First publ. in: Journal of Ecology 95 (2007), 4, pp. 674-681

DOI: 10.1111/j.1365-2745.2007.01250.x

South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions

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Summary

1 Plant invasions constitute a large biological problem and screening protocols are needed to assess the invasive potential of species considered for introduction. However, insufficient information is available on species characteristics associated with successful establishment outside their native range.

2 We tested experimentally whether seed and seedling emergence characteristics and early growth of seedlings are associated with naturalization of South African Iridaceae. In a common garden experiment, we compared these characteristics between 30 species that have become naturalized elsewhere and 30 congeneric species that have been introduced elsewhere but have failed to become naturalized.

3 The average seed mass did not differ between naturalized and non-naturalized species but seedlings of naturalized species emerged faster and more profusely than their non-naturalized congeners. As a consequence of fast seedling emergence, naturalized species reached a larger size early in the season than did non-naturalized species.

4 The results of our study indicate that rapid and profuse seedling emergence play important roles during naturalization, at least for Iridaceae from South Africa.

Key-words: alien species, establishment, exotic species, germination, growth, horticulture, introduced species, non-indigenous, seed mass.

Introduction

During the past few centuries many species have been introduced into new areas from their native regions. Some of these alien species have become naturalized and, in many cases, also invasive. Biological invasions homogenize the Earth's biota (Wilson 1975), and constitute a threat to agriculture, natural ecosystems and biodiversity (Drake *et al.* 1989; Vitousek *et al.* 1997). The control of invasive organisms is expensive, labour intensive and usually has limited success (e.g. Myers *et al.* 2000). Therefore, it is important to prevent new introductions of potentially invasive species. The development of screening protocols for potential invasiveness of species considered for introduction into new regions requires information on which species characteristics are associated with successful establishment outside the native range (e.g. Daehler & Carino 2000).

Based on personal experience and theory, Baker (1965, 1974) compiled the first list of potential traits of the ideal weed. This included, among other traits, rapid and profuse germination and rapid growth. Although this list was not specifically compiled for alien invasive plants, it has frequently been referred to in this context (e.g. Liu *et al.* 2006; Richards *et al.* 2006). To date, however, there is very little empirical evidence that the traits that theoretically should promote invasiveness actually do so. As a consequence, it has been suggested that invasions are fully idiosyncratic (Crawley 1987; Roy 1990). Others, however, have pointed out that traits have to matter for invasiveness but that crucial information is lacking for most species (Gilpin 1990; Rejmánek 1996; Pyšek & Richardson 2007).

Although the number of empirical studies that have assessed traits of invasive species has steadily increased

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(Pyšek & Richardson 2007), most have included only a few species (but see references in Kolar & Lodge 2001; Cadotte *et al.* 2006), and as a consequence generalizations are hard to make. Moreover, most studies compared invasive and native species (e.g. Daehler 2003; also see Pyšek & Richardson 2007), which can be useful to unravel why alien species can invade native plant communities, but do not necessarily help to show why some introduced species establish natural populations whereas others do not (Hamilton *et al.* 2005; Muth & Pigliucci 2006). Therefore, a better approach is to compare traits among introduced species that have either become naturalized or have not.

Many existing studies compared species in the same non-native region (the so-called 'target area' approach) rather than species from the same source region. The latter approach, especially when focused on comparisons among congeners, offers more possibilities for identifying traits involved in naturalization because it eliminates or reduces the bias and variation associated with different species origins (Pyšek *et al.* 2004; Pyšek & Richardson 2007). So far, this approach has been used only in a few studies that compiled data from electronic data bases or floral guides (Scott & Panetta 1993; Goodwin *et al.* 1999; Prinzing *et al.* 2002; van Kleunen *et al.* 2007), and only one of these studies (van Kleunen *et al.* 2007) controlled for whether the non-naturalized species have actually been introduced in other regions. Additional limitations of these studies are that accurate data on many potentially important traits are not available in the published sources (Pyšek & Richardson 2007; van Kleunen *et al.* 2007) and also that any traits that are included have generally not been assessed under common environmental conditions. Therefore, studies are needed that empirically assess trait differences between large numbers of successfully and non-successfully introduced congeners in a common environment.

The probability of an alien species' naturalization is determined by the number of introduced propagules and the species' intrinsic rate of increase (Warren *et al.* 2006). This implies that once propagules, usually seeds, have arrived at a new site, naturalization depends on the intrinsic rate of increase, which is determined by seedling emergence characteristics and growth of seedlings. We tested this experimentally for the South African Iridaceae (iris family) by comparing seed mass, seedling emergence and early growth of 30 species that have become naturalized elsewhere and 30 congeneric species that have been introduced elsewhere but have not become naturalized. We used the Iridaceae as a study system because more than 300 of the *c.* 1000 species native to southern Africa (Goldblatt *et al.* 2003) are used in international horticulture (i.e. they have been introduced elsewhere) and, of these, more than 60 have become naturalized (van Kleunen *et al.* 2007). Some of these species are among the world's most invasive (Weber 2003). Moreover, it is likely that more species of Iridaceae will be considered for horticultural introduction elsewhere (Manning *et al.* 2002).

Methods

STUDY SYSTEM AND SEED MATERIAL

The Iridaceae is a cosmopolitan family of *c.* 1800 species. Most of these species are geophytes and more than half are native to southern Africa (Goldblatt *et al.* 2003). Because most species of the Iridaceae have attractive colourful flowers, hundreds of them have been introduced outside their native range for horticultural purposes (Manning *et al.* 2002; van Kleunen *et al.* 2007).

We used 30 species of South African Iridaceae that have become naturalized elsewhere, mainly in Australia, New Zealand and California, and 30 species that are used in international horticulture (i.e. have been introduced elsewhere) but have not become naturalized (Table 1). The choice of these study species was restricted by seed availability from local commercial seed providers. We

Table 1 The 30 naturalized and 30 non-naturalized congeneric species of Iridaceae used in this study

Genus	Naturalized species	Non-naturalized species
Babiana	*angustifolia*[2], *stricta*[1*,2]	*odorata*[1*], *villosa*[1*,2]
Chasmanthe	*floribunda*[1*,2]	*aethiopica*[1*,2]
Dierama	*pendulum*[1,2], *pulcherrimum*[1*]	*reynoldsii*[1*], *robustum*[1*]
Dietes	*bicolor*[1], *iridioides*[1*,2]	*butcheriana*[1,2], *flavida*[1]
Gladiolus	*alatus*[1*,2], *cardinalis*[1*], *carneus*[1,2], *caryophyllaceus*[1*], *floribundus*[1*], *tristis*[1]	*carmineus*[1*], *hirsutus*[1], *liliaceus*[1*,2], *scullyi*[1*], *teretifolius*[1*], *virescens*[1*]
Hesperantha	*falcata*[1*]	*cucullata*[1*]
Ixia	*flexuosa*[1], *longituba*[1], *maculata*[1*]	*dubia*[1*], *monadelpha*[1], *rapunculoides*[1*]
Moraea	*fugax*[1*]	*ramosissima*[1], *tulbaghensis*[1*,2]
Romulea	*flava*[1*], *minutiflora*[1], *obscura*[1], *rosea*[1*]	*barkerae*[1], *camerooniana*[1], *kaminensis*[1], *sabulosa*[1*]
Sparaxis	*bulbifera*[1*], *tricolor*[1*], *villosa*[1*]	*elegans*[1]
Tritonia	*lineate*[1]	*deusta*[1*], *flabellifolia*[1*]
Watsonia	*aletroides*[1*], *borbonica*[2], *marginata*[1], *meriana*[1,2]	*coccinea*[1,2], *laccata*[1*,2], *pillansii*[1], *wilmaniae*[1]

Obtained from [1]Silverhill Seeds, [2]Kirstenbosch.
*Collected in natural population.

assessed the horticultural usage status of these 60 species outside South Africa by checking their presence in horticultural data bases (Plant Finder of the Royal Horticultural Society, http://www.rhs.org.uk/rhsplantfinder/plantfinder.asp; PlantFiles of Dave's Garden, http://davesgarden.com/pf/; HortiPlex Plant Database of GardenWeb, http://hortiplex.gardenweb.com/plants/; also see van Kleunen *et al.* 2007). We assessed the naturalization status of the 60 species by checking their presence in *A Global Compendium of Weeds* (Randall 2002). This book presents the most comprehensive list of naturalized and weedy plants worldwide that is currently available. This book, however, also includes some species that are only weedy in their native range or that are considered as potential alien weeds although they have not yet become naturalized. Therefore, we only considered species as naturalized when they were specifically labelled as such [i.e. were defined by Randall (2002) as alien species that have self-sustaining and spreading populations with no human assistance]. Further, all of the species categorized as naturalized were listed as naturalized in the United States (USDA Plants Database, http://plants.usda.gov/), Australia (Australian Plant Census Database, http://chabg.gov.au/chah/apc/), New Zealand (New Zealand Plants Database, http://nzflora.landcareresearch.co.nz/) or a combination of these three countries. Only one of our study species that was not listed as naturalized in Randall (2002), *Sparaxis villosa*, was listed as naturalized in Southern Australia.

The 60 study species represent 12 genera, and for each genus we had at least one naturalized and one non-naturalized species. We bought, when possible, 100 or more seeds of each of the 60 species from two commercial seed suppliers in South Africa. Forty-five species (23 non-naturalized and 22 naturalized species) were bought from Silverhill Seeds (Capetown, South Africa) only, two species (both naturalized) were bought from Kirstenbosch Botanical Gardens (Capetown, South Africa) only, and 13 species (seven non-naturalized and six naturalized species) were bought from both seed providers (Table 1). Seeds of Silverhill Seeds have usually been collected from several individuals in a population and mixed, while seeds of Kirstenbosch have usually been collected from few individuals per population. The different collection protocols used by the two seed suppliers are unlikely to affect the results because near-equal numbers of non-naturalized and naturalized species were obtained from each seed provider (Table 1). Of the 58 species obtained from Silverhill Seeds, seeds of 35 species (18 non-naturalized and 17 naturalized species) had been collected in natural populations (one population per species), while all remaining species obtained from Silverhill Seeds and Kirstenbosch had been collected in gardens (one garden per species). This is also unlikely to affect the results because near-equal proportions of non-naturalized and naturalized species had been collected in natural and garden populations (Table 1).

EXPERIMENTAL SET-UP AND MEASUREMENTS

To determine individual seed mass for each of the species, we randomly selected 10 seeds per species per seed provider (i.e. for each of the 13 species bought from both seed providers, we selected 20 seeds) and weighed them individually on a micro-balance with a precision of 10^{-4} mg. To determine the time to seedling emergence and the proportion of emerging seedlings, we sowed 10 portions of 10 seeds of each species in pots (18 cm diameter, 8 cm high) filled with a 1 : 1 mixture of sand and compost that had been sterilized with methyl bromide. We covered the seeds with a thin layer of soil. For three species, *Moraea ramosissima*, *Romulea barkerae* and *Ixia monadelpha*, we only had sufficient seeds for five, seven and eight pots, respectively. For one species, *Gladiolus liliaceus*, we mistakenly sowed seeds in 11 pots instead of 10. We assigned the 601 pots to random positions on two shade house benches in the Botanical Gardens of the University of KwaZulu-Natal in Pietermaritzburg, South Africa. We checked the pots for newly emerged seedlings every second day from when all the seeds were sown (6 February 2006). On 6 October 2006 (7 months after start of the experiment), when no new seedlings had emerged for over 2 weeks, we ended the experiment. We re-randomized the pots three times during the experiment. From the collected data, we determined the time to emergence (taken as the number of days from sowing to the appearance of the first seedling in each pot) and the proportion of emerging seedlings.

On 21 and 22 July 2006 (i.e. 5.5 months after sowing the seeds), we estimated the size of the largest seedling in each pot by measuring the length and width of the longest leaf and counting the number of leaves. As an overall measure of plant size, we calculated total leaf area by multiplying leaf length, leaf width and the number of leaves. During the experiments, pots were watered daily with an automatic sprinkler system.

ANALYSES

Because the number of species was unbalanced among genera (Table 1), we analysed seed mass, time to seedling emergence, the proportion of emerging seedlings and leaf area with restricted maximum likelihood analysis of variance (REML) using the statistical software GenStat (Lawes Agricultural Trust, Rothamsted, UK). Although analyses of variance gave similar results, REML provides more efficient estimates of treatment effects in unbalanced designs with more than one source of error (Payne *et al.* 2005). The fixed model of the REML analyses included the factors 'naturalized' and was tested with the Wald test statistic, which has an asymptotic chi-squared distribution (Dobson 1990). The random model of the REML analyses included the factor 'genus', the interaction 'naturalized-by-genus' and the factor 'species' nested within 'naturalized' and 'genus'. We tested the significance of random factors and their

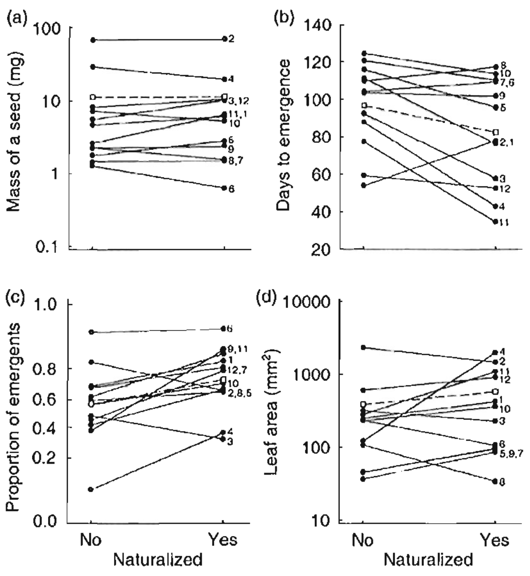

Fig. 1 Average trait values (closed circles connected by solid lines) of naturalized and non-naturalized species in 12 genera of South African Iridaceae for (a) mass of a seed, (b) time to seedling emergence, (c) proportion of emerging seedlings and (d) leaf area of seedlings. The averages of non-naturalized and naturalized species across all genera are indicated by open squares connected by dashed lines. Proportion of emerging seedlings, and mass of a seed and leaf area were arcsin-square-root and $\log_{10}$ transformed, respectively. 1 = *Babiana*, 2 = *Chasmanthe*, 3 = *Dierama*, 4 = *Dietes*, 5 = *Gladiolus*, 6 = *Hesperantha*, 7 = *Ixia*, 8 = *Moraea*, 9 = *Romulea*, 10 = *Sparaxis*, 11 = *Tritonia*, 12 = *Watsonia*.

interactions using the change in deviance after removing these terms from the model. The change in deviance is approximately chi-squared distributed (Littell *et al.* 1996). For all traits, variance components of the 'naturalized-by-genus' interactions were estimated to be negative and resulted in unstable model outcomes. Therefore, the variance components were constrained to positive values. Effectively, this means that the 'naturalized-by-genus' interactions were removed from the models.

Because there may be phylogenetic non-independence among naturalized and among non-naturalized species within each genus, we additionally performed paired *t*-tests on mean values of naturalized and non-naturalized species of each genus. To achieve normality and homoscedasticity, proportion of emerging seedlings was arcsin-square-root transformed, and seed mass and leaf area were $\log_{10}$ transformed prior to all analyses.

Results

The mass of seeds varied significantly among genera and among species within genera but did not differ significantly between naturalized and non-naturalized species ($t_{11} = 0.52$, $P = 0.614$; Fig. 1a; Table 2). However, seedlings of naturalized species emerged significantly earlier, by 14 days (−14.6%), on average, and naturalized species showed overall a higher proportion of emerging seedlings (+27.4%) than non-naturalized species (Fig. 1b,c; Table 2). These effects remained significant after correction for potential phylogenetic non-independence among naturalized and among non-naturalized species within genera ($t_{11} = 2.24$, $P = 0.046$ and $t_{11} = 2.64$, $P = 0.023$ for time to seedling emergence and proportion of emerging seedlings, respectively). Time to seedling emergence also differed significantly among genera and both time to seedling emergence and the proportion of emerging seedlings differed between species nested within genera and naturalization status (Table 2).

The largest leaf area produced by a seedling was found for a non-naturalized species, *Chasmanthe aethiopica*, but, on average, naturalized species had 53.8% more leaf area than non-naturalized species (Fig. 1d; Wald statistic = 4.91, $P = 0.027$). This, however, was not significant when we corrected for potential phylogenetic non-independence among naturalized and among non-naturalized species within genera ($t_{11} = 1.42$, $P = 0.183$). Moreover, when we corrected for the time to seedling emergence by including it as a

Table 2 Summary of restricted maximum likelihood analyses of variance testing for differences between naturalized and non-naturalized species of Iridaceae, and variation among genera and species nested within genera and naturalization status for seed mass, time to seedling emergence, proportion of emergents and leaf area. For leaf area, we also included time to seedling emergence as a covariable. The fixed effects were tested with Wald tests, and random effects with the changes in deviance after removing the effects from the full model. Both the Wald test and the change in deviance are chi-squared distributed with 1 d.f. Proportion of emergents was arcsin-square-root transformed, and seed mass and leaf area were $\log_{10}$ transformed prior to analyses

Effect	Seed mass	Time to emergence	Proportion of emergents	Leaf area
Fixed model				
Time to germination	–	–	–	198.35***
Naturalization status	1.66	5.48*	5.00*	2.27
Random model				
Genus	21.80***	8.87**	0.30	12.58***
Species	638.12***	250.47***	250.97***	75.74***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

covariable, the difference between naturalized and non-naturalized species was also not significant (Table 2). Genera and species nested within genera and naturalization status differed significantly in leaf area (Table 2).

Discussion

Our study shows that naturalization of South African Iridaceae is associated with rapid and profuse seedling emergence. These two traits are likely to form important components of a species' intrinsic rate of increase (Warren *et al.* 2006). Naturalization did not, however, appear to be associated with seed mass and growth rate. Below we discuss further the association, or lack thereof, between each of these traits and naturalization or invasiveness, and compare these results to those obtained in other studies.

SEED MASS

It has been suggested that seed mass is a key trait determining the structure of plant communities (Rees 1995), and it would therefore be expected to play an important role in naturalization of plants. Moles & Westoby (2006) showed in a recent meta-analysis that species with large seeds have higher survival through post-dispersal seed predation, through a given time as seedlings and probably through storage in the soil than species with small seeds. However, Moles & Westoby (2006) also showed that the advantages of species with large seeds are balanced by the greater annual seed production per adult plant of species with small seeds, and their shorter time to reproduction. Moreover, small seeds have a lower terminal velocity (Soons & Heil 2002), and as a result can be dispersed over longer distances by wind (Soons *et al.* 2004). Given the potential balance between advantages and disadvantages of small and large seeds, it is not surprising that we did not find a significant association between seed mass and naturalization of Iridaceae.

The results from other studies on seed mass of exotic species are mixed. In a field study, Lambrinos (2002) found that *Cortaderia selloane*, which has rapidly invaded California, has heavier seeds than the more slowly invading *Cortaderia jubata*. Similarly, Lake & Leishman (2004) found that among 57 exotic species in urban bushland in Sydney, Australia, the invasive species tended to have heavier seeds than the non-invasive species. Further, Daws *et al.* (2007) found that of 114 invasive species in their study, 71 species produced heavier seeds in the introduced than in the native range, suggesting selection for heavy seeds in the introduced range. This was also found by Buckley *et al.* (2003) for *Cytisus scoparius* but not for *Ulex europaeus*. By contrast, Rejmánek & Richardson (1996) found that low seed mass is one of the three characteristics that most clearly distinguish 12 invasive *Pinus* species from 12 non-invasive ones. This was also confirmed by Grotkopp *et al.* (2002) in another study on the same system. Similarly, Forcella *et al.* (1986) found that among three alien *Echium* species in Australia, seed mass is lowest for the two most common species. In a recent study, Hamilton *et al.* (2005) found that regional and continental abundance of 152 alien species in eastern Australia is associated with small seeds.

In agreement with the current study, several previous studies did not find a clear association between seed mass and naturalization or invasiveness. Richardson *et al.* (1987) found that differences in seed mass among one highly invasive, two moderately invasive and one non-invasive *Hakea* species in South Africa are not clearly related to invasiveness. Similarly, Mihulka *et al.* (2003) found that among 15 alien *Oenothera* species in central Europe, seed mass is not associated with invasiveness. Based on our study and the others, we conclude that although seed mass might be useful as a predictor of invasiveness for certain groups of plants, such as pine species, it does not apply to all groups of plants.

SEEDLING EMERGENCE

Obviously, once a seed has arrived at a new site it can only result in establishment when it produces a seedling. Rapid and profuse seedling emergence is therefore likely to increase species establishment and abundance. This has been shown for native species among which the rare ones have lesser capacity for immediate germination (Hodgson 1986). Our results clearly show that rapid and profuse seedling emergence is an attribute associated with species of South African Iridaceae that have become naturalized in other regions. A recent review (Pyšek & Richardson 2007) and a meta-analysis (Colautti *et al.* 2006) of the literature also concluded that germination rate is generally positively associated with invasiveness. Unfortunately, however, this review and meta-analysis did not distinguish studies comparing successfully and unsuccessfully introduced species from studies comparing invasive and native species. Moreover, the meta-analysis only included studies that mentioned the trait in the abstract, and thus might be biased against non-significant associations of germination and invasiveness.

The importance of rapid and profuse seedling emergence for naturalization is also supported by several other studies. In his seminal paper on characteristics of weedy species, Baker (1965) mentioned that seeds of the weedy *Ageratum conyzoides* germinate under a wider range of conditions than the seeds of congeneric non-weedy species. Similarly, Mihulka *et al.* (2003) found that among 15 alien species of *Oenothera* in central Europe, the most successful invaders are those that germinate best in the light. Lambrinos (2002) found that the percentage germination is higher for *Cortaderia selloana*, which has rapidly invaded California, than for the more slowly invading *C. jubata*. Forcella *et al.* (1986) found that among three alien *Echium* species in Australia, seeds of the most invasive one germinate faster and over a larger range of temperature conditions. Richardson *et al.* (1987) found that among four alien *Hakea* species in South Africa, seed germinability in the non-invasive species *Hakea salicifolia* is lower than in both the highly invasive *H. sericea* and the moderately invasive *H. suaveolens*, but is not lower than the other moderately invasive *Hakea* species, *H. gibbosa*.

Only a few studies report the absence of, or a negative association between, seedling emergence characteristics and naturalization or invasiveness. Gerlach & Rice (2003) found that among three alien *Centaurea* species differing in their invasiveness in California there are minimal differences in seed germination which are not related to invasiveness. Mandák (2003) found that seeds of the invasive *Atriplex sagittata* germinate slower and less profusely than the seeds of the non-invasive *A. hortensis* but that another pair of invasive and non-invasive *Atriplex* species do not differ in their germination characteristics. In conclusion, with the exception of these two studies [which included only small numbers of species (< 5)], all studies to date, including the present study, indicate that establishment of alien species is associated with rapid and profuse seedling emergence.

GROWTH

Several studies have found that plant size is positively associated with naturalization or invasiveness (e.g. Pyšek *et al.* 1995; Goodwin *et al.* 1999; but see Hamilton *et al.* 2005). It has also been suggested that plants might evolve a larger size in their introduced range (e.g. Blossey & Nötzold 1995). In a previous data base study on southern African Iridaceae, van Kleunen *et al.* (2007) also found that naturalization is positively associated with maximum plant height.

For initial establishment of a plant, however, it might be less important what the final size is and more important how rapidly it can achieve a certain size in order to compete with other species. Seedlings can achieve this by having a high relative growth rate. Grotkopp *et al.* (2002) found that among 29 *Pinus* species the 13 species classified as invasive have, on average, a higher relative growth rate than the eight species classified as non-invasive. Similarly, Burns (2004) found that among four species of alien Commelinaceae, the two invasive species have the highest relative growth rates, at least when nutrient levels are high. Forcella *et al.* (1986) also found that among three alien *Echium* species in Australia, the most invasive species also possesses the highest growth rate. On the other hand, Bellingham *et al.* (2004) found no relationship between relative growth rate and the rate of spread among 33 naturalized woody plants in New Zealand. Similarly, Mihulka *et al.* (2006) found no association between relative growth rate and the number of localities among 11 alien *Oenothera* species in Europe. This indicates that relative growth rate is sometimes but not generally associated with naturalization and invasiveness.

Our study shows that, 5.5 months after sowing, the species of Iridaceae which have become naturalized elsewhere were larger than those that had not. This might suggest that naturalized Iridaceae also had a higher growth rate. However, when we corrected for time of seedling emergence, the difference in size between naturalized and non-naturalized species was no longer significant. This indicates that the larger size of naturalized Iridaceae is a consequence of earlier seedling emergence rather than of a higher relative growth rate. In conclusion, most studies point to an important role of plant size for establishment of introduced species. A large size, however, can be achieved by a high relative growth rate or by rapid seedling emergence as appears to be the case for Iridaceae from South Africa.

PREDICTING NATURALIZATION

The development of screening protocols for predicting invasiveness of species considered for introduction into new regions depends on information on which species attributes are associated with invasiveness (e.g. Daehler & Carino 2000). In particular, more information is needed on traits associated with the earlier stages of invasion (i.e. naturalization; Kolar & Lodge 2001). Generalizations about species traits associated with naturalization and invasiveness can only be made based on studies that compare large numbers of naturalized and non-naturalized species and invasive and non-invasive species, respectively. Such studies have mainly been restricted to species characteristics that are easily available from floral guides or electronic databases (Scott & Panetta 1993; Goodwin *et al.* 1999; Prinzing *et al.* 2002; van Kleunen *et al.* 2007) and often do not correct for phylogeny or taxonomy. As a consequence, the power to predict naturalization or invasiveness from species characteristics is still relatively low (Prinzing *et al.* 2002; van Kleunen *et al.* 2007). Therefore, there is a need for more studies like the present one that experimentally assess the association between species characteristics and naturalization or invasiveness for large numbers of species from the same source region.

Conclusions

To the best of our knowledge, this is the first experimental common garden experiment to include a large number of introduced species from the same source area to test for traits associated with naturalization. In a previous data base study including 1036 southern African Iridaceae (van Kleunen *et al.* 2007), we showed that naturalization is associated with maximum plant height, the number of subtaxa per species and a low maximum altitude, but not with size of the native range. The current study shows, in addition, that although naturalized and non-naturalized species of Iridaceae did not differ in average seed mass, naturalized species had faster and more profuse seedling emergence than non-naturalized species. As a consequence, seedlings of naturalized species reached a larger size early in the growing season. Therefore, we recommend that the seedling emergence characteristics of a species be assessed before it is introduced elsewhere.

Acknowledgements

We thank Vanessa Pasqualetto, Alison Young, Ian Kippel and James Rodger for practical assistance, and Angela Moles and two anonymous referees for helpful comments on an earlier version of this manuscript. Part of this work was supported by a postdoctoral fellowship of the Swiss Science Foundation to M.v.k. and by funding of the DST-NRF Centre for Invasion Biology to S.D.J.

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