



Seed characteristics in Cactaceae: Useful diagnostic features for screening species for invasiveness?



A. Novoa^{a,b,*}, J. Rodríguez^c, A. López-Nogueira^c, D.M. Richardson^a, L. González^c

^a Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa

^b Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont, South Africa

^c Departamento de Biología Vegetal e Ciencias do Solo, Faculdade de Biología, Universidade de Vigo, Vigo, Spain

ARTICLE INFO

Article history:

Received 30 April 2015

Received in revised form 14 December 2015

Accepted 18 January 2016

Available online 6 April 2016

Edited by C Seal

Keywords:

Biological invasions

Biosecurity

Cacti

Ornamental plants

Prevention

Seed mass

Seed size

ABSTRACT

Invasive alien species impose a wide range of negative impacts in invaded ecosystems. Management strategies aiming to minimize these impacts include measures to prevent the introduction of potentially invasive species, early detection and eradication, and control/containment of widespread invaders. Prevention is the most cost-efficient component of these strategies. Therefore, accurate screening of potentially invasive species and practical measures for identifying and intercepting such species along introduction pathways are crucial. Many studies have identified correlates of invasive success in plant species, but few have identified traits that are easy to measure and can be applied practically in screening protocols. Because hundreds of species in the Cactaceae family are being moved around the world, and many of them are already invaders, we assessed the potential for using seed characteristics to identify potentially invasive cacti. We reviewed websites advertising cactus seeds for sale and found that at least seeds of 266 cactus species are being traded worldwide, including 24 species already known to be invasive. We bought seeds of each species and recorded their mass, size and appearance (form, color, brilliance and surface). Already-invasive species had significantly larger and heavier seeds than non-invasive species. All cactus species identified as potentially invasive taxa in a previous study also had significantly larger and heavier seeds than non-invaders. We found no clear link between seed appearance and invasiveness. Overall, our study shows that the traits seed mass and size should be used for improving screening protocols for cactus species as they are easy to measure and provide an indication of invasiveness in this group.

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1. Introduction

The current rate of human-mediated introductions of species to areas outside their native ranges is enormous and is still increasing rapidly (van Kleunen et al., 2011). Although only a small proportion of introduced species naturalize and even fewer become invasive, many invasive species have major ecological, social, and/or economic impacts (Richardson, 2011; Simberloff and Rejmánek, 2011). Invasive alien species are one of the greatest threats to global biodiversity and they cause huge economic costs worldwide (Pimentel et al., 2000).

Management strategies aimed at minimizing the negative impacts of invasive species are in place or under development in many parts of the world (Pyšek and Richardson, 2010). These strategies can be divided into three broad components (Simberloff et al., 2005; van Wilgen et al., 2012): prevention (avoid new introductions by predicting potentially invasive species and detecting them on the ports of entry), early detection and eradication (if invasive species get in, find and eradicate them quickly), and control (if they cannot be eradicated, manage

them to reduce population levels/extent and impacts). Prevention is the most cost-efficient component of such strategies (Simberloff et al., 1997; Leung et al., 2002).

To prevent the introduction of new invasive species, evidence-based criteria are needed for identifying future potential invaders (Kolar and Lodge, 2001). Identifying traits associated with invasive success, and using these in practice to screen new introductions for invasiveness, are fundamental challenges in invasion science. Many studies have searched for features of plant species that are associated with invasiveness (Rejmánek and Richardson, 1996; Pyšek and Richardson, 2007; Küster et al., 2008; van Kleunen et al., 2010). This work has followed two major approaches. First, many studies have compared invasive species with native species (e.g. Strauss et al., 2006; Chrobok et al., 2011; Davidson et al., 2011; Godoy et al., 2011; Flores-Moreno and Moles, 2013). Although such comparisons may shed light on many questions – e.g. why a given invasive species out-competes native species –, the studied native species could themselves be invasive elsewhere. Therefore, such comparisons do little to elucidate mechanisms that might favor a potential invasive species over a non-invasive alien species (Burns, 2004). A second approach involves comparing traits in invasive and non-invasive species within groups of alien species. Studies following this approach typically identify high propagule pressure, other

* Corresponding author at: Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa. Tel.: +27 79 365 9258.

E-mail address: novoa.perez.ana@gmail.com (A. Novoa).

Table 1
Cactus seed characteristics used in this study to look for signs of invasiveness among ornamental cacti

Category	Characteristic	Description	Method	Type of variable
Mass			Measure seed mass with a precision balance	Numeric
Size	Width Length		Record seed width with the program Image J	Numeric
Form	1. Globular	Spherical form	Observe a picture taken with a digital camera coupled to a magnifying lamp	Categorical
	2. Hat-like	Ovoid with a curved extreme		
	3. Irregular ^a	Uneven form		
	4. Lens-shaped	Ovoid to flat		
	5. Match head ^a	Ovoid and blunt extreme		
	6. Mussel-shaped	Mussel shell like		
	7. Ovoid	Elliptical		
	8. Piriform	Conical		
	9. Reniform	Kidney like		
	10. Snail shell ^a	Spiral-shaped		
Color	1. Black		Observe a picture taken with a digital camera coupled to a magnifying lamp	Categorical
	2. Brown			
	3. Black to dark brown ^a			
	4. Reddish dark brown			
	5. Reddish brown			
	6. Tan			
	7. White			
Brilliance	1. Slightly shiny ^a		Observe a picture taken with a digital camera coupled to a magnifying lamp	Categorical
	2. Opaque			
	3. Shiny			
Surface	1. Porous ^a	Uniform holes on the surface	Observe a picture taken with a digital camera coupled to a magnifying lamp	Categorical
	2. Rough ^a	Uneven holes or lumpy surface		
	3. Smooth ^a	Flat surface		

^a Indicates new characteristics added in this study to the list published by Rojas-Arechiga and Vazquez-Yanes (2000).

factors associated with human usage (e.g. number of introduction events), certain reproductive traits (e.g. seed size or clonal growth), and features of the native range size as important mediators of invasive success (e.g. Lockwood et al., 2005; Muth and Pigliucci, 2006; Feng et al., 2008; Castro-Díez et al., 2011; Gallagher et al., 2011; Novoa et al., 2015a, 2015b).

Seed mass and/or size have been considered in many assessments of plant invasiveness (Leishman and Harris (2011) provide an excellent review; see also Hamilton et al. (2005) and Westcott and Fletcher (2011)). Several studies have shown that seed size and/or mass are strongly associated with invasiveness within taxa or functional groups (Rejmánek, 2000). However, the relation between seed size and invasiveness is highly context specific (Pyšek and Richardson, 2007; Leishman and Harris, 2011), being positive or negative depending on the studied taxa or functional group. For example, within the genus *Pinus* and the *Proteaceae* family, invasive species have smaller seeds than non-invaders (Rejmánek, 1996). In these particular cases, smaller seed mass improves long-distance dispersal (Moodley et al., 2013). However, in *Quercus* and some herbaceous species, species with larger seeds present strong advantages for survival in certain habitats and are more suitable for dispersal by animals – which may improve invasiveness (Aizen and Patterson, 1990; Burke and Grime, 1996).

A critical aspect of any prevention effort is the ability to accurately identify, detect and intercept species with features identified as being associated with invasiveness (Armstrong and Ball, 2005). This is particularly challenging in large taxonomic groups where identification of taxa requires expert knowledge, such as in the Cactaceae (Pyšek et al., 2013). DNA barcoding is a promising tool in such cases (Dunning and

Savolainen, 2010), but there are many significant challenges associated with this technique (Valentini et al., 2009), and target organisms cannot always be identified to species or even genus level (Will and Rubinoff, 2004). In this context, seed features such as size and mass could be important and simple measures for intercepting invasive plants along introduction pathways – i.e. if the higher taxonomic group is known, seed mass and size could be useful for identifying potentially invasive alien plants at ports of entry, if there is a clear link between these features and invasiveness. Moreover, in taxa with diverse seed features (e.g. color or form), such features, although not necessary ecologically implicated in invasiveness, could also be important for separating seeds of potentially invasive from non-invasive plant species- e.g. if within a taxonomic group the seeds of invasive or potentially invasive species differ in seed color from those of non-invasive species, the color (although not responsible for invasive success) would be a useful feature to identify potentially invasive species introductions.

The Cactaceae is a clearly defined plant family with an estimated 1919 species (Novoa et al., 2015b). The large native range of cacti extends from southern Patagonia in Argentina to Alberta and British Columbia in Canada (Edwards et al., 2005). The only exception is *Rhipsalis baccifera* (mistletoe cactus) which is native to Central and South America, the Caribbean, and Florida, South Africa, Madagascar and Sri Lanka (Rebman and Pinkava, 2001). Cacti are economically important and species have been introduced to many parts of the world for human consumption, animal fodder, and for medicinal and ornamental purposes (Novoa et al., 2015b). In the last few decades, cactus trade via nurseries, seed companies, and botanical gardens has developed into a substantial industry and has become the primary pathway for the intentional introduction and dissemination of cacti around the world (Walters et al., 2011). Moreover, the Cactaceae constitutes an important group in terms of their position among invasive plants worldwide – about 57 species have already become invasive in several countries, exerting a range of ecological, social and economic impacts (Vilà et al., 2003; Zimmermann, 2006; Smith and Figueiredo, 2012; Lloyd and Reeves, 2014).

A genus-level approach has been used to identify cactus taxa with a high risk of becoming invasive (Novoa et al., 2015a). Following this approach cactus species in genera that include invasive species are

Table 2
Ornamental cactus species divided in non-invasive, potentially invasive (sensu Novoa et al., 2015a) and invasive (sensu Novoa et al., 2015b) cactus invaders.

Number of non-invasive species	Number of potentially invasive species (by a genus approach)	Number of invasive species	Total number of species
228	13	25	266

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