. 1989	<i>Bromus diandrus</i>	ann grass	<i>Quercus douglasii</i>	tree, seedl	AE in pots	A	savanna	California
Hobbs and Atkins 1991	<i>Ursinia anthemoides</i>	ann grass	<i>Allocasuarina campestris</i>	shrub, seedl	AE	A	heathland	W. Australia
Huenneke and Thompson 1994	<i>Dipsacus sylvestris</i>	bien forb	<i>Cirsium vinaceum</i>	per forb	RSE	A, N	grassland	New Mexico
Janes et al. 1996	<i>Azolla filiculoides</i>	hydrophyte	<i>Potamogeton crispus</i>	hydrophyte	AE greenhouse	A	aquatic system	UK
Janes et al. 1996	<i>Lemna minuta</i>	hydrophyte	<i>Potamogeton crispus</i>	hydrophyte	AE greenhouse	A	aquatic system	UK
Lindquist et al. 1996	<i>Centaurea maculosa</i>	ann forb	<i>Festuca idahoensis</i>	bunchgrass	RSE in pots	A, N	prairie	Nebraska
Lindquist et al. 1996	<i>Centaurea maculosa</i>	ann forb	<i>Pseudoroegneria spicatum</i>	bunchgrass	RSE in pots	A, N	prairie	Nebraska
Makepeace et al. 1985	<i>Pilosella officinarum</i>	ann forb	<i>Festuca novae-zelandiae</i>	per grass	RSE greenhouse	A, N	grassland	New Zealand
Melgoza et al. 1990	<i>Bromus tectorum</i>	ann grass	<i>Chrysothamnus viscidiflorus</i>	shrub	RE	A	bunchgrass com	Nevada
Melgoza et al. 1990	<i>Bromus tectorum</i>	ann grass	<i>Stipa comata</i>	per grass	RE	A	bunchgrass com	Nevada
Mesléard et al. 1993	<i>Paspalum paspalodes</i>	per grass	<i>Aeluropus litoralis</i>	per grass	RSE in pots	A, N	marsh	Camargue (France)
Nelson and Allen 1993	<i>Avena barbata</i>	ann grass	<i>Stipa pulchra</i>	per grass	AE, AE greenhouse	A, N	grassland	California
Quinos et al. 1998	<i>Lotus tenuis</i>	per forb	<i>Paspalum dilatatum</i>	per grass	AE	A	grassland	Argentina
Ridenour and Callaway 2001	<i>Centaurea maculosa</i>	ann forb	<i>Festuca idahoensis</i>	bunchgrass	AE greenhouse	A	oldfield	Montana
Romo and Eddleman 1987	<i>Bromus japonicus</i>	ann grass	<i>Agropyron spicatum</i>	per grass	RE	A	prairie	Great Plains
Romo and Eddleman 1987	<i>Bromus japonicus</i>	ann grass	<i>Koeleria cristata</i>	per grass	RE	A	prairie	Great Plains
Romo and Eddleman 1987	<i>Bromus japonicus</i>	ann grass	<i>Sitanion hystrix</i>	per grass	RE	A	prairie	Great Plains
Sheley and Jacobs 1997	<i>Centaurea maculosa</i>	ann forb	<i>Agropyron spicatum</i>	per grass	RSE	A, N	grassland?	Montana
Van Auken and Bush 1991	<i>Cynodon dactylon</i>	per grass	<i>Baccharis neglecta</i>	shrub, seedl	RSE greenhouse	A, N	prairies	California
Weber and D'Antonio 1999	<i>Carpobrotus edulis</i>	succulent, seedl	<i>Carpobrotus chilensis</i>	succulent, seedl	AE in pots	A, N	coastal scrub	California
Welker et al. 1991	<i>Bromus mollis</i>	ann grass	<i>Quercus douglasii</i>	tree, seedl	AE in pots	A, N	savanna	California
Willis et al. 1998	<i>Hypericum perforatum</i>	per forb	<i>Themeda triandra</i>	grass	AE greenhouse	N	grassland	Australia
Witkowski 1991b	<i>Acacia saligna</i>	tree, seedl	<i>Protea repens</i>	tree, seedl	AE greenhouse	A, N	shrubland	South africa
Zedler et al. 1990	<i>Typha orientalis</i>	halophyte	<i>Juncus kraussii</i>	halophyte	RSE in pots	A, N	marsh	SW Australia

Life form, stage: per = perennial, ann = annual, seedl = seedling.

Study type: RE = removal experiment, AE = addition experiment, RSE = replacement series experiment. All are field experiments otherwise noticed.

Effect: A = effect of the alien on the native species, N = effect of the native on the alien species.

System and Region refer to the community type and geographical region where the alien is invading, respectively.

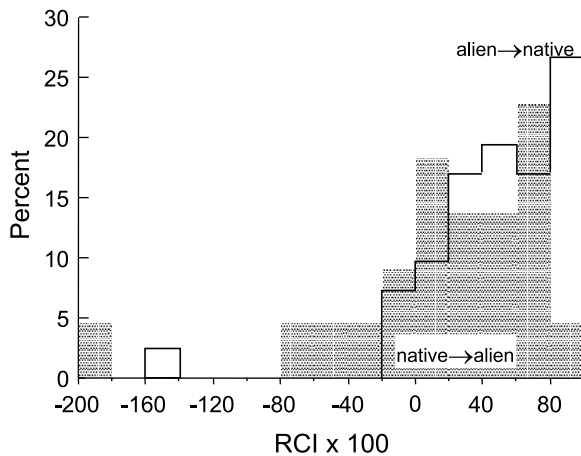


Fig. 1. Frequency distribution of the relative competition intensity indexes (RCI) for removal and additive experiments of the effect of alien species on native species (outlined bars, $n = 39$) and the effect of native species on alien species (grey bars, $n = 24$).

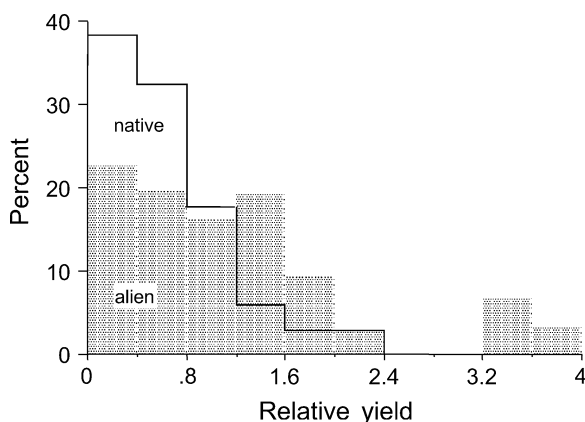


Fig. 2. Frequency distribution of the relative yields (RY) from replacement series experiments between native and alien species. Outlined bars represent RY for native species ($n = 34$) and grey bars represent RY for alien species ($n = 31$). The sample size is smaller for aliens because some publications do not present data on monocultures of the alien species.

of *Lantana camara* (Gentle and Duggin 1997). Similarly, there is some field evidence that *Pilosella officinarum* and *P. praealta* introduced to New Zealand can affect tussock grasslands by allelopathic exudates (Makepeace et al. 1985). However, although there is evidence that resource competition affects several components of performance of native plants (i.e. size, growth, reproduction, survivorship and germination), most studies do not assess the resources for which the plants are competing or how competition varies along environmental gradients. This information is needed if we are to predict

under which conditions the threat of aliens on natives will be greatest.

What do we mean by “competition” in the context of plant invasions?

No word has been used in more different ways and has been the source of more confusion in ecology than “competition” (Keddy 2001). Competition has different meanings at different scales in ecology, and these different meanings are often confused in the literature (O’Neill et al. 1986). Even at one scale, the word competition is used to refer to all negative neighbour effects in some cases and only resource-mediated effects in other cases. This has been the cause of much of the confusion in the literature on competition and invasion.

Is the dominance of some invading species in a recipient community due to its superior competitive ability? If one sees the process of invasion, i.e. the increase in population size of an alien species and the concurrent decrease in population size of some native species, as a competitive process, the statement that invaders are better competitors is tautological. On the other hand, if we define competition more narrowly, for example as negative effects of neighbours due to consumption of limiting resources, then the dominance of an invader can be attributed to factors other than competition itself, such as indirect effects (e.g. “apparent competition” or allelopathy).

One can distinguish between an inherent and a non-inherent competitive advantage. One leading theory for the success of invasive plants is that they have escaped the co-evolved natural enemies that hold them in check in their region of origin (Elton 1958). Much emphasis has been put on the potential role of phytophagous invertebrates and pathogens in controlling plant invasions. It is likely that the interaction between competition and natural enemies results in the advantage that invaders often have. This could be because the invader’s competitive advantage is not innate but mediated by the decreased load of natural enemies experienced by the invader compared to the native species (Keane and Crawley 2002). If a reduced load of natural enemies tips the competitive balance in favour of an invading species, this will be observed as a “competitive advantage” in the field and in field experiments. This may incorrectly be interpreted as an inherent competitive advantage for the invading species. Generalist herbivores reduce invasive plant growth, seed set and survival but can also act as seed dispersers and alter the outcome of native and non-native plant competitive interactions, often having overall a positive effect on the invasion process (Maron and Vilà 2001). As often the case in ecology, explanations for many of the most important

phenomena may lie in the interactions among factors, such as competition and herbivory, not in single factors.

We attempted to test the hypothesis that natural enemies mediate the competitive advantage of invaders by comparing experiments conducted under highly controlled glasshouse conditions with field experiments. The assumption is that the latter will be more influenced by natural enemies. The competition indices were very similar for the two types of experiments, so there was no support for the hypothesis. Another possibility is that the release from natural enemies in the new community results in the evolution of a more competitive allocation strategy by the invader, resulting in increased competitive ability of invaders (Blossey and Nötzold 1995).

Limits of the available data

There are several reasons why the conclusion that invasive species are superior competitors than native species should be considered tentative. First, the alien species studied are not a random sample of the pool of available introduced species. Researchers usually tend to choose to study those alien species that have the largest impact, i.e. invaders that dominate native vegetation or at least suppress specific native species. Similarly, researchers may tend to choose the native species that seem to be especially threatened by an alien, such as rare or endemic species with small populations (Huenneke and Thompson 1994). If these species' rarity reflects poor competitive ability then competition between a rare native species and a dominant invader may not represent a typical case of native versus alien species (Aplet and Laven 1993).

The process of invasion can be described in four stages that may be driven by very different processes (Williamson and Fitter 1996): (1) introduction, (2) establishment, (3) naturalization and (4) outbreak. The factors that determine whether or not an alien species establishes and naturalizes may be very different than those that determine if, after establishment, it undergoes a population explosion, suppressing other species and becoming a pest. The role of competition between natives and aliens may be very different in these different stages. The competitive effect is most commonly tested in alien plant species in stage (4), but the question whether aliens generally are better competitors than natives should be addressed to species in stages (2) or (3). Perhaps invading (outbreak) species are those among the naturalized aliens that have highest competitive ability. Thus alien (i.e. naturalized) species may not generally be better competitors than natives, but invaders (i.e. those aliens that become pests) are.

Finally, the choice of dissimilar alien–native species pairs in terms of size, life form, life-history stages and taxonomic relatedness may also bias the available data

towards higher competitive superiority of aliens over natives. For example, several studies focus on the effect of mature fast growing grasses on native seedlings of woody species (Cohn et al. 1989, Gordon et al. 1989, Hobbs and Atkins 1991). It is well known that different life forms respond very differently to competition (Gerry and Wilson 1995). It can be argued that to generalize that aliens are superior competitors than natives, one should pair alien and native species with the same life form because studies have demonstrated that the larger effects will be found when the introduced species does not match the characteristics of the resident species (Chapin et al. 1995). On the other hand, if invaders often have superior competitive ability because they have a different and more competitive growth form than natives, then this difference is part of the explanation for their competitive advantage. Replacement series experiments are much more meaningful if the initial biomass (e.g. propagule or seedling biomass) of the competitors is included in the analyses (Connolly 1986), but most studies do not contain this important information.

Proposed pair-wise experimental approaches

To test if invasive species have superior competitive ability than native species both the impact and resistance components of invasion should be estimated. We propose the following two approaches based on pair-wise experiments and competition indices such as RCI or In RR to experimentally test the hypothesis that alien species are better competitors than native species (Fig. 3).

In the first approach, the effect of an alien species on one or more target native species should be compared with the effect of other coexisting natives on the same target native species (Fig. 3a). If the alien species were competitively superior to natives we would expect the alien species to reduce the growth of the target native species more than it is reduced by other coexisting natives (invader's relative impact). This has rarely been attempted. The effect of root competition by the alien vine *Lonicera japonica* on the growth of *Liquidambar styraciflua* saplings was stronger than the effect of the native vine *Parthenocissus quinquefolia* (Dillenburg et al. 1993). This could be because the alien vine is evergreen while the native is not. Similarly, the alien annual grass *Bromus mollis* reduced soil water availability more than the native perennial grass *Stipa pulchra* and consequently shoot and root mass of *Quercus douglassii* seedlings was more reduced by *Bromus* than by *Stipa* (Welker et al. 1991). Ideally, both alien and native competitors should be closely related if one wants to avoid confounding effects due to different life forms. The microcosm setting used by Dukes (2001) exemplifies this

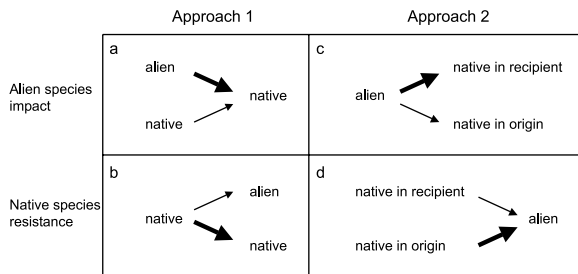


Fig. 3. Schematic representation of hypotheses based on two approaches to test experimentally that alien species are better competitors than native species by considering the effect of aliens on natives (alien species impact) and the effect of natives on aliens (native species resistance). Approach 1 (a, b) represents an alien advantage over natives in the recipient community, whereas Approach 2 (c, d) represents an alien advantage in the recipient community in comparison with its community of origin. Thicker arrows signify stronger effects of competition. (a) The alien affects natives more than natives affect one another. (b) Native species affect each other more than they affect the alien species. (c) The alien affects natives in the recipient community more than it affects natives in its original community. (d) Natives from the community of origin affect the alien more than natives in the recipient community do.

approach. He found that the annual alien grasses *Avena barbata* and *Bromus hordeaceus* had a more suppressive effect on the alien herb *Centaurea solstitialis* than perennial grasses.

Similarly, a native's effects on an alien should be compared with its effects on other native species that are similar to the invader (native species' relative resistance; Fig. 3b). If invaders were better competitors, we would expect the effect of competition by native species on coexisting natives to be stronger than the effect on the alien species. We know of no study that has made this comparison.

Another approach attempts to compare competition between the alien species and native species from the region of its origin with competition between the alien and native species in the recipient community (Fig. 3c, d). If the alien species is competitively superior, the effect on natives in the recipient community will be stronger than the effect on natives in the community of origin. Similarly, the alien species will have a higher resistance to the competition exerted by natives in the recipient community than in the community of origin. We know of only one study that has used such approach. The Eurasian forb *Centaurea diffusa*, which is invading western USA, had a more negative effect on North American grasses (a decrease of 85% of the biomass) than on Eurasian grasses (a decrease of 50% of the biomass; Callaway and Aschehoug 2000). Correspondingly, North American grasses did not reduce the biomass of the alien forb, while one of the Eurasian species did. Experimental addition of activated carbon in the soil revealed that *C. diffusa* produces root

exudates to which Eurasian grasses might be adapted and which affect competition for resources.

Invasion and plant community biomass

What are the implications of pair-wise competition experiments to understand the effects of invaders on vegetation structure? How can we detect invader competition superiority in a plant community context? The effect of invasion on local plant community biomass provides important clues concerning the nature of the changes the community is undergoing and the competitive interactions between the native and the alien species. However, studies on the impact of plant invasions on community structure usually focus on the effect of the invader on the biomass of specific species or groups of species (e.g. native herbs, seedlings), not the whole plant community.

There are three possible responses of plant community biomass to invasion:

1) If the invasion does not affect plant community biomass, then the invasion can be considered as a resource competitive process: a species that initially contributes relatively little to community biomass because of its small population size, is able to increase its share of the biomass over time at the expense of native species.

2) If an invasion increases plant community biomass significantly, then the invading species can tolerate the conditions created by the native vegetation and produce additional biomass, presumably by utilizing previously unutilised resources (niche differentiation). An extreme theoretical case would be if the invading species contributes only additional biomass to the community, not affecting the abundance of native species. In such a case, there would be no evidence for competition between the invading species and the native vegetation.

3) Two alternative scenarios are possible if an invasion reduces community biomass. It could result from strong indirect effects of the alien, such as allelopathy (Rice 1984), salt deposition (Vivrette and Muller 1977), or "ecological engineering" (Crooks 2002) by the invader, which changes the environment in ways other than resource consumption. In these cases an invader has major ecosystem effects, which one would not usually call competition. In a second possible scenario, an invasion can reduce community biomass if the invader suppresses native species by light competition but the invader is less efficient than native species in using soil resources to make biomass. For example, climax forests do not always have more biomass than sub-climax forests (Golley 1977), because the highly shade-tolerant climax species are not always larger than the sub-climax species. It is possible that an invading species could have such behaviour.

Conclusions

The aim of most of the reviewed pair-wise experiments was to determine the effects of fast-spreading, well-established alien plants on native species. We would need random samples of native and alien species to test that alien species are generally superior competitors. On the other hand, some experiments tested the effect of native species on alien species to explain one component of resistance posed by particular species to invasion. The small-scale trials reviewed in this paper are a simple approach to test for alien superiority and represent only a first attempt to generalize on the role of competition on plant invasions. Some invasive plants tend to form monospecific stands while the population of dominant native species decreases rapidly, which suggests a strong competitive effect on native species (Bakker and Wilson 2001). More studies comparing similar native and invading species are needed to test for the generality of invading species superiority. Field experiments comparing the effects of invasive and non-invasive species on intact native plant communities are necessary if we are to answer these questions more definitively.

Acknowledgements – This paper contributes to the Global Change and Terrestrial Ecosystems Project (GCTE core project of the IGBP on Biological Invasions). We are grateful to J. Canadell and M. Lonsdale for facilitating this study, and M. Erneberg and M. Williamson for critical comments on earlier drafts of this paper. This research was partially funded by grants from the Spanish Ministerio de Ciencia y Tecnología (REN2000-0361/GLO) and the European Science Foundation to M.V.

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