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Mechanisms of resistance of Mediterranean annual communities to invasion by *Conyza bonariensis*: effects of native functional composition

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Recent studies have shown that a high species or functional group richness may not always lead to a greater resistance of plant communities to invasion, whereas species and/or functional group composition can more reliably predict invasion resistance. The aim of this study was to understand the mechanisms through which functional group composition can influence the resistance of Mediterranean annual communities to invasion by the exotic *Conyza bonariensis*. To analyse the effects of functional composition on the performance of individuals introduced as seedlings we first examined the relationships between the demographic and vegetative parameters of *C. bonariensis* and the biomass achieved by each functional group (grasses, legumes and *Asteraceae* rosettes) in synthetic communities. As a further step to approach the mechanisms involved in community resistance to invasion, we included in the analyses measurements of functional variables taken within the synthetic communities.

In agreement with earlier results and theory suggesting that high nutrient availability can favour invasions, an abundant legume biomass in communities increased the final biomass and net fecundity of *C. bonariensis*, due to positive effects on soil nitrate concentration. Survival and establishment of *C. bonariensis* were mainly favoured by a high biomass of *Asteraceae*. Additional results from measurements of herbivory suggested that *C. bonariensis* survival wasn't related to abiotic conditions but may be owed to a protection against herbivores in plots with abundant *Asteraceae*. Establishment was on the other hand likely to be hindered by the effects of abundant grass and legume foliage on light quality, and therefore easier within an *Asteraceae* canopy.

We conclude that invasion of Mediterranean old fields by species with biologies similar to *C. bonariensis* could be limited by favouring communities dominated by annual grasses.

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'Invasion' refers to the set of processes concerning the introduction, installation, maintenance and spread of a species in a community in which the species was previously absent (Mack 1985, Groves 1986). Invasions by exotic species are a special case of introduction and spread of a species that was historically absent from a region (Richardson et al. 2000). The increase in human activities, and especially intercontinental transport, has led to an increase of invasion rates around the world (Hodkinson and Thompson 1997, Vitousek et al. 1997). Invasions can have impacts on ecosystem stability by modifying their diversity (Pimm 1993) and their func-

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tioning (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). Several hypotheses have been proposed to explain why some communities are more susceptible to invasions. A classic hypothesis proposed that a high native diversity could limit the establishment of alien species (Elton 1958, Fox and Fox 1986, but see Rejmánek 1989). However experimental studies of the relationships between plant community species richness and invasion by exotic weeds or ruderal species have yielded inconsistent patterns, with both positive (Palmer and Maurer 1997, Robinson et al. 1995) and negative relationships (Tilman 1997). These discrepancies occur in part because many studies have not separated the effects of different components of community structure, especially community richness and community composition (Prieur-Richard and Lavorel 2000). Recent studies have shown that the species (Crawley et al. 1999) or functional group (Prieur-Richard et al. 2000, Symstad 2000) composition of plant communities may be more relevant than their richness to their resistance to invasion.

Prieur-Richard et al. (2000) showed that the impact of functional group composition varied across life stages of two exotic species of Mediterranean old fields, *C. bonariensis* and *C. canadensis*. Survival increased with an increase in *Asteraceae* species richness. Biomass and reproduction decreased in the presence of a higher annual grass species richness but increased in the presence of annual legumes. Resource competition was hypothesised to explain these patterns: an increase in resources would increase invasion by *C. bonariensis* and *C. canadensis*. This hypothesis would conform with the theory of invasion proposed by Davis et al. (2000) to explain why species-rich communities may be invaded when the resources are not limiting due, for example, to spatial or temporal variation in resource supply. To further our results about the effects of functional composition on invasion into Mediterranean annual communities we hypothesised that modifications of resource availability by resident communities may be the mechanism underlying changes in invasive species performance. We tested this hypothesis only for *Conyza bonariensis* because the high mortality in *Conyza canadensis* would affect the robustness of statistical analyses, except for survival which will be included in the discussion.

It has been argued that the proportion of the total biomass of a community represented by a functional group or species is more relevant to the functioning of ecosystems than their mere presence (Grime 1998, Sala et al. 1996). For example, the productivity of a grassland (McNaughton 1983) or the maintenance of water balance in a savanna (Knoop and Walker 1985) were better explained using the biomass fraction for each functional group than the list of functional groups present. Hence to identify the effects of functional composition on invader performance, we used biomass of each functional group within a community in multiple stepwise regression analyses rather than the number of species within each functional group.

As a second step, to address the hypothesis that resource availability underlies the effects of functional composition, we included in the regressions a series of functional parameters: soil water content, light interception and soil nitrate content. The robustness over vegetation development of the mechanisms identified for resistance to invasion was insured by repeating the analyses for two consecutive years.

These analyses addressed two questions: 1) can effects of functional composition on *Conyza bonariensis* performance, expressed by species richness per functional group (Prieur-Richard et al. 2000), be explained by effects of the biomasses of the functional groups? 2) Through which ecosystem functional process(es) do particular functional groups limit *C. bonariensis* colonisation success?

Materials and methods

Synthetic field communities

The study site is located at the field station of Camp Redon, CNRS, in Montpellier in the French Mediterranean region (43°39′N, 3°51′E, altitude 56 m). Synthetic annual plant communities presenting different functional compositions (i.e. identities of functional groups, *Poaceae*, *Asteraceae* and *Fabaceae*) for a fixed richness of 6 species were sown in October 1996. Detailed information about the characteristics of the study site and the synthetic communities are presented in Prieur-Richard et al. (2000).

The annual peak of vegetation, which occurs in May in our region, is the time when the biomass of native species and, hence their competitive ability against exotic species, are the highest. In May 1997 and May 1998, five 10×10 cm samples of aboveground biomass were collected from a 1 m^2 quadrat within each plot. The total list of functional groups used for each plot were, according to its intended composition: sown *Poaceae*, unsown *Poaceae* and other monocots, sown *Asteraceae*, unsown *Asteraceae* and other rosettes, sown and unsown *Fabaceae*, unsown other species with leafy stems (e.g. *Caryophyllaceae*, *Borraginaceae*). Litter was also separated in an attempt to account for accumulation of non-decomposed dead material. Biomass samples were then dried to constant mass at 60°C during 36 hours, and weighed. Community composition for each plot was thus described by the biomass of different functional groups and total litter. The use of functional group biomass made it possible to take into account in our statistical analyses the fact that plots may present a different number of functional groups. This approach made it possible to address indirectly the mechanisms of competition in our analyses.

Measurement of functional parameters in the field synthetic communities

To approach the mechanisms that mediate the effects of functional group identities on the resistance of plant community to invasion, we measured a set of functional parameters during the peak of native vegetation in May of each year. These measurements were carried out within a 1 m^2 quadrat adjacent to biomass sampling and transplantation quadrats. In May 1997 we measured the percentage of incident photosynthetic active radiation reaching ground level using a one-meter integrating light sensor (AccuPAR). In order to integrate small scale vegetation heterogeneity we took five non-overlapping measurements per 1 m^2 quadrat. In May 1997 and 1998 five soil cores (each 10 cm depth, 2 cm diameter) were sampled within each quadrat. These five samples were mixed and dried before analysing nutrient concentrations. Total organic nitrogen (N) using the Kjeldahl method, phospohorus (P_2O_5) using the Joret–Hebert method, nitrates (NO_3) and ammonium (NH_4) were analysed by the soil analysis services of National Agronomic Research Institute (Arras, France).

Measurements of *Conyza bonariensis* performance in field synthetic communities

To assess the variation of invasibility across the different types of synthetic communities we used an exotic annual *Asteraceae*, *Conyza bonariensis*, as invasion phytometer. Eight seedlings of this species were transplanted into the sown communities in March 1997 and again in 1998. Survival, final dry weight of aboveground biomass and net fecundity of *C. bonariensis* were measured during the two consecutive vegetation seasons. Detailed information about this species, the transplantation experiment and the measurements are presented in Prieur-Richard et al. (2000).

Experimental establishment of *Conyza bonariensis* in the glasshouse

The field experiment addressed the effects of community composition on the performance of seedling and adult *C. bonariensis*. However, it lacked an essential component to invasion success, in situ establishment fractions. A first estimation of how these vary according to functional composition was obtained using a glasshouse microscosm experiment described by Prieur-Richard et al. (2000). This experiment (establishment experiment 1 henceforth) examined establishment as a function of numbers of species per functional group in pots where we sowed the same species and functional group mixes as in the field. Here we re-analysed these results using additional measurements of the biomass reached by each of the resident functional groups in the pots by the end of the experiment.

To assess the effects of light quantity and quality on *C. bonariensis* establishment we carried out a second controlled experiment (establishment experiment 2 henceforth), examining establishment of 120 *C. bonariensis* seeds sown in 8×8 cm pots under the following five light treatments: 1) 100% of incident light; 2) 57% of incident light (neutral shadecloth filter); 3) 18% of incident light (neutral shadecloth filter); 4) vegetation filtered light (a filter of fresh leaves changed every two days); and 5) litter filtered light (a filter of field collected litter). The percentage of intercepted light reaching ground level was measured with a LICOR quantum sensor. The percentage light extinction in the vegetation and litter filtered light treatments approximated that of the 18% neutral shadecloth filter, which therefore acted as a control for changes in the quality of transmitted light. These treatments were designed to test the response of *C. bonariensis* establishment to changes in incident light levels and changes in light quality, specifically changes in the red/far red ratio which may occur when incident light traverses a vegetation canopy. Each treatment was replicated in five pots. Pots were kept moist and the experiment was continued for one month with the first seedlings appearing during the first week. At the end of the experiment the number of individuals of *C. bonariensis* was recorded for each pot.

Data analyses

A first set of analyses identified functional groups responsible for the variation in performances of *C. bonariensis* across communities. Multiple stepwise regressions were used to analyse the effects of the biomass of different functional groups within communities on the vegetative and demographic performances of *C. bonariensis* described by four response variables: final dry biomass, survival, net fecundity in the field, and number of established seedlings in establishment experiment 1. Biomass and net fecundity had a normal distribution while survival and establishment distributions were binomial. *C. bonariensis* biomass was transformed using logarithms and survival was transformed using arcsin (squareroot). Because *C. bonariensis* is an annual species, its biomass and net fecundity were correlated ($r^2_{104} = 0.216$, $p = 0.017$), hence multiple regressions for the net fecundity of *C. bonariensis* used the biomass of *C. bonariensis* as a covariable in combination with the biomasses of different functional groups. For the 1998 data, all analyses included biomasses of unsown species that germinated during the second year of the experiment, and which were expected to affect response patterns.

For each of the two growing seasons, relationships between the biomass of each of the three functional groups (*Poaceae*, *Fabaceae*, and *Asteraceae* – sown and unsown) and ecosystem functional parameters were analysed by linear regression.

To approach the mechanisms underlying the relationships between performances of *Conyza bonariensis* and biomasses of the different functional groups present in the resident communities, we carried out further multiple stepwise regressions in which we added soil nitrate concentration for 1997 and 1998, percentage of light reaching the ground for 1997 and the biomass of litter for 1998. Nitrates alone were considered in these analyses because it was the only soil nutrient concentration significantly modified by community composition (Serrano 1999).

We analysed separately the effects of light quantity and quality on establishment fractions of *C. bonariensis* in pots (establishment experiment 2) using General Linear Models (GLM). A first analysis considered the effects of light levels and a second one examined the effects of light interception media. Establishment rates of *Conyza bonariensis* were treated using a binomial distribution with a logit link.

These analyses were performed using respectively the procedures "proc reg" and "GLM" of the software package SAS-PC (version 6.12, SAS Institute 1990).

Results

Relationships between functional group biomass and functional parameters

In May 1997, the percentage of light reaching the ground was negatively correlated with the biomass of annual grasses present in the communities (Fig. 1). In May 1997 and May 1998, nitrates were the only soil nutrient that changed in concentration in response to different sown species mixtures (Serrano 1999). Soil nitrate concentration was also negatively correlated

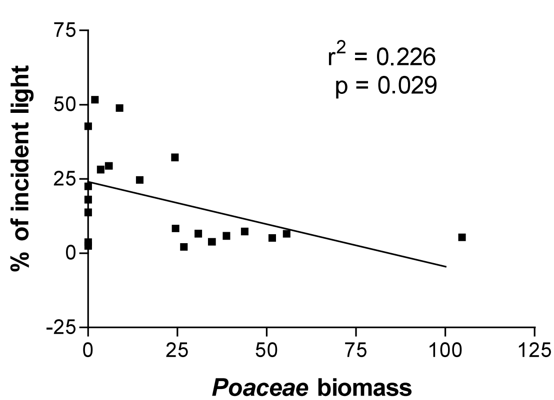

Fig. 1. Regression between the percentage of incident light at ground level and *Poaceae* biomass in 1997.

with grass biomass (Fig. 2a) and positively with legume biomass (Fig. 2b), with a response twice stronger to legume biomass (regression slope: $+0.113$) than to grass biomass (regression slope: -0.051). The relationship to legume biomass was also the one that was conserved in May 1998 (Fig. 2c).

Mechanisms limiting growth and reproduction of *Conyza bonariensis*

Table 1 presents the significant results of multiple regression of the different life cycle parameters of *Conyza bonariensis*. Each significant explanatory variable is preceeded by its estimated parameter within the model. For each demographic parameter of *C. bonariensis* Table 1 presents two models: model 1 presents significant functional group biomass variables; model 2 presents the significant functional group biomass and/or functional variables.

In 1997 final *C. bonariensis* biomass was negatively affected by grass biomass and positively by legume biomass in the resident communities (Table 1). When functional parameters were included in the multiple stepwise regression the only significant effect was that of soil nitrate concentration, with a positive relationship with *C. bonariensis* biomass (Table 1, Fig. 3a). The relationship between *C. bonariensis* biomass and soil nitrate concentration was essentially due to the species mix with 6 legume species. The positive effect of legume biomass on the covariance between net fecundity and biomass was also explained by a positive effect of soil nitrate concentration (Table 1). Hence soil nitrates had effects on *C. bonariensis* net fecundity both indirectly via its biomass and directly on its allocation to reproduction.

The analyses of the effects of functional composition on performances of *C. bonariensis* in 1998 showed fewer significant results than for the first year (Table 1). Final biomass and net fecundity of *C. bonariensis* were not significantly influenced by any of the tested factors (Table 1). This lack of effects was related to the drift in community composition, whereby the most significant component for biomass and fecundity responses, legume biomass, was drastically reduced in 1998 as compared to 1997. As a result, when in 1997 soil nitrate concentration ranged between 1 and 10 g/kg across diversity treatments, in 1998 the variation was only between 1 and 3 g/kg. Accordingly, when analyses aggregated 1997 and 1998 as a single data set for multiple regression with biomass of sown and unsown functional groups and nitrate concentration, the positive relationship between nitrate concentration and *C. bonariensis* biomass identified for 1997 alone appeared as robust, with 1998 data appearing as a restricted subsample of low *Fabaceae* biomass and therefore low

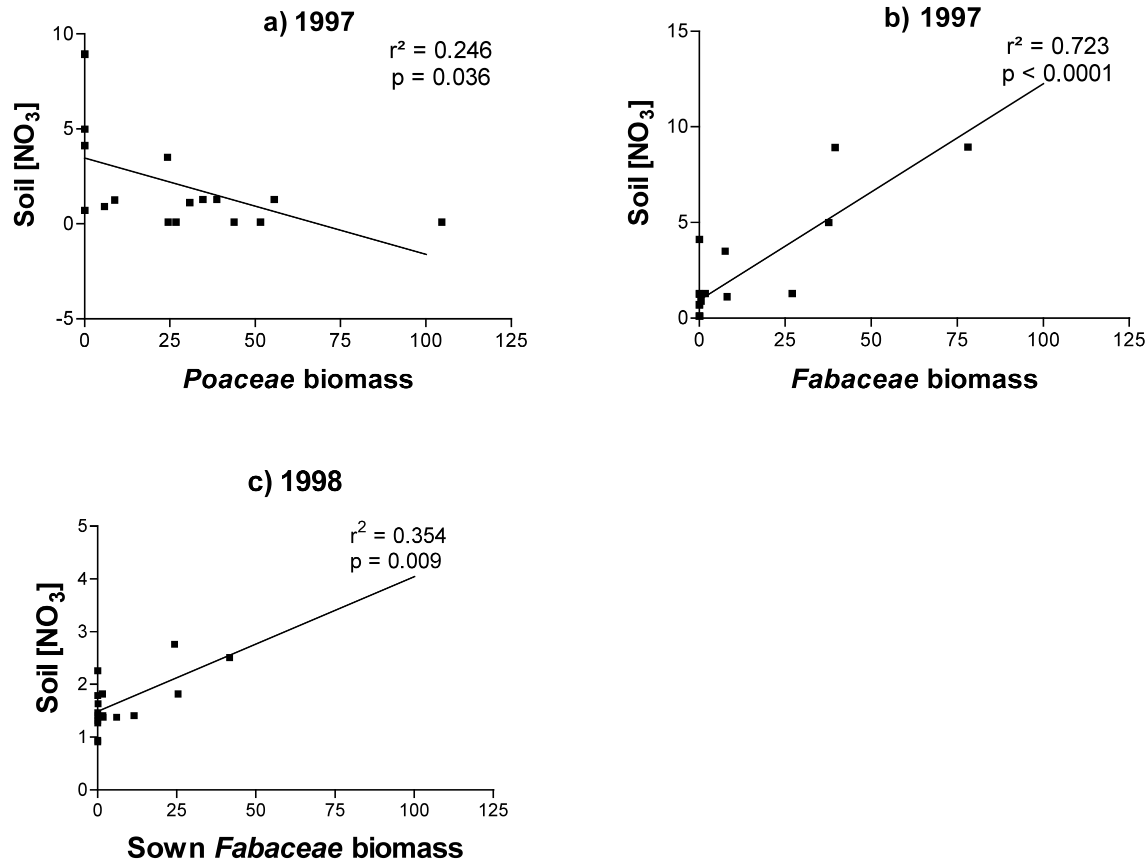

Fig. 2. Regressions between soil nitrate concentration and functional group biomass a) 1997 *Poaceae* biomass, b) 1997 *Fabaceae* biomass and c) 1998 *Fabaceae* biomass.

Table 1. Multiple stepwise regressions of *Conyza bonariensis* performances as a function of significant explanatory variables for the data of 1997, 1998 and 1997 and 1998 together (significance level ≤5%). The first model, M1, is presenting the effects of functional composition represented by the biomass of the functional groups (A: sown *Asteraceae*; P: sown *Poaceae*; F: sown *Fabaceae*; Lit: litter; us: unsown). The second model, M2, included in addition two functional parameters: the percentage of incident light at ground level (PAR) and soil nitrate concentration (NO_3). The number shown before significant variables is the estimated parameter with the trend of its impact, negative or positive.

Conyza bonariensis demograhic parameters	Estimated parameters of the significant explanatory variables		
	1997	1998	1997 & 1998
Survival	M1 = 0.08 A	M1 = 22.01 Lit	
	M2 = 0.08 A	M2 = 0.04 Aus	
Biomass	M1 = −0.02 P + 0.04 F	/	/
	M2 = 0.50 NO_3	/	M2 = 0.08 Lit
Net fecundity	M1 = 1856 F	/	
	M2 = 18815 NO_3	/	
% of establishment	M1 = 0.01 A		

soil nitrate concentrations (Fig. 3b, $r^2_{25} = 0.499$, $p < 0.0001$). However in the multiple regression including soil nitrates and litter, this nitrogen fertilisation effect was no longer significant (Table 1). A positive effect of litter was detected (Table 1) but was an in fact a statistical artefact stemming from the combination of 1997 data, where litter was absent, with 1998 data containing larger amounts.

Mechanisms limiting survival and establishment of *Conyza bonariensis*

In 1997 survival in the field was positively correlated with the biomass of *Asteraceae* in multiple regression analyses with or without functional parameters (Table 1). Hence neither percentage of incident light, nor soil nitrate concentration or soil water content influenced

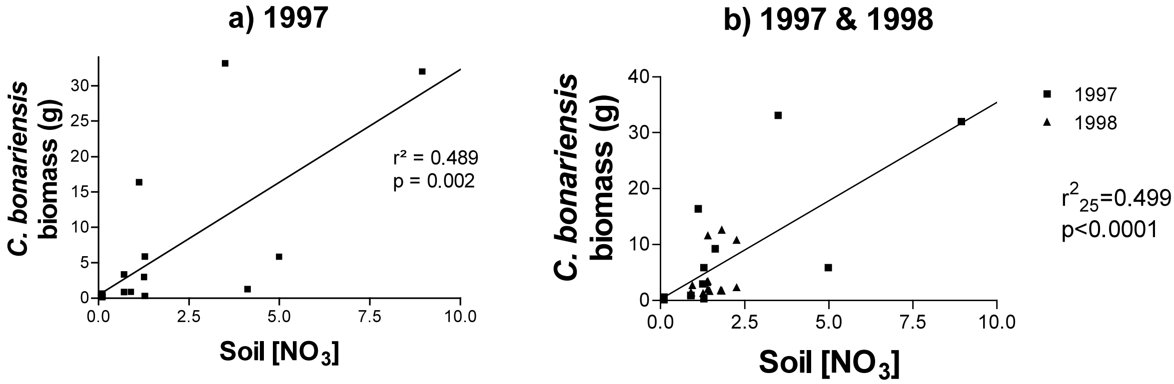

Fig. 3. Regression between soil nitrate concentration and the biomass of *Conyza bonariensis* for the data of a) 1997 and b) 1997 and 1998.

the survival of this exotic species. In 1998 survival was positively influenced by litter biomass showing a beneficial effect of litter protection during dry spring conditions prevalent that year. This effect was replaced by a positive effect of the biomass of unsown *Asteraceae* when the analysis included functional parameters. This latter model, which included a greater number of explanatory variables (addition of soil nitrate concentration), leading to a larger amount of total variance explained, was more powerful than the model with functional group biomass alone. Hence the effect of the biomass of unsown *Asteraceae* is expected to be more robust than the effect of the litter biomass.

In the glasshouse, the establishment of *C. bonariensis* was also positively correlated with the biomass of *Asteraceae* species in pots (establishment experiment 1) (Table 1) and negatively affected by full light conditions (establishment experiment 2) (Fig. 4, $F_{(3,12)} = 216.4$, $p = 0.0001$). Light quality, as affected by different interception media (shade cloth, live vegetation or litter), also had a significant effect on establishment fractions (Fig. 4, $F_{(2,12)} = 5.91$, $p = 0.016$). For a fixed level of light availability (18% of incident light at ground level), establishment of *C. bonariensis* decreased when live vegetation was used for light interception rather than inactive material.

Discussion

Effects of nitrate concentration on invasion success of *Conyza bonariensis* into annual old fields

Our analyses indicated that light competition, proposed by Prieur-Richard et al. (2000) as one potential mechanism limiting invader performance, was not particularly important to explain the variations of *C. bonariensis* biomass in response to community functional composition. Instead biomass and net fecundity of *C. bonariensis* were clearly controlled by soil nitrate concentration. One of the main effects of functional composition on invaders' performance was thus indirect and resulted from the effects of particular functional groups on soil nitrate availability. Observed positive effects of annual legume abundance on the biomass and fecundity of *C. bonariensis*, and negative effects of annual grass abundance on its biomass, were respectively the reflection of symbiotic nitrogen fixation and of direct underground competition. In adddition, although no direct measurements of the effects of functional composition on water availability were taken in these plots, measurements in a complementary experiment in the same field (described in Prieur-Richard et al. 2000) indicated that increasing legume biomass tended to decrease soil moisture in the soil's top 15 and 30 cm (Serrano 1999). Therefore positive effects of legumes on the growth and reproduction of *C. bonariensis* could not be confounded by a decrease in competition for soil water when legumes replace grasses in the synthetic communities.

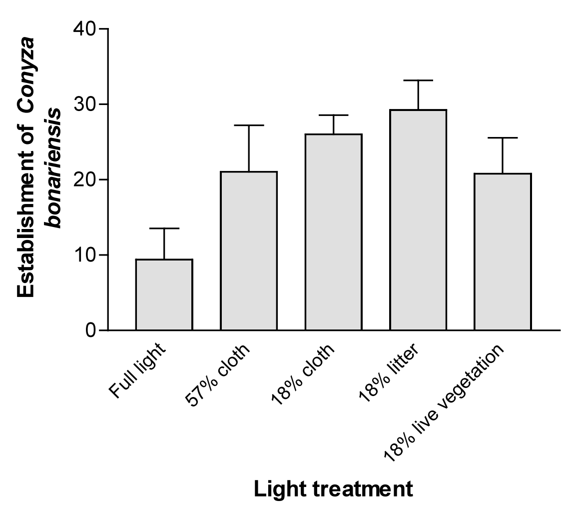

Fig. 4. Establishment fractions of *Conyza bonariensis* according to the different light treatments.

Our results demonstrating the role of nitrate concentration on the performance of *C. bonariensis* concurs with those found for two other congeneric exotic species of our region, *Conyza canadensis* and *C. sumatrensis*, whose performances in Mediterranean old fields increased with the experimental addition of nitrogen (Thébaud et al. 1996). Hector et al. (2001) also found, in addition to an overwhelming positive effect of light availability, a positive correlation between soil nitrogen concentration and the establishment of weeds into synthetic perennial grassland communities. Fertilisation is a well-known factor facilitating invasions (Hobbs and Huenneke 1992, Davis et al. 2000), whose effects have been detected for a range of Mediterranean vegetation types (Hobbs and Atkins 1988, Huenneke et al. 1990). The discrepancy between our findings and those by others (Tilman 1996, Knops et al. 1999, Hector et al. 2001) that the presence of perennial legumes decreased grassland invasibility resulted from the fundamental difference between an increase in resource availability for plant growth in our case, and a decrease in available space for colonisation from seeds in their cases.

Such results support doubts that community richness should ever be the best predictor of community invasibility, as opposed to community composition (Prieur-Richard et al. 2000, Symstad 2000) and its effects on resource availability (Davis et al. 2000). Rather than low species richness, as proposed by Elton (1958), abundant legume biomass would be one factor favouring invasion of annual weed species such as *Conyza bonariensis* into early successional communities.

Effect of *Asteraceae* rosettes on the invasion of annual old fields by *Conyza bonariensis*

For both years of experimentationn, survival of *C. bonariensis* was increased in plots having an abundant *Asteraceae* biomass. Based on our experimental design, which was substitutive for functional group identities, we previously hypothesised that the positive effect of *Asteraceae* on survival of *C. bonariensis* could be explained in an inverse manner, where the absence of *Fabaceae* and *Poaceae* would favour *C. bonariensis* survival through decreased above- and belowground competition (Prieur-Richard et al. 2000). The lack of effects of either light or nitrates in the multiple regression models would instead suggest that the property favouring *C. bonariensis* survival is not resource-related but specific to another characteristic of *Asteraceae*. The same response of survival to functional composition was observed for *C. canadensis* in 1997 and 1998. Likewise in 1999 survival of a perennial grass, *Bromus erectus*, transplanted into the same experimental plots increased with *Asteraceae* biomass (S. Lavorel, unpubl.), suggesting that the positive effect of *Asteraceae* on survival may be valid for exotic and native as well as for annual and perennial species. For *C. bonariensis* and *C. canadensis* we showed specifically that the underlying mechanism was a decrease in the rate of herbivory on seedlings in communities dominated by *Asteraceae*, which we interpreted as evidence that these communities were acting as refuges against insect and mollusc herbivores (Prieur-Richard et al. 2002).

Seedling establishment of *C. bonariensis* was also highest in pots with a large *Asteraceae* biomass. This would suggest that, in addition to herbivore protection in the field provided by this group, there was little intra-functional group competition. These results contrast with findings that the recruitment of dicots and grasses of British grasslands was more limited by intra- than inter-functional group resident species (Leishman 1999). On the other hand, Pyšek and Pyšek (1995) showed that invasion by *Heracleum mantegazziani* increased in a community made of species with equivalent life history traits. Based on our substitutive design, we hypothesise that the absence of *Poaceae* or *Fabaceae* was the factor favouring establishment rather than the presence of *Asteraceae* per se. Light competition can however be excluded as a potential mechanism since establishment rates were highest in pots with the lowest light availability at ground level (18% of incident light), a value similar to that measured in field communities dominated by *Poaceae* (Serrano 1999). However the quality of light, with a modification of the far red light radiation by live vegetation, could explain the decrease of establishment of *Conyza bonariensis* in communities dominated by *Poaceae* that present a greater leaf area index than communities dominated by *Asteraceae* (Lavorel et al. 1999). Litter biomass did not have any significant effect on the establishment of unsown species into synthetic grassland communities of the BIODEPTH Silwood Park site either (Hector et al. 2001). Competition for water, which is a prevalent mechanism in Mediterranean communities, especially during the establishment stage (Vilà and Sardans 1999), would also deserve further consideration.

Conclusion

Hector et al. (2001) observed that a decrease in nitrogen, light and space availability due to changes in species richness and composition suppressed the establishment of weedy species into perennial grasslands. In our study we established for the first time in a direct manipulation of community functional composition the full linkage from effects of functional groups on resources (nitrates in our case) to their effects on the growth and reproductive output of an invading species, *C. bonariensis*. Multiple stepwise regression models of *C. bonariensis* performance including the biomass of functional groups present in communities and functional parameters made it possible to highlight the mechanisms through which functional composition can determine plant community resistance to invasion. We identified two different types of mechanisms through which functional group composition affects different parts of the life cycle of *C. bonariensis*: 1) resource competition: high soil nitrate concentration with abundant legumes and few grasses led to greater growth and reproduction, while better light quality in the absence of grasses led to higher establishment; 2) survival was favoured by increased *Asteraceae* biomass through a reduction in herbivory (Prieur-Richard et al. 2002). To combine these two mechanisms of resistance communities dominated by *Poaceae* would then be most efficient to limit invasion by *C. bonariensis*. Sowing grasses after agricultural abandonment should therefore help limit invasion by annual weed species similar to *C. bonariensis*, directly by affecting their performances and indirectly by pre-empting the establishment of annual legumes and rosettes like *Asteraceae*.

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