First publ. in: Basic and Applied Ecology 12 (2011), 3, pp. 244–250

Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland

Thomas Chrobock*, Anne Kempel, Markus Fischer, Mark van Kleunen[1]

Institute of Plant Sciences and Oeschger Centre, University of Bern, Altenbergrain 21, CH – 3013 Bern, Switzerland

Abstract

Traits that differ between invasive alien and native plant species are frequently interpreted as traits conferring invasiveness. However, such differences could reflect an introduction bias of alien species, particularly cultivated ones, or human-mediated selection of cultivars of these species with certain traits. We tested whether this is the case for germination characteristics that are frequently reported to be associated with invasiveness. In a glasshouse experiment, we compared germination characteristics of 42 plant species native to Switzerland and 47 cultivated alien species including 26 cultivars. To test whether differences in germination between these groups of species depend on an important environmental factor, we used two light levels. Cultivated alien plant species germinated earlier and more successfully than related native plant species under both light conditions. Similarly, among cultivated alien species, cultivars germinated earlier and with higher proportions than non-cultivars. Our results indicate that previously reported differences in germination characteristics between invasive alien and native species might reflect introduction bias and human-mediated selection for these characteristics. Nevertheless, because fast and abundant germination is also frequently associated with naturalization and invasiveness among alien introduced species, our results suggest that biased introduction and human-mediated selection of ornamental plants with these characteristics might increase the risk that these species ultimately become invasive. Therefore, it is important that studies testing for determinants of invasiveness include non-invasive alien species in addition to invasive alien species.

Zusammenfassung

Merkmalsunterschiede zwischen invasiven gebietsfremden und heimischen Pflanzenarten werden oft dahingehend interpretiert, dass sie Invasionen ermöglichen. Allerdings könnten diese Unterschiede auch auf selektiver Einführung und Selektion von gebietsfremden Arten, insbesondere Zierpflanzenarten oder Kulturvarietäten mit diesen Eigenschaften beruhen. Wir untersuchten, ob dies für Keimungseigenschaften, die oft mit Invasivität verbunden werden, der Fall ist. In einem Gewächshaus- experiment verglichen wir die Keimungseigenschaften von 42 in der Schweiz heimischen Arten und 47 gebietsfremden Zierpflanzenarten, darunter 26 Kulturvarietäten. Um zu testen, ob Keimungsunterschiede zwischen Zierpflanzenarten und heimischen Arten von einem wichtigen Umweltfaktor abhängig sind, nutzten wir zwei unterschiedliche Lichtintensitäten. Gebietsfremde Zierpflanzenarten keimten im Vergleich zu heimischen Arten früher und mit höheren Keimungsraten unter beiden Lichtintensitäten. Von den Zierpflanzenarten keimten die Kulturvarietäten früher und mit höheren Keimungsraten. Unsere

*Corresponding author. Tel.: +41 0 31 6314938; fax: +41 0 31 6314942.
E-mail address: thomas.chrobock@ips.unibe.ch (T. Chrobock).
[1] Present address: Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D – 78457 Konstanz, Germany.

Resultate weisen darauf hin, dass die bisher gefundenen Keimungsmerkmalunterschiede zwischen invasiven gebietsfremden und heimischen Arten selektive Einführung und Selektion widerspiegeln. Da schnelle und reichliche Keimung oft mit Naturalisierung und Invasivität verbunden ist, suggerieren unsere Resultate dass selektive Einführung und Selektion von Kulturpflanzenarten mit diesen Eigenschaften das Invasionsrisiko dieser Arten erhöhen. Aus diesem Grund ist es wichtig, dass Studien, die nach diesen Merkmalen suchen, sowohl invasive als auch nicht-invasive gebietsfremde Arten berücksichtigen.

Keywords: Alien plant; Exotic plant; Horticulture; Human-mediated selection; Introduction bias; Multi-species comparison; Non-native plant; Ornamentals; Plant invasion

Introduction

A major objective in invasion ecology is to identify traits that promote naturalization and invasiveness of alien plant species. Recent studies indicate that certain traits related to physiology, morphology and reproduction are indeed frequently associated with naturalized and invasive plant species (see Pyšek & Richardson 2007; van Kleunen, Weber, & Fischer 2010b). Among these traits are fast and abundant germination (Klink 1996; Pérez-Fernández, Lamont, Marwick, & Lamont 2000; Goergen & Daehler 2001; Gruberová, Bendová, & Prach 2001; Mihulka, Pyšek, & Martínková 2003; van Kleunen & Johnson 2007; Fisher, Loneragan, Dixon, & Veneklaas 2009; Flory & Clay 2009; Schlaepfer, Glättli, Fischer & van Kleunen, 2010), and the ability to germinate under contrasting environmental conditions (Gruberová et al. 2001; Mihulka et al. 2003; Cervera & Parra-Tabla 2009). Although fast and abundant germination could be disadvantageous under certain conditions, it is likely to result in size advantages (van Kleunen & Johnson 2007), which may facilitate establishment in disturbed habitats by suppression of slower and less-profusely germinating species through asymmetric resource competition (Weiner & Thomas 1986; Milberg & Lamont 1995; Verdu & Traveset 2005; Damgaard & Weiner 2008) and fast population growth. Moreover, for establishment in (semi-)natural vegetation, it is also relevant that a species is able to germinate under shaded conditions as found in these habitats.

Most experiments on traits associated with invasiveness compared invasive alien to native species (van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer 2010). A limitation of such studies is that the traits that appear associated with invasiveness might reflect traits of the introduced species – many of which have not become invasive (i.e. have not spread in the landscape) – rather than traits that truly confer invasiveness. Such a biased introduction of plant species with certain traits has rarely been tested explicitly (van Kleunen et al. 2010a).

Most invasive alien plant species appear to have been introduced for ornamental or horticultural purposes (Forman 2003; Weber 2003; Lambdon et al. 2008), and their cultivation use increases the likelihood that these species escape and spread into the landscape (Dehnen-Schmutz, Touza, Perrings, & Williamson 2007; Dehnen-Schmutz, Touza, Perrings, & Williamson 2007). Human preferences for specific characteristics of cultivated species might thus strongly bias the traits of introduced species. Moreover, many cultivated species have been in breeding programs to create new varieties (Cheers 1997; Hogan 2003; Drew, Anderson, & Andow 2010). The resulting cultivars, some of which have become invasive (Wilson & Mecca 2003; Trusty, Lockaby, Zipperer, & Goertzen 2008), may differ from wild-type species in ornamental traits such as flower shape and color but also in other ecological attributes. Consequently, human-mediated selection for particular traits of cultivars might have contributed to observed trait differences between invasive alien and native species. Thus, introduction bias and human-mediated selection could result in erroneous conclusions with regard to traits promoting invasiveness. Moreover, in some cases, they could also favour traits that truly promote invasiveness (Wilson & Mecca 2003; Anderson, Galatowitsch, & Gomez 2006).

To test whether there is an introduction bias and subsequent human-mediated selection for fast and abundant germination in cultivated alien species, we compared germination characteristics between 42 species native to Switzerland and 47 related, cultivated alien species that are not invasive and of which 26 were cultivars. All 89 study species are herbaceous dicots of mostly open habitats. To test whether differences between native and cultivated alien species and between cultivars and non-cultivars are consistent across different environments, we sowed seeds of these 89 species under shaded and unshaded conditions. In addition, to test whether germination characteristics depend on the region of origin of cultivated alien species, we included alien species from other parts of Europe and from other continents.

Materials and methods

Experimental setup and data collection

To determine whether germination characteristics differ between native and cultivated alien species, and between alien cultivars and non-cultivars, we ordered seeds of 42 species native to Switzerland and 47 related non-invasive cultivated alien species from commercial seed suppliers. These 89 species represented 14 families, and 26 of the alien species were cultivars (see Appendix B for details on the selection of the species and the species list). For each species, we sowed 50 seeds onto each of 12 trays (i.e. 600 seeds per species) filled with a 1:1:1 mixture of sand, plain field soil from agricultural fields in the Bern region ("Landerde", Ricoter Erdaufbereitung AG, Aarberg, Switzerland) and seedling soil ("Aussaat- und Pikiererde 191", Ricoter) on 15 May 2008. Prior to sowing, damaged and empty seeds had been sorted out. To account for spatial heterogeneity in our glasshouse (Muri near Bern, Switzerland), we randomly assigned one tray per species to one of 12 blocks. Six of the blocks were shaded with a green mesh ("Poly-Schattentuch", Neeser AG, Reiden, Switzerland) reducing light intensity by 60%. Trays were watered as needed.

We counted seedlings (with visible cotyledons) three times a week, every Monday, Wednesday and Friday, for a period of 107 days. During the last two weeks of this period, no new seedlings had emerged. We calculated for each tray the number of days until the first seedling emerged (i.e. germination delay), the number of days until 50% of the final number of germinated seeds had germinated (i.e. half-germination time) and the proportion of germinated seeds.

Statistical analysis

Because of unequal numbers of native vs. cultivated alien species and cultivars vs. non-cultivars per family, we analyzed the data with linear mixed models based on REML (restricted maximum likelihood) estimation, which can handle unbalanced data (Payne et al. 2008), using GenStat (Release 12.1, Lawes Agricultural Trust, Rothamsted Experimental Station, UK). Germination delay and half-germination time were $\log_{10}$-transformed to meet model assumptions.

To test for differences in germination characteristics between native and cultivated alien species and their responses to shading, we analyzed the data including the fixed terms 'status' (native or alien), 'cultivar' (cultivar or non-cultivar), 'shade' (shaded or unshaded) and their interactions. Because we did not include native cultivars, we restricted the comparison of cultivars and non-cultivars of alien species by fitting 'cultivar' after 'status'. To test whether region of origin of the alien species affected germination characteristics, we also included 'European origin' (European or non-European origin) and its interactions with the other fixed factors as fixed terms. As random terms, we included 'block', 'family', 'species' nested within 'family', and the interactions of 'family' and of 'species' with 'shade'. Additionally, we included '$\log_{10}$-1000-seed mass', determined by calculating the mean mass of five portions of 1000 seeds of each species, as a covariate in the random model to account for a potential association between seed mass and germination characteristics.

Because 'status' and/or 'cultivar' may be confounded with taxonomic levels above the family level, life-history and seed supplier, we also ran a model (see Supplementary Table 3) in which we added the fixed factors 'subclass' (species member of Asteridae or not), 'life-history' (perennial or non-perennial), 'native supplier' (supplier of native species only or not), and the interactions of 'life-history' with 'status', 'subclass' and 'cultivar'. As random factors, we included 'supplier' (i.e. individual suppliers) nested in 'native supplier' and the interaction of 'shade' with 'supplier' nested in 'native supplier'. We also tested explicitly whether the results of our experiment could be biased due to phylogenetic non-independence of species (see Appendix B).

We determined the significance of fixed factors with *F*-ratio tests and numerically estimated denominator degrees of freedom (Payne et al. 2008). We tested whether random factors and their interactions explained a significant proportion of variation by using the change in deviance after removing these terms from the full model. The change in deviance is approximately Chi-squared distributed with one degree of freedom (Payne et al. 2008). For all analyses, we report the significance of both fixed and random terms in Table 1 and Appendix B, but because only the fixed terms were of major interest, we focus on these in the results section.

Results

By the end of the experiment, 85 of the 89 species had germinated (Supplementary Table 1). Averaged over all species, germination occurred significantly earlier (germination delay: −23%, half-germination time: −29%), and proportions of germinated seeds were significantly higher (+42%) in shaded than in unshaded conditions (Fig. 1, Table 1).

Germination of native and cultivated alien species

Cultivated alien species germinated significantly earlier (germination delay: −39%, half-germination time: −31%; averaged over both light treatments; Fig. 1A and B), and had significantly higher proportions of germinated seeds (+145%) than native species (Fig. 1C, Table 1). This pattern was consistent within almost all plant families (Supplementary Fig. 1). Moreover, the positive effect of shading on the proportion of germinated seeds was larger for cultivated alien than for native species (Fig. 1C, significant shade × status interaction in Table 1). Neither the origin of the species (European or non-European origin) nor its interaction with shade had significant effects on germination characteristics (Table 1).

The results remained qualitatively the same when we accounted for possible confounding effects due to differences in life-history, seed supplier and taxonomic subclass of the species (Supplementary Table 3). These additional analyses showed that differences in germination characteristics between cultivated alien and native species were consistent across subclasses (as indicated by non-significant subclass × status interactions; Supplementary Table 3). Concordantly, we did not detect significant phylogenetic signals

Table 1. Results of REML analysis of variance of germination characteristics of 42 Swiss native and 47 cultivated alien plant species of 14 families under shaded and unshaded conditions obtained in a glasshouse experiment. The table gives F-test statistics for fixed terms, χ^2-test statistics (i.e. changes in deviance) for random terms, degrees of freedom (d.f.) and probabilities (p).

	Germination delay			Half-germination time			Proportion of germinated seeds		
	Statistic	d.f.	p	Statistic	d.f.	p	Statistic	d.f.	p
Fixed terms									
Shade	21.80	1, 14.7	**<0.001**	37.05	1, 15.7	**<0.001**	43.46	1, 19.0	**<0.001**
Status	21.83	1, 73.3	**<0.001**	24.36	1, 73.0	**<0.001**	54.50	1, 78.2	**<0.001**
Cultivar	5.40	1, 71.5	**0.023**	5.52	1, 71.0	**0.022**	3.48	1, 76.5	0.066
European origin	1.60	1, 74.6	0.209	2.13	1, 74.7	0.149	2.23	1, 76.6	0.140
Shade × Status	0.20	1, 66.5	0.660	3.53	1, 70.2	0.064	25.20	1, 68.7	**<0.001**
Shade × Cultivar	0.96	1, 64.2	0.330	0.07	1, 68.4	0.788	1.62	1, 67.3	0.207
Shade × European origin	0.13	1, 61.8	0.716	0.05	1, 61.7	0.816	0.02	1, 71.8	0.900
Random terms									
Block	35.50	1	**<0.001**	17.36	1	**<0.001**	46.51	1	**<0.001**
Log_{10}-1000-seed mass	3.11	1	0.078	10.43	1	**0.001**	12.50	1	**<0.001**
Family	5.92	1	**0.015**	4.31	1	**0.038**	0.76	1	0.383
Species (family)	108.77	1	**<0.001**	47.67	1	**<0.001**	112.94	1	**<0.001**
Shade × Family	0.19	1	0.663	0.06	1	0.806	2.94	1	0.086
Shade × Species (family)	23.95	1	**<0.001**	90.94	1	**<0.001**	65.15	1	**<0.001**

for any of the germination characteristics (Supplementary Table 2). These analyses also showed that germination delay and half-germination time differed significantly among life-histories of species (means ± SE; germination delay: non-perennials 7.71 ± 0.27 days, perennials 10.19 ± 0.35 days; half-germination time: non-perennials 13.98 ± 0.43 days, perennials 16.64 ± 0.50 days, averaged over both treatments; Supplementary Table 3), but there were no significant interactions of 'life-history' with other factors. Overall, these additional analyses indicate that the differences in germination characteristics between alien and native species are robust with respect to taxonomy, life-history and seed supplier.

Germination of cultivars and non-cultivars of cultivated alien species

Among cultivated alien species, cultivars germinated significantly earlier (germination delay: −30.8%, half-germination time: −24.7%; averaged over both treatments) than non-cultivars (Fig. 1A and B, Table 1), and had marginally significantly higher proportions of germinated seeds (+29.3%, Fig. 1C, Table 1). Responses to shading were not significantly different between cultivars and non-cultivars (Table 1). Again, we did not detect a significant phylogenetic signal in this comparison (Supplementary Table 2), indicating that the differences between cultivars and non-cultivars are robust with respect to phylogeny. However, when we incorporated additional factors in the model, the significant differences between cultivars and non-cultivars disappeared (Supplementary Table 3). Most likely, this reflects that 'cultivar' was confounded with 'seed supplier'.

Discussion

Many studies have reported that invasive alien plant species frequently germinate faster and more abundantly than native species (e.g. Callaway & Josselyn 1992; Klink 1996; Pérez-Fernández et al. 2000; Goergen & Daehler 2001; Gruberová et al. 2001; Fisher et al. 2009; Flory & Clay 2009), and that invasive alien and native species also differ in other life-history traits (Lake & Leishman 2004; Pyšek & Richardson 2007; Küster, Kühn, Bruelheide, & Klotz 2008; van Kleunen et al. 2010b; Fenesi & Botta-Dukat 2010). However, few studies have considered that the observed trait differences between invasive alien and native species could reflect an introduction bias or human-mediated selection rather than traits promoting invasiveness (van Kleunen et al. 2010a). Here, using a large number of species representing different families, we showed that alien species introduced for cultivation and subsequent human-mediated selection may be biased in favour of species and cultivars that germinate fast and abundantly under different light conditions.

Biased introduction of cultivated alien plant species

Most of the cultivated alien plant species tested in our experiment germinated earlier than native confamilial species, and also had higher proportions of germinated seeds. Although some of the cultivated alien species in our study are sometimes found in the wild (Supplementary Table 1), none of them are considered invasive in Switzerland (Moser, Gygax, Bäumler, Wyler, & Palese 2002; Wittenberg et al. 2006). Nevertheless, the fast and abundant germination of

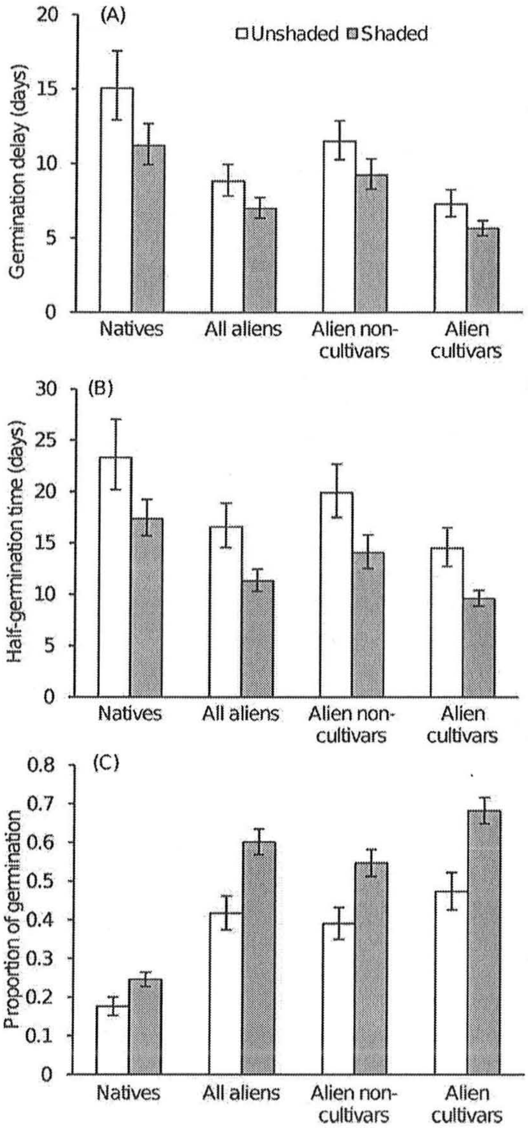

Fig. 1. Germination characteristics of plant species as assessed in a glasshouse experiment under shaded and unshaded conditions, including 42 Swiss native and 47 cultivated alien plant species (21 non-cultivars, 26 cultivars). Shown are means ± 1 SE. Values of germination delay and half-germination time were back-transformed from $\log_{10}$-values.

non-invasive alien species in our study strongly resembles the pattern found in studies comparing invasive alien species to native species (Callaway & Josselyn 1992; Klink 1996; Pérez-Fernández et al. 2000; Gruberová et al. 2001; Goergen & Daehler 2001; Fisher et al. 2009; Flory & Clay 2009). Therefore, our results suggest that many of the trait differences reported in studies comparing invasive alien and native species might reflect, at least partly, an introduction bias and not necessarily traits that confer invasiveness. However, previous studies showed that among alien plant species, the more invasive ones (or the more widely naturalized ones) frequently germinate faster and more successfully than the less invasive ones (e.g. Forcella, Wood, & Dillon 1986; van Clef & Stiles 2001; Lambrinos 2002; Mihulka et al. 2003). Therefore, our results suggest that plant species introduced for cultivation are biased towards having germination characteristics that may promote invasiveness. To further explore the importance of biased introduction of alien species, future studies should compare traits among large numbers of native, invasive and non-invasive alien species.

Plant species in our experiment germinated faster and more abundantly in shaded than in unshaded conditions, which may reflect that germination requires constantly moist conditions (Pérez-Fernández et al. 2000) along with less stressful light conditions. Interestingly, cultivated alien species took more advantage of the benign shade conditions in terms of proportion of germinated seeds than native species. Nevertheless, cultivated alien species also germinated earlier and had higher proportions of germinated seeds in the more stressful unshaded environment. Similarly, for alien species in the later stages of the invasion process (i.e. naturalized or invasive species), high environmental tolerance of germination (i.e. higher proportion of germinated seeds and/or shorter time to germination) over broad gradients of environmental factors compared to native (Köck 1988; Gruberová et al. 2001) and non-invasive alien species (Radford & Cousens 2000; Cervera & Parra-Tabla 2009) has been reported. This further exemplifies that there might be an introduction bias towards germination characteristics that are also likely to promote invasiveness.

The low proportions of germinated seeds of native species may reflect that, in contrast to cultivated alien species, native species had lower seed viability or that they are not adapted to germinate under glasshouse conditions. We cannot fully exclude the possibility that some seeds in our study were dormant or not viable, but we reduced the likelihood that seeds were unviable by excluding damaged and empty seeds prior to sowing. Moreover, although we included one major ecological factor (light intensity) in our experiment, we cannot exclude the possibility that under certain environmental conditions, such as field conditions, differences in germination characteristics between native and alien species might be absent or opposite to the results that we found. This does, however, not invalidate our finding that native and cultivated alien species have different germination characteristics.

Human-mediated selection for germination characteristics

In our experiment, alien cultivars germinated earlier and had higher proportions of germinated seeds than alien non-cultivars. Since cultivars have been selected for traits attractive to customers, these results might have been expected but, to the best of our knowledge, it has never been tested before in a large comparative study. Because it is likely that many of the invasive cultivated alien species are cultivars, cryptic (i.e. hardly identifiable) cultivars, or even hybrids of cultivars (Trusty et al. 2008; Culley & Hardiman 2009), it is likely that reported differences between invasive alien and native species partly reflect human-mediated selection for specific characteristics of cultivars.

The potential invasiveness of cultivated alien plants is of growing interest in the horticultural literature (e.g. Reichard & White 2001; Bell, Wilen, & Stanton 2003; Mack 2005). Wilson and Mecca (2003) found that cultivars of *Ruellia tweediana* have higher germination rates than the wild type, possibly contributing to their superior invasiveness compared to the wild type. In line with our results this suggests that inadvertent breeding bias or targeted selection towards plant cultivars with "best-seller" attributes demanded by customers, such as fast and complete germination, could potentially increase the likelihood of becoming invasive. The differences between cultivars and non-cultivars were, however, no longer significant when we corrected for possible confounding effects of seed supplier. This likely reflects that cultivars were ordered from two seed suppliers, whereas non-cultivars were ordered from these and two additional seed suppliers. As a consequence, the cultivar effect cannot be separated from the supplier effect. Therefore, future studies should compare cultivars and non-cultivars from the same seed suppliers. Moreover, it would be interesting to test for differences in germination characteristics between cultivars and non-cultivars of the same species, and to do this for a large number of species.

Conclusions

Our results indicate that previously reported differences in germination characteristics between invasive alien and native species might reflect introduction bias and human-mediated selection for these characteristics. Nevertheless, because fast and abundant germination is also frequently associated with naturalization and invasiveness among alien introduced species (e.g. Forcella et al. 1986; Mihulka et al. 2003; van Kleunen & Johnson 2007; Schlaepfer et al. 2010), our results suggest that biased introduction and human-mediated selection of ornamental plants with these characteristics might increase the risk that these species ultimately become invasive. The importance of introduction bias and human-mediated selection for certain traits of cultivated alien species has been largely neglected in invasion ecology (van Kleunen et al. 2010a). Therefore, future studies should also test whether other life-history characteristics frequently reported to be associated with invasiveness, such as fast growth and self-compatibility, could result entirely or partly from biased introduction and human-mediated selection.

Acknowledgements

We thank Delphine Kolly for helping to count seedlings. The comments of three anonymous reviewers helped to improve the manuscript. This study was financed by the Swiss National Found (SNF), grant no. 31003A-117722.

References

Anderson, N. O., Galatowitsch, S. M., & Gomez, N. (2006). Selection strategies to reduce invasive potential in introduced plants. *Euphytica*, *148*, 203–216.

Bell, C. E., Wilen, C. A., & Stanton, A. E. (2003). Invasive plants of horticultural origin. *Hortscience*, *38*, 14–16.

Callaway, J. C., & Josselyn, M. N. (1992). The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries*, *15*, 218–226.

Cervera, J. C., & Parra-Tabla, V. (2009). Seed germination and seedling survival traits of invasive and non-invasive Ruellia species (Acanthaceae) in Yucatan, Mexico. *Plant Ecology*, *205*, 285–293.

Cheers, G. (1997). *Botanica, the illustrated A–Z of over 10000 garden plants and how to cultivate them.* Milsons Point, Australia: Random House.

Culley, T. M., & Hardiman, N. A. (2009). The role of intraspecific hybridization in the evolution of invasiveness: A case study of the ornamental pear tree *Pyrus calleryana*. *Biological Invasions*, *11*, 1107–1119.

Damgaard, C., & Weiner, J. (2008). Modeling the growth of individuals in crowded plant populations. *Journal of Plant Ecology*, *1*, 111–116.

Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007a). A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, *13*, 527–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007b). The horticultural trade and ornamental plant invasions in Britain. *Conservation Biology*, *21*, 224–231.

Drew, J., Anderson, N., & Andow, D. (2010). Conundrums of a complex vector for invasive species control: A detailed examination of the horticultural industry. *Biological Invasions*, *12*, 2837–2851.

Fenesi, A., & Botta-Dukat, Z. (2010). Do short-lived and long-lived alien plant species differ regarding the traits associated with their success in the introduced range? *Biological Invasions*, *12*, 611–623.

Fisher, J. L., Loneragan, W. A., Dixon, K., & Veneklaas, E. J. (2009). Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation*, *142*, 256–269.

Flory, S. L., & Clay, K. (2009). Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation*, *142*, 2531–2537.

Forcella, F., Wood, J. T., & Dillon, S. P. (1986). Characteristics distinguishing invasive weeds within Echium (Buglos). *Weed Research*, *26*, 351–364.

Forman, J. (2003). The introduction of American plant species into Europe: Issues and consequences. In G. Brundu, J. H. Brock, I. Camarda, L. Child, & M. Wade (Eds.), *Plant invasions: Species ecology and ecosystem management*. Leiden, The Netherlands: Backhuys Publishers.

Goergen, E., & Daehler, C. C. (2001). Reproductive ecology of a native Hawaiian grass (*Hetropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae). *International Journal of Plant Sciences, 162*, 317–326.

Gruberová, H., Bendová, K., & Prach, K. (2001). Seed ecology of alien *Bidens frondosa* in comparison with native species of the genus. In G. Brundu, J. H. Brock, I. Camarda, L. Child, & M. Wade (Eds.), *Plant invasions: Species ecology and ecosystem management*. Leiden, The Netherlands: Backhuys Publishers.

Hogan, S. (2003). *Flora – A gardener's encyclopedia* Portland, USA: Timber Press.

Klink, C. A. (1996). Germination and seedling establishment of two native and one invading African grass species in the Brazilian Cerrado. *Journal of Tropical Ecology, 12*, 139–147.

Köck, U. V. (1988). Ökologische Aspekte der Ausbreitung von *Bidens frondosa* L. in Mitteleuropa. Verdrängt er *Bidens tripartita* L.? *Flora, 180*, 177–190.

Küster, E. C., Kühn, I., Bruelheide, H., & Klotz, S. (2008). Trait interactions help explain invasion success in the German flora. *Journal of Ecology, 96*, 860–868.

Lake, J. C., & Leishman, M. R. (2004). Invasion success of exotic plants in natural ecosystems: The role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation, 117*, 215–226.

Lambdon, P. W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., et al. (2008). Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia, 80*, 101–149.

Lambrinos, J. G. (2002). The variable invasive success of Cortaderia species in a complex landscape. *Ecology, 83*, 518–529.

Mack, R. N. (2005). Predicting the identity of plant invaders: Future contributions from horticulture. *Hortscience, 40*, 1168–1174.

Mihulka, S., Pyšek, P., & Martínková, J. (2003). Invasiveness of Oenothera congeners in Europe related to their seed characteristics. In L. E. Child, J. H. Brock, G. Brundu, K. Prach, P. Pyšek, P. M. Wade, & M. Williamson (Eds.), *Plant invasions: Ecological threats and management solutions*. Leiden, The Netherlands: Backhuys Publishers.

Milberg, P., & Lamont, B. B. (1995). Fire enhances weed invasion of roadside vegetation in southwestern Australia. *Biological Conservation, 73*, 45–49.

Moser, D., Gygax, A., Bäumler, B., Wyler, N., & Palese, R. (2002). *Rote Liste der gefährdeten Arten der Schweiz*. Bern, Switzerland: BUWAL, ZDSF/CRSF, CJBG.

Payne, R. W., Harding, S. A., Murray, D. A., Soutar, D. M., Baird, D. B., Glaser, A. I., et al. (2008). *The guide to GenStat release 11. Part 2. Statistics*. Hempsted, UK: VSN International, Hempel Hempsted.

Pérez-Fernández, M. A., Lamont, B. B., Marwick, A. L., & Lamont, W. G. (2000). Germination of seven exotic weeds and seven native species in south-western Australia under steady and fluctuating water supply. *Acta Oecologica, 21*, 323–336.

Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants: Where do we stand? In W. Nentwig (Ed.), *Biological invasions, Ecological Studies, 193*. Berlin, Germany: Springer-Verlag.

Radford, I. J., & Cousens, R. D. (2000). Invasiveness and comparative life-history traits of exotic and indigenous Senecio species in Australia. *Oecologia, 125*, 531–542.

Reichard, S. H., & White, P. (2001). Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience, 51*, 103–113.

Schlaepfer, D. R., Glättli, M., Fischer, M., & van Kleunen, M. (2010). A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. *New Phytologist, 185*, 1087–1099.

Trusty, J. L., Lockaby, B. G., Zipperer, W. C., & Goertzen, L. R. (2008). Horticulture, hybrid cultivars and exotic plant invasion: a case study of *Wisteria* (Fabaceae). *Botanical Journal of the Linnean Society, 158*, 593–601.

van Clef, M., & Stiles, E. W. (2001). Seed longevity in three pairs of native and non-native congeners: Assessing invasive potential. *Northeastern Naturalist, 8*, 301–310.

van Kleunen, M., Dawson, W., Schlaepfer, D. R., Jeschke, J. M., & Fischer, M. (2010). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, doi:10.1111/j.1461-0248.2010.01503.x

van Kleunen, M., & Johnson, S. D. (2007). South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions. *Journal of Ecology, 95*, 674–681.

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters, 13*, 235–245.

Verdu, M., & Traveset, A. (2005). Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. *Ecology, 86*, 1385–1394.

Weber, E. (2003). *Invasive species of the world: A reference guide to environmental weeds*. Oxford, UK: CABI Publishing.

Weiner, J., & Thomas, S. C. (1986). Size variability and competition in plant monocultures. *Oikos, 47*, 211–222.

Wilson, S. B., & Mecca, L. K. (2003). Seed production and germination of eight cultivars and the wild type of *Ruellia tweediana*: A potentially invasive ornamental. *Journal of Environmental Horticulture, 21*, 137–143.

Wittenberg, R., Kenis, M., Blick, T., Hänggi, A., Gassmann, A., & Weber, E. (Eds.). (2006). *Invasive alien species in Switzerland – An inventory of alien species and their threat to biodiversity and economy in Switzerland*. Bern, Switzerland: Federal Office for the Environment.