Sensitivity of the Invasive Geophyte Oxalis pes-caprae to Nutrient Availability and Competition

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INTRODUCTION

Invasions by alien species are a global phenomenon that can cause irreversible changes in community structure and ecosystem function (Levine et al., 2003). The success of introduced species depends on their biological traits, propagule pressure and ecosystem invasibility (Lonsdale, 1999; Lloret et al., 2005). The invasibility of plant communities (i.e. the intrinsic vulnerability to invasion) is strongly influenced by the interplay between available resources (e.g. water, nutrients and light) and plant–plant interactions (Keane and Crawley, 2002). For example, disturbance is known to increase invasibility (D’Antonio et al., 1999) mainly due to reduced competitive pressure from other plants and increased resource levels (Hobbs and Huenneke, 1992). While many studies have examined the relative competitive strength of exotic vs. native species (see Vilà and Weiner, 2004; Bruno et al., 2005) and the influence of resource availability on invasive success (e.g. Davis et al., 2000; Blumenthal et al., 2003), relatively fewer studies have examined experimentally the combined effects of competition and resource availability (Hansjörg et al., 2002; Suding et al., 2004). These type of studies are necessary in order to understand the ability of exotic plants to spread in new areas.

In Mediterranean regions, invasions by non-native plant species are common (di Castri et al., 1990) and are regarded as one of the most important drivers of global change (Sala et al., 2000). One of the most widespread invasive species of many temperate and Mediterranean areas of the world is Oxalis pes-caprae (Oxalidaceae, hereafter Oxalis), a winter annual geophyte from South Africa (Peirce, 1997). Oxalis invasion is particularly evident in many islands of the Mediterranean basin and is probably enhanced by its distinct winter phenology and its short life cycle relative to many native species (with spring–summer phenology and longer life cycles), and by its prolific vegetative reproduction by daughter bulbs.
availability and competition as Lolium monly co-occurs with was chosen as a target native species because it com-

output of Oxalis (Pu¨tz, 1994).

and orchards, compared with less-disturbed sites such as shrublands and forests (Gimeno et al., 2006). In addition to propagate pressure, Oxalis invasion along disturbance and nutrient availability gradients may partially depend on its sensitivity to nutrient availability and to competitive interactions with dominant native species. Such interactions may occur if warm temperatures advance the phenology of native species (Pu¨telas et al., 2002; Gordo and Sanz, 2005), therefore increasing the temporal overlap between Oxalis and native species. Therefore, knowledge of Oxalis sensitivity to nutrient availability and to competition with native species may prove useful for predicting Oxalis inva-
sion along disturbance gradients and with climate change. Experimental manipulations of single factors are needed to disentangle the relative effect of these two factors on Oxalis invasion in different environments.

Oxalis invasion in Mediterranean islands has been shown to decrease overall native plant diversity by about 10 %, especially with regard to annual grasses (Vila¨ et al., 2006b). However, this effect was lower than that measured for other invasive plant species. The lower negative impact of Oxalis on native species relative to other plant invaders may relate to its winter phenology, but also to species-specific traits. For instance, Oxalis is known to accumulate oxalic acid in its leaves, which is toxic to herbivore vertebrates if eaten in large quantities (Hulme, 2004). Oxalate is known to be a chelating agent for phosphorous, thus increasing its availability to other plants (Cannon et al., 1995). This raises the possibility that heavy Oxalis invasion increases soil phosphorous availability due to the release of oxalic acid-rich litter. If so, spring pulses of phosphorous in Oxalis-invaded fields could enhance sub-
sequent germination and growth of native species, thereby contributing to their maintenance.

In this study, a full-factorial greenhouse pot experi-
ment was conducted with nutrient availability (high and low) and competition (Oxalis alone, the annual grass Lolium rigidum alone, and the two species together) in order to address the following questions. (1) Does nutrient availability affect the growth and vegetative reproductive output (i.e. bulb production) of Oxalis? (2) Does competition with Lolium reduce the reproductive output of Oxalis? (3) Is Oxalis as affected by nutrient availability and competition as Lolium? Lolium rigidum was chosen as a target native species because it commonly co-occurs with Oxalis (Vil¨a et al., 2006b). Soil sampling in the field was also conducted in Menorca (Balearic Islands, Spain) in order to address an additional question: does the presence of Oxalis alter soil P avail-

ability? Due to the distribution of Oxalis in disturbed habitats, it was hypothesized that both nutrients and competition would have significant effects on Oxalis, although we did not have specific predictions on the rela-
tive magnitude of these effects. It was anticipated that competition by Oxalis on Lolium would be moderate due to differences in size between the two species (Oxalis is small relative to Lolium).

MATERIALS AND METHODS

Study species

Oxalis is a small annual, bulbous herb native to South Africa (Peirce, 1997) that has invaded the Mediterranean Basin, Australia, India, New Zealand, Portugal, the southwest of England and warm regions of the USA (Peirce, 1997). Oxalis was introduced into the Mediterranean Basin in 1796 and it is now found in Italy, Greece, the Iberian Peninsula and North Africa (Damanakis and Markaki, 1990; Brandes, 1991).

Oxalis spreads vegetatively by rooting at nodes and via numerous daughter bulbs (or bulblets) produced by each mother plant during late spring and early summer (Pu¨tz, 1994). On average, each plant produces 20 daughter bulbs (Vil¨a et al., 2006a). Daughter bulbs remain dormant in the summer and sprout in the autumn (Vil¨a et al., 2006a). The peak of vegetative growth occurs during autumn and winter (from November to March), after which flowering starts. During vegetative growth an underground tuber develops. Because viable seed production is rare or absent (see Marshall, 1987), the invading potential of Oxalis relies largely on bulb production. Oxalis leaves senesce in spring (March–May), at which time bulblet buds start to fill from reserves stored in the tuber (Chawdhyr and Sagar, 1973).

Glasshouse experiment

Comencing on 6 October, 2003, a factorial greenhouse experiment was conducted with species, nutrient avail-

ability (high and low) and interspecific competition (Oxalis pes-caprae and Lolium rigidum alone or in compe-

tition with each other). The experiment was conducted at the glasshouse facilities of the University of Barcelona (north-east Spain). Bulbs of Oxalis were harvested from plants grown in a common garden at the University of Barcelona, which originated from bulbs collected in the field (Menorca, Spain; see Vilˆa et al. 2006a). Lolium rigidum (hereafter Lolium) seeds were collected from natural field populations in Lleida (Catalonia, Spain), which had similar distribution, growth patterns and charac-
teristics as populations in Menorca. Oxalis bulbs from 50 different plants were mixed in a bag and sorted into ten size classes (from an average weight of 0.04 g in the small-
est size class to 1.06 g in the largest size class). Eight sets of ten bulbs each were prepared, with each bulb in the set selected from a different bulb-size class. Bulb-size distri-

bution was similar among sets, resulting in similar average bulb weight per set [0.39 ± 0.03 g (± s.d.); P > 0.05]. Two randomly selected sets were assigned to each of the following four treatments: (1) high nutrients with Lolium; (2) high nutrients alone; (3) low nutrients with Lolium; and (4) low nutrients alone. Two sets of bulbs per treat-

ment allowed for one set to be harvested at the time of peak Oxalis above-ground biomass, and the other for a final harvest at the end of the experiment.

Each Oxalis bulb was sown 3 cm below the soil surface in 2-L plastic pots (11.5 × 21 cm, diameter × depth) filled with silica sand. Several Lolium seeds were planted on the
soil surface in all pots assigned to the competition treatments, and in 40 additional pots assigned to the Lolium-alone treatments under high and low nutrients. Lolium seedlings were subsequently thinned to one seedling per pot. Initial Oxalis bulb emergence occurred 10 d after sowing. The experimental design was set up to test the effects of nutrients and interspecific competition, and had a total of 160 pots (2 species × 2 nutrient levels × 2 competition levels × 2 sets × 10 pots each). Effects of intraspecific competition are addressed in Vilà et al. (2006a).

All pots were completely randomized and initially watered to field capacity (200 mL). During the first 2 weeks, pots were subjected to a 60-s surface misting three times a day in order to maintain surface soil moisture and ensure emergence of Oxalis and germination of Lolium. Fertilization treatments started approximately 3 weeks after sowing (20 October). Pots assigned to the high and low nutrient treatments were watered every 6 d with 200 mL of 1/2 and 1/16 strength modified Hoagland solution (\( \text{NO}_3^- : \text{NH}_4^+ : \text{PO}_4^{3-} : \text{K}^+ : \text{Ca}^{2+} : \text{Mg}^{2+} : \text{SO}_4^{2-} \) at concentrations of 7 : 1 : 1 : 3 : 25 : 2 : 0.5 : 0.5 mm), respectively. High nutrient levels were estimated to provide approximately 0.015 g mineral N Kg \(^{-1}\) soil, to mimic nitrogen availability in productive Mediterranean soils (Serrasolsas et al., 1999). Low nutrient levels were chosen to represent unfertile field soils, such as those in areas where Oxalis is native (Read and Mitchell, 1983). After 8 weeks, pots were watered every 3 d until the end of the experiment, with nutrients added every 6 d. Pots were rotated every 2–3 weeks to prevent glasshouse location effects. Glasshouse temperature was set at 20/10 °C day/night (with daylight from 0900 to 1800; there was an approx. 3-h transition period), providing an average temperature of 15.5 °C during the experiment, with average maximum and minimum temperatures of 19.6 and 13.0 °C, respectively. No supplemental light was supplied in the glasshouse. The average temperature in Menorca (1977–2000) from September to April (when Oxalis is present in the field) is 14.3 °C, with average maximum and minimum temperatures of 17.8 and 11.0 °C, respectively. Thus, temperature fluctuations in the glasshouse were representative of the mild climate in the field. It is worth noting that the slightly warmer conditions in the glasshouse (approx. 2 °C) fall within the variation recorded in the field.

On 14–15 January, 2004, at the onset of Lolium leaf senescence and maximum flowering, the final Lolium harvest was conducted using the second set of pots. At this point, Oxalis above-ground biomass had completely decayed, although bulblet development was still in progress. Therefore, only above-ground Lolium biomass was harvested. Tillers and spikes were harvested separately, oven-dried as before, and weighed. Pots that had Oxalis (alone or in competition with Lolium) were left untouched until 10 July, 2004, when they were emptied and daughter bulbs were harvested.

### Soil field survey

In December 2002, twenty-three 2 × 2 m paired invaded and non-invaded plots were selected across Menorca (Balearic Islands), one of the most invaded islands of the eastern Mediterranean Basin (Gimeno et al., 2006). One plot of each pair was centred on an Oxalis patch (invaded plot). The other plot of each pair was then selected at approx. 2 m distance from the edge of the invaded plot (control plot). Paired-plots were selected based on a subjective decision following dedicated land surveys to make sure that the two paired-plots shared similar substrate and habitat characteristics. To reduce invaded plot variability, all plots were selected on the basis of having a high cover of the invader (present in ≥ 14 out of a total of 16 subplots within each plot). The minimum distance between different paired-plots was 1 km.

During the spring of 2002, at the peak of native vegetative cover and species’ richness, soil was collected at random from three different subplots and subsequently pooled for each plot. For each sample, surface litter (if present) was removed, and the top 12 cm of soil was sampled to a total plot volume ranging from 0.0005–0.001 m\(^3\) of bulk soil. Samples were air-dried to constant weight, sieved with a 2-mm pore-size sieve and ground in a standard ball mill grinder.

### Chemical analyses

Oxalis and Lolium leaves from the first glasshouse harvest were dried and ground to a powder (passing through a 2-mm mesh screen) for measurement of total nitrogen (N) and phosphorous (P) content, conducted at the Chemical Analyses Services of the Autonomous University of Barcelona, Spain. Leaf N was analysed with a CNS analyser, and leaf P by atomic emission spectroscopy with Inductively Coupled Plasma analysis after bi-acid digestion (nitric : perchloric, 2 : 1) in a microwave oven (Mateo and Sabaté, 1993).

Soils from invaded and non-invaded field sites were air-dried, sieved and analysed for available P (Olsen method) at the Escudero Laboratories (Reus, Spain) following standard protocols (Klute, 1986). No attempt was made to examine differences in soil P availability from the glasshouse experiment because we predicted minimal differences due to the short duration of the experiment and the minimal P retention in the irrigated silica sand.
Statistical analysis

Statistical analyses were first performed separately per species. For Oxalis, the effects of competition and nutrient treatments on above-ground biomass (first harvest), and on number, total and average weight of daughter bulbs (second harvest) were tested using an ANCOVA with initial bulb mass as covariate for Oxalis, and using a t-test for Lolium. The competition effect on roots was not tested as the roots of the two species could not be separated when grown together. Two-way ANOVAs were used to test the effects of nutrient and competition treatments on Oxalis and Lolium leaf N, P and N/P ratio, and on Lolium biomass at the first (tillers) and final (tillers and spikes) harvests.

A three-way ANOVA with species, nutrients and competition was used to test whether responses to nutrients and to competition differed between species (i.e. whether the interactions nutrient × species and competition × species were significant). In this case, bulb mass was not used as a covariate since there was no such covariate for Lolium.

A paired t-test was used to test differences between field soil P content. Variables were Ln-transformed (Lolium and Oxalis above-ground biomass, leaf nitrogen and phosphorous concentrations, and Oxalis mother bulb weight) or square-root transformed (total number and total biomass of Oxalis daughter bulbs) to meet model assumptions. All tests were considered significant at P < 0.05. All statistical analyses were conducted using SPSS 11.5 (SPSS, Inc., Chicago).

RESULTS

Ten days after planting (16 October, 2003), 12.5% of the bulbs had emerged. Emergence rapidly increased to 72% after a further week, reaching a maximum of 95% one month after planting. Emergence tended to be delayed in the smallest bulbs, with 5% of bulbs (all less than 0.09 g) failing to emerge. While failure to emerge tended to occur in smaller bulbs, the three smallest bulbs (less than 0.033 g) did emerge. Oxalis attained maximum biomass and flowering 3.5 months earlier (mid-January) than Lolium (mid- to late-April), with complete die-back of Oxalis above-ground biomass at the time of Lolium maximum biomass.

Oxalis responded to high nutrients with a significant increase in above-ground biomass (F_{1,36} = 106.2, P < 0.0001; Fig. 1), and a significant decrease in root biomass (F_{1,18} = 12.6, P = 0.003; Fig. 2A) and root mass ratio (RMR; F_{1,18} = 47.8, P < 0.0001; Fig. 2B). High nutrients also caused a significant increase in leaf N (F_{1,36} = 28.0, P < 0.0001; Fig. 3A) and, to a lesser degree, P concentration (F_{1,36} = 11.5, P = 0.002; Fig. 3B), but did not significantly change N/P ratios (F_{1,36} = 3.7, P = 0.064; Fig. 3C). High nutrients increased the total

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number of *Oxalis* daughter bulbs ($F_{1,38} = 73.2$, $P < 0.0001$; Fig. 4A), but did not have an overall effect on total daughter bulb biomass (Fig. 4B). However, the increase in the number of daughter bulbs was due to much higher values under no competition compared with all other treatments, while under competition the total number and biomass of bulbs was as low as under low nutrients ($F_{N \times C; 1,38} = 46.2$, $P < 0.0001$ and $F_{N \times C; 1,38} = 13.4$, $P < 0.001$).
Daughter bulbs were smaller (lower weight) at high than at low nutrient levels ($F_{1,36} = 21.3$, $P < 0.0001$; Fig. 4C). 

Competition by *Lolium* caused a significant decrease in above-ground biomass ($F_{1,36} = 7.0$, $P = 0.012$; Fig. 1) and of leaf N concentration in *Oxalis* ($F_{1,36} = 5.5$, $P = 0.025$; Fig. 3A) but it did not affect leaf P concentration and N/P ratios ($F_{1,36} = 0.39$, $P = 0.54$, and $F_{1,36} = 0.99$, $P = 0.33$, respectively; Fig. 3B, C). The effect on leaf N concentration tended to be stronger under low nutrients ($F_{N \times C, 1,36} = 3.8$, $P = 0.06$; Fig. 3A). Competition by *Lolium* strongly reduced the total number and total biomass of *Oxalis* daughter bulbs ($F_{1,38} = 215.4$ and 60.2, respectively; $P < 0.0001$ for both), with a much stronger effect at high nutrients (see above; Fig. 4A, B); however, it did not affect the mass of individual daughter bulbs (Fig. 4C).

Larger initial bulbs in *Oxalis* resulted in higher above- and below-ground biomass ($F_{1,36} = 40.0$, $P < 0.0001$, and $F_{1,18} = 21.2$, $P < 0.0001$, respectively; Fig. 5A, B). However, this effect was mostly restricted to smaller bulbs up to approx. 0.2 g, after which there was no change in the response variables (Fig. 5). An exception was when *Oxalis* was grown alone under low nutrients, where below-ground biomass continued to increase (although not linearly) with initial bulb mass (Fig. 5B). Larger mother bulbs also produced larger daughter bulbs (i.e. higher mass per bulb; $F_{1,38} = 10.2$, $P < 0.003$; Fig. 4C) and tended to result in an increase in the total biomass of daughter bulbs (i.e. a nearly significant effect of the initial bulb mass covariate in the ANOVA; $F_{1,38} = 3.9$, $P = 0.055$). When treatments were considered separately, a positive linear correlation between initial bulb mass and total daughter bulb biomass was only significant when *Oxalis* was grown alone under low nutrients ($r^2 = 0.4$, $P = 0.04$, $F_{1,8} = 6.4$; data not shown).

In *Lolium*, high nutrients increased tiller biomass in the first ($F_{1,38} = 94.8$, $P < 0.0001$) and final ($F_{1,40} = 89.9$, $P < 0.0001$) harvests, and the total spike biomass in the final harvest ($F_{1,40} = 41.8$, $P < 0.0001$; Figs 1 and 6). While *Lolium* root biomass in the first harvest was not affected by the nutrient treatment (Fig. 2A), RMR decreased significantly under high nutrients ($F_{1,20} = 6.3$, $P = 0.02$; Fig. 2B). Nutrients resulted in a significant increase of *Lolium* leaf N concentration in the first harvest ($F_{1,38} = 28.8$, $P < 0.0001$; Fig. 3A), but a significant decrease in leaf P ($F_{1,38} = 11.4$, $P = 0.002$; Fig. 3B). Consequently, *Lolium* leaf N/P ratios for the first harvest decreased under low nutrients ($F_{1,38} = 50.5$, $P < 0.0001$; Fig. 3C).

Competition by *Oxalis* significantly reduced the first-harvest above-ground biomass of *Lolium* regardless of nutrient treatment ($F_{1,38} = 12.0$, $P = 0.001$; Fig. 1). However, *Oxalis* competition did not affect final *Lolium* tiller and spike biomass ($F_{1,40} = 0.5$, $P = 0.13$ and $F_{1,40} = 2.3$, $P = 0.14$, respectively; Fig. 6). Leaf N concentration and N/P ratios of *Lolium* were significantly reduced under competition with *Oxalis* ($F_{1,38} = 5.2$, $P = 0.03$ and $F_{1,38} = 5.1$, $P = 0.03$, respectively; Fig. 3A, C), while leaf P concentration was not affected by competition ($F_{1,38} = 0.05$, $P = 0.55$; Fig. 3B).

Overall, biomass responses to nutrients and to competition were similar for both species ($F_{N \times C, 1,75} = 0.61$, $P = 0.08$; $F_{C \times SP, 1,75} = 0.3$, $P = 0.21$; three-way ANOVA.
with species, nutrients and competition; Figs 1 and 2). Decreases in leaf N concentration under low nutrients were greater for Oxalis than for Lolium ($F_{N_{SP}1,75} = 5.2$, $P = 0.03$; Fig. 3A). In contrast, under low nutrients leaf P concentration decreased in Oxalis while it increased in Lolium ($F_{N_{SP}1,75} = 22.8$, $P = 0.0001$; Fig. 3B). Consequently, nutrient effects on the N/P ratio were stronger for Lolium than for Oxalis ($F_{N_{SP}1,75} = 4.6$, $P = 0.04$; Fig. 3C).

Oxalis-invaded soils sampled in Menorca during 2003 had significantly higher P concentrations than paired non-invaded soils (one-tail paired $t$-test; $t_{22} = 1.7$, $P = 0.02$; Fig. 7).

**DISCUSSION**

The invasive success of alien species has been associated, among other factors, to disturbance-related increases in resource availability and reductions of competition with native species (Hobbs and Huenneke, 1992). Our results show that Oxalis pes-caprae growth and reproductive output is enhanced by increased nutrient availability and absence of competition with the common annual grass Lolium rigidum.

Decreases in nutrient availability caused stronger negative effects on Oxalis vegetative biomass than did increases in competition with Lolium. Oxalis responded to increased nutrient availability with increases in above- and below-ground biomass, decreases in root mass ratio, and increases in leaf N and P concentrations. However, competition with Lolium had a much stronger negative effect on the total number of daughter bulbs and their total biomass than was caused by reduced nutrients: when Oxalis was grown in competition with Lolium the total number and biomass of daughter bulbs was dramatically reduced regardless of nutrient availability. In a glasshouse experiment using the same pot size, Vila et al. (2006a) reported that Oxalis daughter-bulb production per plant decreased from an average of 50 bulbs when one mother plant was grown per pot (which is consistent with our results) to approx. 30 when there were two mother plants per pot, and to approx. ten when there were fifteen plants per pot. In our experiment, the number of daughter bulbs decreased to below ten bulbs per plant when Oxalis was grown with a single Lolium plant. These results suggest that the effect of intraspecific competition is much smaller than the effect of interspecific competition. The relative responses to competition and nutrient availability in plants reproducing exclusively by bulbs are poorly documented and, to our knowledge, no study has addressed these interactions in an invasive bulb-reproducing plant. Our results are in accordance with studies on asexual-reproducing plants; increases in asexual propagules and vegetative spread in response to nutrient addition have been documented by Wookye et al. (1994), Ronsheim and Bever (2000) and Hansjörg et al. (2002). Ronsheim (1996) also reported decreases in aerial bulbil production under intraspecific competition in Allium vineale, although nutrient effects were not studied. The strong negative effect of competition by Lolium (relative to nutrient availability) on Oxalis reproductive output increased even more under high nutrients: not only was the number of daughter bulbs reduced to that produced under low nutrients and competition, but the bulbs were significantly smaller. Consistent with these results, Hansjörg et al. (2002) also reported stronger negative effects of competition by natives relative to nutrient reductions on vegetative growth of the invasive clonal forb Rorippa austriaca.

The larger size of daughter bulbs produced under low nutrients regardless of competition may be ecologically relevant for the maintenance of subsequent populations in nutrient-deficient soils: under stressful conditions a few, large bulbs may increase population emergence relative to many, small bulbs. Indeed, emergence and growth of Oxalis have been shown to depend on bulb size and the depth at which the bulb resides in the soil (Lane, 1984). Smaller bulbs take longer to emerge at the soil surface as initial below-ground growth depends on stored reserves in the bulb. Consistent with this, the few bulbs in the current experiment that failed to emerge were in the smallest category. As reported by Lane (1984), we also found that for bulbs smaller than 0.2 g, increases in mother-bulb mass resulted in higher vegetative biomass. Smaller plants are more likely to exhibit lower daughter-bulb production as bulblet development depends on tuber size, which in turn depends on mother-bulb stored resources and, upon depletion of these, on photosynthates from above-ground structures (Chawdhry and Sagar, 1973). Consistent with this, under low nutrients and no competition, reduced mother-bulb size significantly reduced the biomass of daughter bulbs. Together these results suggest that increased bulb size under nutrient deficient conditions may improve emergence, growth and reproductive output of future plants in the field. Increased bulb size under low nutrients could be an evolutionary response of Oxalis, as soils from its native South African range are notoriously nutrient-poor (Read and Mitchell, 1983).

It is unlikely that the decrease of bulb size under high nutrients limits bulb emergence in the more fertile field soils that Oxalis tends to prefer in its invasive range. This
is because average bulb size under the high nutrient treatment was about 0.2 g, which is the threshold above which bulb size does not affect above-ground growth and daughter-bulb production. Further, disturbances involving soil mixing (e.g. ploughing) bring bulbs close to the soil surface, potentially offsetting the small size effect.

Some invasive species have been shown to be more responsive to nutrient addition than co-occurring native species (e.g. Leishman and Thomson, 2005). This was not the case in our experiment as biomass responses were generally similar for both species. Further, while in Oxalis leaf P concentration under low nutrients at the first harvest decreased, there was an increase in Lolium. We suspect that this increase was due to a concentration effect, as Lolium plants had not yet reached their maximum growth at the first harvested and their above-ground biomass was significantly reduced.

Invasive species are often superior competitors than natives. If this is the case, invaders should affect native plant performance more, and be more resistant to their presence than vice versa (Vilà and Weiner, 2004). This was not the case in our study system: Lolium competition reduced both Oxalis vegetative biomass and asexual reproductive output while Oxalis competition reduced the biomass of Lolium at the first harvest but, as predicted, not its final biomass and reproductive output. Although the advantages of initial plant size have been highly emphasized (Gerry and Wilson, 1995), it is probable that the rapid growth of Oxalis (with peak growth in the greenhouse by mid-January) relative to Lolium (peak growth in April) resulted in only a transient competitive effect of Oxalis on Lolium. Thereafter, upon Oxalis senescence and during bulb maturation, Lolium continued to grow to its peak regardless of prior competition with Oxalis. While the winter phenology of Oxalis minimizes competition with native species, overlap between Oxalis and native species occurs during the later stages of the life cycle of Oxalis in the spring and early summer, particularly when native species germinate early after warm winters. If climate change advances the phenology of Mediterranean native species (Peñuelas et al., 2002; Gordo and Sanz, 2005), these results point to a potential increase of the competitive effect of native species on Oxalis.

Many alien species are known to alter nutrient cycling in invaded areas (Ehrenfeld, 2003). In the field it was found that Oxalis-invaded soils had significantly greater available P than non invaded soils. Oxalis is known to accumulate oxalic acid in its leaves (Marshall, 1987), which is a chelating agent known for its ability to improve P availability (Cannon et al., 1995). The annual return of Oxalis leaf litter and its oxalate to the soil may, therefore, be the mechanism responsible for the observed P increase. Interestingly, in the greenhouse, while soil P amelioration was expected to be minimal, Lolium leaf P did not decrease when grown in competition, which is in contrast to the significant decrease in leaf N. These results are consistent with our field data and suggest that Oxalis may improve P availability in the field. Such an effect may explain the low observed differences in plant species’ diversity in Oxalis-invaded and non-invaded communities (Vilà et al., 2006b). Field experiments are needed to test if P availability counterbalances the competitive effect of Oxalis. Such an effect has been suggested by Bellingham et al. (2005), who observed soil P accumulation in communities invaded by Buddleja davidii without any changes in native species’ diversity relative to non-invaded communities.

In conclusion, our results show that the reproductive output of Oxalis was negatively influenced by reduced nutrient availability and, particularly, by competition with the native Lolium. These results are consistent with the distribution of Oxalis in the field (preferentially in abandoned fields and orchards; Gimeno et al., 2006) and could have important implications for management. For instance, because of the winter phenology of Oxalis, ploughing of agricultural fields in the autumn may enhance Oxalis invasion due to the relatively high fertility in these fields and the removal of native competitors. The results also suggest that planting native grass species may improve restoration of abandoned orchards, particularly if climate change advances the phenology of native species.

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LITERATURE CITED


