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Naturalised and invasive succulents of southern Africa

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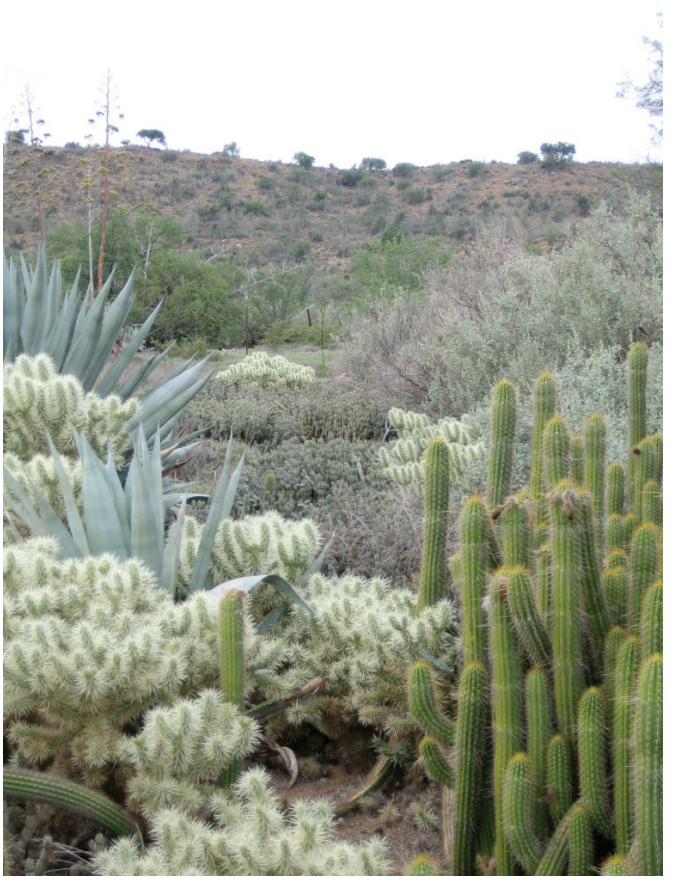

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Captions to figures for *Naturalised and invasive succulents of southern Africa*

Front cover. *Opuntia ficus-indica* (L.) Mill. thriving on an inaccessible cliff ledge in the Karoo, Graaff-Reinet, South Africa. (Picture by Neil R. Crouch)

Half-title page. The exotic *Agave americana* L. var. *americana*, *Echinopsis schickendantzii* F.A.C.Weber and *Cylindropuntia pallida* (Rose) F.M.Knuth firmly established in South Africa's Karoo. (Picture by Helmuth G. Zimmermann)

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Foreword

Many books on plant invasions are published every year dealing with various aspects of the field, ranging from regional atlases to conference proceedings covering a variety of topics and compendia on theoretical issues related to invasion biology with chapters written by invited authors. The first question that a potential buyer or reader of this book would consider is whether they require yet another book on plant invasions, even if it is from South Africa, a country that is greatly impacted by invasive plants. In the current literature the majority of books on invasions focus on the ecology of the organisms. However, while this volume on invasive succulents does provide some ecological and historical background, it is primarily a taxonomic treatment, making it special among the plethora of books bearing the word “invasive” in their title.

Succulents are an important group in terms of their position amongst invasive plants. Although Weber’s compendium of invasive plants of the world from 2003 lists only nine species of perennial succulents among more than 400 global invaders, the group includes some of the prominent invasive species. Everyone interested in biological invasions is aware of the control of *Opuntia* Mill. in Australia using the moth *Cactoblastis cactorum*, which was one of the first examples of successful biological control on invasive plants. In heavily impacted parts of the world, succulent invaders have transformed habitats, exerting a range of ecological and economic impacts. This is true both in South Africa and other parts of the world. Although most of the world’s most noxious succulent invaders come from North America, South Africa itself has donated some prominent succulent invaders, such as *Carpobrotus edulis* (Fig. 1), *Mesembryanthemum crystallinum* or *Conicosia pugioniformis* to other parts of the world.

As a rule in biological invasions, only a few taxa from the whole species pool are successful as invaders. However, it is also important to be aware of those that are not successful, as future invaders could be recruited from taxa that are currently naturalised. Therefore, comprehensive regional accounts on alien species should be praised. This volume deals with about seventy succulent species that have become naturalised in South Africa and neighbouring countries, providing detailed descriptions and illustrations. However, it is not just an atlas of alien succulents because this information is placed into a wider ecological and historical context through chapters on their ecological impacts, the history of their invasion in South Africa, pathways of introduction and reasons for their invasiveness, and also legislation on invasive species in South Africa. An outline of the current classification of each of the families and genera is provided, along with dichotomous identification keys, and a guide on how to collect succulents for deposition in an herbarium.

Fig. 1. *Carpobrotus edulis* (L.) N.E.Br. subsp. *edulis* (sour fig) is an indigenous South African succulent that has become established in other parts of the world. (Picture by Neil R. Crouch)

The taxonomic emphasis present throughout the book highlights the role of taxonomy in current research on biological invasions. Field botanists and researchers in invasion biology are often confronted with new species that may have come to their regions from virtually any part of the world. The ability to identify new invaders is essential to develop an early warning system and facilitate immediate response to potential invasions that may cause problems in the future. Therefore, close cooperation between ecologists and taxonomists is vital for successful management of invasive species. This book exemplifies how fruitful such cooperation can be.

The authors state that the book is targeted at the general public, policymakers, fellow scientists, agricultural researchers, horticulturalists, customs officials, and commercial and subsistence farmers. Special consideration has been given to make it accessible to the general public. Indeed, one can imagine an enthusiastic amateur naturalist using the dichotomous keys contained in this book, as a guide on his or her field trips to identify the species he or she finds. Of equal importance is the fact that the user will *not* be able to identify some species, simply because they are not in the book and could therefore be future invaders. Fortunately the authors provide some guidance in such cases by providing information on how to collect an herbarium specimen and to seek expert help. Every collector knows how difficult it is to collect a succulent for an herbarium specimen resulting in succulents being fairly under-represented in herbaria. If the book contributes to improving this situation, it will gain even greater credibility.

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Abstract

Taxonomic information is provided for 69 exotic succulent plant species that have become naturalised or invasive - or may potentially do so - in South Africa and some of its neighbouring countries. Informative descriptive text and illustrations are provided for all the species, as well as synonymies and geographical distribution maps. Ancillary chapters cover brief introductions to the ecological impacts of invasiveness, a history of invasive succulents in South Africa, the means of introduction and reasons for their success, legislation governing invasive species in South Africa, and how to collect succulents for deposition in an herbarium. However, emphasis throughout is on the taxonomy of these species.

Keywords - alien species, early detection, eradication, invaders, naturalised, southern Africa, succulent plants

Table of contents

1. About this book

The primary aim of this book is to provide taxonomic information on the alien succulent plant species that have become established as part of the naturalised flora of southern Africa. The formal taxonomy of the species which form the main part of the book therefore includes descriptions of families, genera and species, synonymies, illustrations, and distribution information and maps. As far as possible the taxonomy is complemented with natural history observations and cultural information applicable to the species within both its natural and adopted distribution ranges. Given the devastating impact aliens can have on the natural environment, and by implication on human livelihoods, one of the primary objectives of the book is to bring the scourge of alien plant invaders to the attention of many. This book targets the general public, policymakers, fellow scientists, agricultural researchers, horticulturalists, customs officials, and commercial and subsistence farmers. For this reason much of the text is written in non-technical language that is easy to read and understand. We have deliberately opted for a broad definition of what constitutes alien and invasive plants, and species that have contributed extensively to habitat transformation, e.g. *Opuntia stricta* (Haw.) Haw. (sour prickly pear, suurturksvy) (Fig. 2), listed as amongst the 36 worst invasive alien plant species globally (Lowe *et al.*, 2000), as well as those that are little more than troublesome garden or crop weeds, e.g. *Portulaca oleracea* L. (purslane) (Fig. 3), are included in the book.

Fig. 2. *Opuntia stricta* (Haw.) Haw. (sour prickly pear) has contributed to serious habitat transformation in several countries. (Picture by Neil R. Crouch)

Fig. 3. *Portulaca oleracea* L. (purslane) is a widely distributed weed of cultivated lands. (Picture by Neil R. Crouch)

As far as possible we have followed the latest classification and nomenclature applicable to the invasive alien succulents of southern Africa. However, in a few instances we have opted not to use the latest classificatory suggestions; for example we prefer to retain the species of *Agave* L. (century plants) in the family Agavaceae rather than including them in the very broadly conceived Asparagaceae of the most recent Angiosperm Phylogeny Group proposal. In some instances the taxonomies of alien succulents that are firmly entrenched in South Africa—and have been so for decades—remain poorly understood locally and sometimes even in their native ranges, particularly in the case of the Cactaceae (cactus family). This publication therefore reflects the current state of our knowledge of the taxonomy of these, as well as the rest of the exotic succulent plants that have become established in natural settings in South Africa and sometimes in neighbouring countries, and beyond. The descriptions of the families and genera provided in this book cover the full variation of the taxa and therefore include the characters of the taxa naturalised in southern Africa.

The geographic coverage of the book is mainly South Africa, but several of the included species have become more widely established, occurring in neighbouring countries, and often much further afield. Where the information was available to us, we have also reflected the occurrence of the species beyond the borders of South Africa.

Chapters in the first part of the book cover several topics that are relevant to studies of biological invasions. These include the ecological impacts of invasiveness, a history of invasive succulents in South Africa, e.g. the means of introduction and reasons for their success, legislation governing invasive species in South Africa, and how to collect succulents for deposition in an herbarium.

In the second part of the book all the species are provided with informative taxonomic descriptions that are useful in identifying them, with special emphasis on those characters important in distinguishing them from related or similar-looking entities, in particular those known to be indigenous to South Africa. An outline of the current classification within each of the families and genera is provided, along with dichotomous identification keys. Colour and black and white images, line drawings, where available, and geographical distribution maps reflecting the best available knowledge, are provided for each taxon.

Past and present species occurrence data (from individual casual aliens to naturalised or invasive stands) for South Africa were obtained from as many sources as possible, including personal observations, interrogating the Agricultural Research Council's Southern African Plant Invaders Atlas (SAPIA), *SAPIA Newsletters* and the South African National Herbarium Pretoria (PRE) Computerised Information System (PRECIS). For other southern African countries, books on invaders, national plant checklists and websites, for instance, Swaziland's Alien Plants Database (http://www.sntc.org.sz/alienplants/index.asp), were used. Standard reference works such as published volumes of the *Flora of Southern Africa (FSA)* and *'Contributions to the FSA'*, an occasional column included in *Bothalia*, were also used and are referenced in the various chapters where the

families are treated taxonomically. In the absence of systematic surveys of many of these species, however, occurrence data usually remain scanty.

The following abbreviations are used throughout the book for the five countries included in the *Flora of Southern Africa* region: B-Botswana; L-Lesotho; N-Namibia; S-Swaziland; SA-South Africa.

It should be noted that some common names given in the book are better known in other parts of the world and not widely used in southern Africa. They are listed here for the sake of completeness.

2. Biology and impact of invasive succulent plants

by James S. Boatwright, Gideon F. Smith, Helmuth G. Zimmermann, Thulisile P. Jaca, Rethabile F. Motloung and Takalani D. Malotsha

2.1. Invasive succulent plants in South Africa

Alien or exotic (non-native) plants can be defined as those that occur in a given area outside of their known, natural distribution due to intentional or accidental introduction through human activity. These plants are only considered to be invasive once they have become naturalised (i.e. reproduce successfully without human intervention) and are able to produce reproductively viable offspring significant distances away from the parent population (see Text Box 1 for useful definitions; Richardson *et al.*, 2000). The effects of invasive plants are often destructive to the natural environment and threaten the biodiversity of areas on which they encroach (Richardson & Van Wilgen, 2004).

South Africa has an extremely rich biodiversity, the richest temperate flora in the world, with 20 456 species occurring in the region (Germishuizen *et al*., 2006; Raimondo *et al.*, 2009). Of these 2 577 taxa are threatened with regional or global extinction. These threats are mainly through agriculture, urbanization, habitat loss and encroachment of alien invasive species (Raimondo *et al*., 2009). Currently, in South Africa more than 550 plant species are known to be contributing to the widespread transformation of once pristine habitats. Approximately 550 naturalised alien species are listed by the Southern African Plant Invaders Atlas (SAPIA) (Henderson, 2007). Of these, approximately 70 are succulents with fat (green or non-green) stems (Fig. 4), leaves (Fig. 5) or caudices (Fig. 6), of which almost half are members of the family Cactaceae. These plants are generally spiny, almost invariably leafless succulents characterised by the presence of areoles. All cactus growth occurs from areoles (reduced axillary shoots) (Fig. 7), which are usually evident as small white, yellow or brown furry 'spots' on the cactus plant bodies (Barthlott & Hunt, 1993; Smith, 2006a). A high number of succulent invaders - almost 20% of the recorded invasive plants - is unsurprising, as most succulents, cacti in particular, require very little aftercare and maintenance once in cultivation, and much of the South African landscape is comprised of arid to semi-arid regions in which succulents thrive, such as the Succulent Karoo, Nama-Karoo and Desert Biomes (Mucina & Rutherford, 2006).

Fig. 4. *Myrtillocactus geometrizans* (Pfeiff.) Console is an example of a stem succulent. (Picture by Gideon F. Smith)

Fig. 5. *Bryophyllum daigremontianum* Haw. is an example of a leaf succulent. (Picture by Neil R. Crouch)

Fig. 6. *Phytolacca dioica* L. of which the stem, especially towards the base, is quite succulent, making it popular among succulent collectors with large gardens. (Picture by Geoff R. Nichols)

Fig. 7. *Cylindropuntia imbricata* (Haw.) F.M.Knuth has stems that are sparsely dotted with spiny areoles. (Picture by Neil R. Crouch)

Text Box 1. Definitions relating to plant invasion ecology (from Richardson *et al*., 2000).

Alien plant: Plant taxa that occur in a given area due to intentional or accidental introduction through humans (syn. exotic plants, non-native plants).

Casual alien plants: Alien plants which thrive and even reproduce in an area, but need repeated introductions for their persistence and do not form self-replacing populations.

Naturalised plants: Alien plants which successfully reproduce in an area and sustain populations over numerous life cycles without direct human intervention.

Invasive plants: Naturalised alien plants or native plants which reproduce, often at high frequency, a significant distance from the parent population and can potentially spread over large areas (native plants that become invasive are often referred to as "densifiers").

Weeds: Plants that are not necessarily alien and grow in areas where they are not wanted, usually with detectable economic or environmental effects (syn. pest plants, problem plants). Mostly associated with "crop weeds".

Transformers: Those invasive plants that change the character, condition, nature or form of ecosystems over a considerable area relative to the extent of that ecosystem.

Of course not all succulents found in South Africa are exotic. South Africa and its four immediate neighbours (Namibia, Botswana, Swaziland and Lesotho) harbour the richest succulent flora globally with over 4 700 such species having been recorded for the subcontinent (Smith *et al*., 1997).

In the South African context, many of the succulent plants now established as invasives were originally introduced into the country for economic purposes. One such well-known example is the prickly pear, *Opuntia ficus-indica* (L.) Mill. (Fig. 8). This member of the Cactaceae, probably introduced into South Africa during early European settlement of the Cape in the seventeenth century, is a multi-use commercial crop for arid regions where the fruit are eaten and the cladodes (fleshy, leaf-like stems), which are regarded as delicacies in their native Mexico and elsewhere (Zimmermann & Zimmermann, 1987; Brutsch & Zimmermann, 1993), are used as livestock fodder and vegetables (Van Wyk & Gericke, 2000). It has now become a serious invader in not only South Africa, but also Saudi Arabia, Yemen, Eritrea, Ethiopia, Madagascar, Hawaii and other countries. The near-cosmopolitan common garden weed *Portulaca oleracea* L. or purslane, the natural origin of which remains unresolved, was established at the southern tip of Africa to provide a source of Vitamin C for seafarers rounding the Cape (Smith & Figueiredo, 2010). Both these species have spread rapidly across the subcontinent and beyond, with the former having contributed extensively to the transformation of large tracts of arid landscapes in the southern African interior. Some South African plants are similarly introduced into other parts of the world for their usefulness or economic gain. The South African succulent, *Carpobrotus edulis* (L.) N.E.Br. is

now invasive in coastal dunes of Australia, New Zealand, USA, and southern and western Europe (Roiloa *et al*., 2010). It was, and still is, widely used to stabilise dunes and road cuttings. Interestingly, there is one documented case where an indigenous succulent plant, *Aloe spectabilis* Reynolds, has become successfully established as a viable colony elsewhere in the country following its translocation to a suitable habitat over 100 years ago (Klopper *et al*., 2010). However, this is rare among the succulents of South Africa.

Fig. 8. *Opuntia ficus-indica* (L.) Mill. was introduced into South Africa as a fodder plant and for its sweet, edible fruit, here shown together with fruit of *Opuntia monocantha* Haw. on the right. (Picture by Helmuth G. Zimmermann)

2.2. Biology and success of succulent invasives

Exotic succulents can easily become established in regions remote from their areas of origin as their general biology and lack of specific natural enemies greatly assist their survival and spread in adopted countries. Firstly, succulents are well adapted to easily survive periods of drought, while some can additionally thrive under such and other adverse environmental and climatic conditions, including very low temperatures. One adaptation to drought tolerance is the reduction of water loss through stomatal closure during the day. Most vascular plants concentrate carbon dioxide (CO_2) for photosynthesis through C_3 carbon fixation which limits them to growing in moderate temperatures as RuBisCO, an enzyme which facilitates carbon fixation, binds more oxygen than CO_2 at higher temperatures

(photorespiration) thus limiting photosynthesis (Keeley & Rundel, 2003). However, many succulent plants concentrate CO_2 through Crassulacean Acid Metabolism (CAM). The advantage of CAM is that it gives plants the ability to survive in dry environments because the stomata only open at night to fix CO_2, and stomatal closure during the day significantly reduces water loss (Keeley & Rundel, 2003; Lüttge, 2004). The fixed CO_2 becomes available during the day and increases the efficiency of photosynthesis. Adaptations to CAM generally include thickening of the leaves along with an increase in cell and vacuole size, reduced intercellular air spaces (IAS) and reduced length of mesophyll surface exposed to IAS per unit (Nelson *et al*., 2005). Most succulents are able to reproduce both from seed and through rooting of severed vegetative parts (clonal reproduction). Species with edible fruit are spread by frugivores, which increases the spatial distribution and density of these plants, the dispersal of species of *Opuntia* Mill. by crows and pale- and red-winged starlings in the Karoo region of South Africa being an example (Dean & Milton, 2000). Others such as *Opuntia aurantiaca* Lindl. (jointed cactus) (Fig. 9) and *Cylindropuntia fulgida* (Engelm.) F.M.Knuth var. *mamillata* (A.Schott ex Engelm.) Backeb. (boxing glove cactus), an emerging alien invasive in South Africa, spread exclusively by vegetative means in their adopted country. These plants are small shrubs that produce stem segments that are easily dislodged and quickly root when they fall from the mother plant (Fig. 10). These thorny segments may be distributed by animals such as livestock through attaching to their fur, or by moving water (J.S. Boatwright, *pers. obs.*). Lastly, many invasive succulents are thorny to varying degrees possibly to escape herbivory in order to protect the water stored in their stems. These extremely thorny invasive cacti, for example the jointed cactus and all the chollas (species of *Cylindropuntia* (Engelm.) F.M.Knuth), can cause considerable harm to small livestock and wildlife, and make handling of specimens of these plants by botanists and others cumbersome. Hares and even small antelope get immobilised, preventing movement and feeding which eventually leads to death. Many birds and small reptiles get impaled on the thorns (Fig. 11; H.G. Zimmermann, *pers. obs.*). This is in stark contrast to the co-adapted local fauna living in the Sonoran Desert (North America) where the chollas are native. Many animal species use these thorny thickets for their own protection, coping well with the barbed spines (Fig. 12).

Fig. 9. *Opuntia aurantiaca* Lindl. cladodes (stem segments) easily snap off when passing animals brush against plants. This is the primary way in which it is vegetatively spread. (Picture by Helmuth G. Zimmermann)

Fig. 10. New populations of *Cylindropuntia fulgida* (Engelm.) F.M.Knuth become established from severed stem segments. (Picture by Barbara K. Mashope)

Fig. 11. A bird that became impaled in the spines of *Cylindropuntia fulgida* (Engelm.) F.M.Knuth. (Picture by Helmuth G. Zimmermann)

Fig. 12. An animal nesting/hiding in the protection of the spines of an *Opuntia* species. (Picture by Helmuth G. Zimmermann)

All invasive succulent species were introduced without any of their natural enemies that prevent them from becoming invasive in their countries of origin. None of the local native phytophagous insect fauna has switched hosts to any of the 28 invasive cactus species, despite their abundance and more than a century of exposure. Due to the uniqueness of the Cactaceae their associated insect fauna is equally uniquely adapted to feed on these plants and are thus often extremely host specific. This explains in part why the success rate of biological control projects on cactus invaders is often higher than those of other plant families.