The alien flora of the Cape of Good Hope Nature Reserve

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An annotated species list of the alien vascular plant flora of the Cape of Good Hope Nature Reserve is presented. The flora comprises five gymnosperm and 68 angiosperm species that are definitely alien to the reserve and four angiosperm species that are possibly alien. The life-form distribution of the alien flora is shown to be significantly different from that of the indigenous flora; trees, shrubs and annual herbs are more important in the alien flora, and dwarf shrubs and perennial herbs are much less important. Biotic factors are suggested as being important in determining the success of alien invasions, in particular grazing by ungulates. The invasion rate is currently about one new species per year. By ceasing to introduce tree species and by restricting human disturbance, the rate of invasion of new species could be reduced.

Keywords: Alien plants, Cape, fynbos, invasive species

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Introduction

The invasion of natural vegetation by alien plants constitutes one of the Cape of Good Hope Nature Reserve's major management problems (Taylor 1977; Taylor & Macdonald 1985; Taylor et al. 1985; Clark 1985). In this paper we list for the first time all the species involved, providing details of their history, distribution and status in the reserve, and present some analyses of the problem, based on this information.

The reserve is located at the southern tip of the Cape Peninsula (34°12'S 18°22'E), is 7750 ha in extent, ranges in altitude from 0 to 366 m.a.s.l. and experiences mean annual rainfall ranging from 300 to 700 mm. The geology, ecology and history of the reserve have been described by Opie (1967) and Taylor (1969). The vegetation and flora of the reserve have been documented by Taylor (1984a, b; 1985). The vegetation is primarily mountain fynbos on the central plateau which is underlain by Table Mountain sandstone, with strandveld vegetation on the littoral shelf which is widest on the western side of the Peninsula.

Methods

In order to compile this list the alien species (Wells et al. 1986) were extracted from the published flora of the reserve (Taylor 1985). Additional species were obtained from the published accounts of alien plant invasions of the reserve (Taylor et al. 1985) and from the unpublished observations of the authors. These species were annotated using the conventions of Wells et al. (1986), the data provided by this text being supplemented where necessary from a range of botanical reference books. Details of each species' distribution and status within the reserve were based on field observations of the authors, supplemented by data recorded by H.C. Taylor in his card index of the area's flora and in the raw data and field notes from the fixed-plot surveys (Taylor et al. 1985). Only alien plant species that are known to have self-seeded on the reserve are included. Species that are known to invade areas of natural vegetation within the reserve are asterisked (*). Species that are or have been a major problem in the reserve are given a double asterisk (**). Species were defined as constituting a 'major problem' when they have been observed to form dense stands in areas of natural vegetation. These stands tend to exclude the native flora and have generally required active control measures to prevent their spread. Those species which are not undoubtedly alien to the reserve are bracketed.

The term 'disturbed' is used throughout this paper to refer to anthropogenic disturbance. Within the reserve this mainly takes the form of soil disturbance arising from road building activities and that around picnic sites and human habitation. The clearance of dense stands of alien trees is also considered to give rise to 'disturbed' areas. Prior to the reserve's proclamation, certain areas were cultivated. These are also termed 'disturbed'.

A map giving the location of most of the places named in the present account and the location of the permanently marked alien plant-monitoring plots (numbered 1 to 100) is presented as Figure 1 of Taylor & Macdonald (1985) and Taylor et al. (1985).

In the list that follows, collections are given by the name of the collector followed by the collector's number. In the case of collections by H.C. Taylor these are given in the form (T2355). All the Taylor collections are lodged with STE and the other collections cited are either in NBT or BOL.

The alien flora

Gymnospermae

Pinaceae

*Pinus halepensis Mill.

Aleppo pine. Tree, perennial from Europe and Asia. A single small plant recorded in plot 23 (near Wolfkop) in the 1976 survey.
**P. pinaster** Ait.
Cluster pine. Tree, perennial from Europe and Asia.
Established as plantations and windbreaks in several locations in the north-west of the reserve. Low density self-sown stands had established throughout the central portions of the reserve by 1966 but were relatively easily controlled. Currently only a problem in the previous high density areas.

*P. pinea* L.
Stone pine. Tree, perennial from Europe and Asia.
Planted around homesteads in north-west of reserve with limited spread into immediate surrounds. This species does not pose a problem in the reserve although adult specimens still grow around Klaasjagersberg.

*P. radiata* D. Don
Monterey pine. Tree, perennial from North America.
Only recorded on a single plot (No. 75) in the Hoek van Bobbejaan area of the reserve in 1976. Possibly this species had been planted at a cottage in this vicinity.

Cupressaceae
* Cupressus macrocarpa* Hartweg.
Monterey cypress. Tree, perennial from North America.
A few adult trees planted and still growing around the Homestead Restaurant. A few saplings have established in the natural vegetation in the near vicinity, the furthest of these was growing near the main road some 700 m from the planted specimens.

Angiospermae
Monocotyledones
Poaceae
* Aira cupaniana* Guss.
Herb, annual from Europe. This small grass has been recorded from the hills between Ribboksdam and Platboom in the south of the reserve by Taylor (T5282).

*Ammophila arenaria* (L.) Link.
Marram grass. Herb, perennial from Europe.
Growing on dunes north of Die Monds where it had probably been planted in a dune ‘reclamation’ campaign. Not considered to be spreading in the reserve.

*Avena barbata* Brot.
Wild oats. Herb, annual from Europe.
Widespread in reserve but is mainly confined to disturbed areas such as road verges, old lands and around present and old homesteads and picnic sites. Does not generally invade natural veld. Very palatable and is probably being kept in check by grazers. In areas of 100% alien tree cover that were cleared in 1986, dense stands of *A. barbata* have germinated. These areas were apparently cultivated at some time in the past.

*Briza maxima* L.
Quaking grass. Herb, annual from Europe. Same comments as for *A. barbata*.

*B. minor* L.
Small quaking grass. Herb, annual from Europe.
Not as common as *Briza maxima*. The species shows a preference for damp areas, eg. vleis and stream banks. Frequently found in natural veld in these areas, but usually in vicinity of old homesteads.

*Bromus diandrus* Roth
Ripgut brome. Herb, annual from Europe & Asia.
Associated with disturbed areas, and in and around picnic sites and old and present homesteads. Often in moist areas.

*Bromus molliformis* Lloyd
Soft brome. Herb, annual from Europe & Asia.
Recorded from the reserve in July 1982.

*Cortaderia selloana* (Schult.) Aschers. & Graebn.
Pampas grass. Herb, perennial, South America.
One specimen known from road verge on Circular Drive. New growth (especially after fire) heavily grazed by Hartman’s Mountain Zebra *Equus zebra hartmannii*. Two plants growing in stream at Smitswinkel Bay. No seedlings noticed.

[Digitaria sanguinalis* (L.) Scop. *
Crab finger grass. Herb, annual, pantropical. Occasional in disturbed areas such as road verges, homestead sites, picnic sites and gravel borrow pits.]

*Hordeum murinum* L.
Wild barley. Herb, annual, Europe & Asia.
As for *D. sanguinalis*.

*Lagurus ovatus* L.
Hare’s tail grass. Herb, annual, Europe & Asia.
As for *D. sanguinalis*.

*Lolium perenne* L.
Perennial ryegrass. Herb, perennial, Europe & Asia.
Often found on road verges and in lawns at picnic sites and homesteads.

*Paspalum dilatatum* Poir.
Common paspalum. Herb, perennial, South America.
Common on stream banks in disturbed areas. Found in picnic sites, road verges and homesteads. Collected in 1979 at the Kaasjagers River Bridge (T9938).

*P. urvillei* Steud.
Tall paspalum. Herb, perennial, South America.
Recorded by Taylor (1969) in Appendix 4.

*Pennisetum clandestinum* Chiov.
Kikuyu. Herb, perennial, East Africa.
Found mainly at Klaasjagersberg, Perdekloof, the Homestead Restaurant and at picnic sites. Spreads in wet areas and outcompetes indigenous species. Isolated patches are scattered around the reserve, often where lawn cuttings have been dumped or used in erosion-control operations. This species is currently heavily grazed in the reserve.

*Polypogon monspeliensis* (L.) Desf.
Beardgrass. Herb, annual, Europe & Asia.
Recorded at Buffels Bay near spring (Adamson 728).
*Vulpia myuros* (L.) C.C. Gmel.

Rat's tail fescue. Herb, annual, Europe & Asia.

Recorded from the reserve by Taylor (1985).

**Cyperaceae**

[*Cyperus textilis* Thunb.]

Matsedge. Herb, perennial, elsewhere in South Africa. A few small clumps occur in the Klaasjagersberg river near the offices and a large stand in the lower reaches of this river near Die Mond. Also occurs in the marsh at Olifantsbos. This species has been cultivated in ornamental ponds at Klaasjagersberg and was not included in the reserve's flora by Taylor (1985). If this species is indeed alien to the reserve it could pose a significant conservation problem in the future.

**Arecales**

*Phoenix dactylifera* L.

Date palm. Tree/shrub, perennial, North Africa and Asia. One plant recorded on Plot 7 in the 1976–80 resurvey. Possibly a remnant of past cultivation as there is an old homestead in the vicinity of this plot. *Phoenix* sp. is recorded as spreading in natural vegetation on the slopes of Table Mountain (Moll & Scott 1981).

**Agavaceae**

*Agave sisalana* Perrine.

Sisal. Shrub, perennial, North America. Planted at Klaasjagersberg and at the Main Gate. In the latter locality has shown regeneration in an adjacent firebreak. Not known to spread into undisturbed fynbos on the reserve.

**Dicotyledones**

**Salicaceae**

*Populus × canescens* (Ait.) J.E. Sm.

Grey poplar. Tree, perennial, Europe & Asia.

Found along streams at Olifantsbos and Perdekloof near old homesteads. Does not appear to be spreading rapidly. In these areas it is competing with *Acacia longifolia* and *A. saligna* and spread might be more rapid in pure fynbos communities.

**Urticaceae**

*Urtica urens* L.

Small stinging nettle. Herb, annual, Europe & Asia.

Recorded on the Gifkommetjie Road dune slack in October 1971.

**Proteaceae**

**Hakea gibbosa** (Sm.) Cav.

Rock hakea. Tree/shrub, perennial, Australia.

Currently there are no seed-producing plants of this species in the reserve. Used to occur at scattered localities on the reserve's northern boundary especially near Modderdam, Wolfkop, Spookhuis and The Camp, but never in large numbers. These plants have been removed on discovery, e.g. seven plants from Modderdam in October 1973.

**Hakea suaveloens** R.Br.

Sweet hakea. Tree/shrub perennial, Australia.

Found in relatively moist sites between Modderdam and Tuinkop, in the north-west of the reserve. No seed-producing trees left by 1987. Previous infestations were not really dense but this area held dense stands of both *Acacia saligna* and *Eucalyptus lehmannii* and competition from these species had probably limited the spread of *H. suaveloens*.

**Chenopodiaceae**

*Chenopodium botryodes* Sm.

Herb, ?annual, Europe & Asia.

Found in disturbed areas, e.g. old lands, homesteads and kraals.

**Caryophyllaceae**

*Spergularia media* (L.) C. Presl.

Middle-sized sand spurry. Herb, perennial, Europe & Asia.

Recorded in the rocky coastal strip throughout the reserve, also in dried-up vleis (Olifantsbos) and on the margins of blackwater lakelets (Sirkelsvlei). Collected several times from the reserve, *(Adamson 710)* and *(T6692, 7257, 7413).*

* S. rubra* (L.) J&C. Presl.

Purple sand spurry. Herb, annual, Europe & Asia. Included in Taylor (1985). Apparently only recorded by Adamson (2619) at a locality called Oudekraal. No such locality name currently in use in the reserve.

**Fumariaceae**

*Fumaria muralis* Sond. ex Koch

Fumitory. Herb, annual, Europe & Asia.

Common on lawns of picnic sites. Also found in disturbed areas such as old lands, homesteads and kraals.

**Pittosporaceae**

*Pittosporum undulatum* Vent.

Sweet pittosporum. Tree/shrub, perennial, Australia.

A few specimens along Klaasjagersberg river near office complex. Does not seem to be spreading.

**Rosaceae**

*Rubus* sp. indet

Bramble. Shrub/climber, perennial, ?origin.

A few plants occur at Perdekloof as an understory in alien *Acacia* thicket.

**Pyracantha angustifolia** Schneid.

Orange firethorn. Tree/shrub perennial, Europe & Asia.

A single plant growing on the road verge on Circular Drive. The plant is kept low by persistent heavy browsing.

**Fabaceae** (Leguminosae)

**Acacia cyclops** A. Cunn. ex G. Don

Rooikrans. Tree/shrub, perennial, Australia.

Adult, seed-bearing trees now (1987) occur only south of a line drawn between Paulsberg, the Homestead Restaurant and Platboom. The species occurs throughout the reserve in dry, disturbed areas and is an aggressive invader.

**A. longifolia** (Andr.) Willd.

Long-leaved wattle. Tree/shrub, perennial, Australia.

Predominantly a riverine habitat invader which is often outcompeted by *A. saligna*. With the exception of isolated patches at Klaasjagersberg, Olifantsbos and Schuster river valley, all adult plants have now been removed.
* A. mearnsii * De Wild.  
Black wattle. Tree/shrub, perennial, Australia. Scattered plants occur around the Klaasjagersberg complex and a few individuals have germinated along the Klaasjagersriver — generally in disturbed areas.  

* A. melanoxylon * R. Br. Blackwood.  
Blackwood. Tree/shrub, perennial, Australia. Has been found invading moist fynbos at Klaasjagersberg and near Plot 78 adjacent to the main road near the Homestead Restaurant. Several mature specimens still grow in the Klaasjagersberg complex.  

** A. saligna ** (Labill.) H.L. Wendl.  
Port Jackson willow. Tree/shrub, perennial, Australia. Distribution generally confined to moist habitats. Isolated patches of seeding trees now only occur at Klaasjagersberg and in the southern portion of the reserve. Small plants are scattered throughout the reserve, often on road-verges.  

* Albizia lophantha * (Willd.) Benth.  
Stinkbean. Tree/shrub, perennial, Australia. Occurs in riverine and marshy habitats at Klaasjagersberg, Perdekloof, Olifantsbos, Smitswinkel Bay, Modderdam and near the Homestead Restaurant.  

* Medicago laciniata * (L.) Mill  
Little burweed. Herb, annual, Europe & Asia. Collected in the hills between Ribboksdam and Platboom in October 1963 (T5263).  

* M. polymorpha * L.  
Burclover. Herb, annual, Europe & Asia. Occurs on lawns of picnic sites throughout the reserve. Has been recorded from the hills in the south of the reserve and on disturbed ground near Sirkelsvlei (T5275 & 8224).  

* Melilotus indica * (L.) All.  
Annual yellow sweet clover. Herb, annual, Europe & Asia. Recorded at Ribboksdam near the sea and on the adjacent hills in October 1963 (Taylor).  

* Ornithopus sativus * Brot.  
Seradella. Herb, annual, Europe & Asia. This species was introduced to the reserve as a fodder legume in the Circular Drive area. These plantings were initiated in 1959 in order to improve the reserve’s grazing for large ungulates (Opie 1967). The introductions of forage legumes all failed as a result of over-utilization by these ungulates (Opie 1967; Millar 1970). Apparently this species is now no longer present on the reserve.  

* Sesbania punicea * (Cav.) Benth.  
Red sesbania. Shrub, perennial, South America. One stand of this species was discovered in the reserve in the early 1980s. The plants are growing on a borrow pit adjacent to the main road near Plot 58. The patch is approximately 500 m² in area. Clearing every second year has not proven successful so annual clearing is now being undertaken.  

* Trifolium fragiferum * L.  
Strawberry clover. Herb, annual, Mediterranean & southern Europe.  
Listed by Taylor (1969) in Appendix 4.  

* T. subterraneum * L.  
Subterranean clover. Herb, annual, Mediterranean & Western Europe. Recorded in a plot at the Gifkommetjie turnoff in October 1971 (T7937).  

* Vicia benghalensis * L.  
Narrow-leaved purple vetch. Climber, annual or biennial, Europe & Asia. Scattered plants are found in disturbed areas around homesteads in the north of the reserve.  

* Geraniaceae  
* Erodium moschatum * (L.) L’Herit.  
Musk heron’s bill. Herb, annual or biennial, Europe & Asia. Recorded in a disturbed area at Buffels Bay in September 1972.  

* Tropaeolaceae  
* Tropaeolum majus * L.  
Garden nasturtium. Herb, annual, Central America. Common in the Perdekloof area following the burning of a dense alien * Acacia * stand in 1986.  

* Euphorbiaceae  
* Ricinus communis * L.  
Castor-oil bush. Tree/shrub, variable, elsewhere in Africa. Scattered plants are found in disturbed areas in the reserve. Young plants were found in Plot 56 on the Smitswinkel Flats in 1986 where material had been imported for erosion control.  

* Lythraceae  
* Lythrum hyssopifolium * L.  
Hyssope loosestrife. Herb, variable, North America. Recorded at Klaasjagersberg as a weed near the river in December 1974 (T8875).  

* Myrtaceae  
* Callistemon rigidus * R.Br.  
Australian bottle brush. Tree/shrub, perennial, Australia. One plant known. Occurs in fynbos on road verge on the Circular Drive.  

* Eucalyptus cladocalyx * F. Muell.  
Sugar gum. Tree, perennial, Australia. This species, like the other * Eucalyptus * spp., was planted around homesteads, mainly in the north of the reserve. It shows localized spread, mainly into disturbed areas such as firebreaks. Thinning of the fynbos community around established individuals or patches allows the establishment of further seedlings.  

* E. fictifolia  
Red flowering gum. Tree, perennial, Australia. Found around Klaasjagersberg. Although seedlings are found, the species does not appear to be an aggressive invader.  

* E. globulus * Labill.  
Blue gum. Tree, perennial, Australia. Only recorded in north of the reserve near Perdekloof.  

* E. gomphocephala * A.DC.  
Tuart. Tree, perennial, Australia. As for * E. cladocalyx *.  

* S. Afr. J. Bot., 1987, 53(5)
**E. lehmannii** (Schau.) Benth.
Spider gum. Tree, perennial, Australia.
Found near old human habitations. Invasive capabilities are greatly enhanced by fire. This species has shown itself capable of forming extensive monospecific stands. Recovery of the fynbos after burning of this and other *Eucalyptus* species tends to be slower than where other alien tree species are involved.

*E. sideroxylon* A. Cunn. ex Woolls.
Black iron bark. Tree, perennial, Australia.
Found around Klaasjagersberg. Although seedlings are found, the species does not appear to be an aggressive invader.

*Lantana camara* L.
Tree/shrub, perennial, South America.
Also at old rubbish dump. Occurs at the Homestead Restaurant and below the Home­stead Dam in dunes next to river. Also at the coast in sandy soil. Also present near beaches and at Cape Point next to footpath near the lookout spots.

**Leptospermum laeigatum** (Soland. ex Gaertn.) F.J. Muell.
Australian myrtle. Tree/shrub, perennial, Australia.
Seems to show a preference for drier, sandy areas — occurs at Skilpadsvlei, Old Spookhuis and in the northern area where all adult plants have now been felled. This species spreads rapidly after fires (from seed) although adult plants are killed by fire.

Primulaceae

*Anagalis arvensis* L.
Scarlet pimpernel. Herb, annual, Europe and Asia.
Grows mainly in disturbed areas, e.g. on road verges and where clearing activities have been carried out around old dwellings. Occasionally found in areas of natural vegetation such as in the coastal communities at Booisekerm and the Old Lime Kiln. These areas have been severely disturbed in the past.

Apiaceae (Umbelliferae)

*Centella asiatica* (L.) Urb.
Pennywort. Herb, perennial, Europe & Asia.
Recorded at Smiths Farm (now the Homestead Restaurant) near the vlei margin (*Adamson 912*) and in west coast swamps of the reserve (*Adamson 3329*). Apparently no recent records.

*Torilis arvensis* (Huds.) Link.
Herb, annual, Europe & Asia.
Recorded on sand at Buffels Bay (*Adamson 723*), on the hills between Ribboksdam and Platboom in October 1963 (*TS260*), in the Gifkommetjie turn-off plot in October 1971 and under bushes at Sirkelsvlei in September 1972.

Verbenaceae

*Lantana camara* L.
Lantana. Shrub/climber, perennial, South America.
A single plant was recorded in Plot 24 at the Spookhuis in the 1966 survey. Not known from anywhere on the reserve since this time.

Solanaceae

*Datura* sp.
Thorn apple. Herb, annual, ?North America.
Occurs at the Homestead Restaurant and below the Homestead Dam in dunes next to river. Also at old rubbish dump.

*Nicotiana glauca* R.A. Grah.
Wild tobacco. Tree/shrub, perennial, South America.
A few specimens in the disturbed area around the Theefontein homestead in 1986.

*Solanum nigrum* L. Scop.
Nightshade. Herb, variable, origin uncertain, thought to be alien to South Africa.
This species is found in disturbed areas around old human habitations and in old cultivated fields.

Orobanchaceae

*Orobanche ramosa* L.
Blue broomrape. Herb, root parasite, annual, Europe & Asia.
One patch found at gate at Scarborough in 1986 growing near the coast in sandy soil. Also present near beaches and at Cape Point next to lookout spots.

Myoporaceae

*Myoporum serratum* R.Br.
Manitoka. Tree/shrub, perennial, Australia.
This is a coastal species which occurs in the dunes at the Homestead Restaurant, Olifantsbos and Die Mond. Also found at Black Rocks. Numerous seedlings come up after clearing *Acacia cyclops* in these areas.

Plantaginaceae

*Plantago lanceolata* L.
Narrow-leaved ribwort. Herb, variable, Europe & Asia.
Occurs mainly on road verges and other disturbed sites in the reserve.

Asteraceae (Compositae)

*Conyza canadensis* (L.) Cronq.
Horseweed fleabane. Herb, annual, North America.
Grows on road verges and along gravel tracks. Common around buildings.

*Hypochoeris radicata* L.
Hairy wild lettuce. Herb, perennial, Europe & Asia.
As for *Plantago lanceolata* but also recorded in the Gifkommetjie turn-off plot in October 1971.

*Sonchus oleraceus* L.
Sowthistle. Herb, annual, Europe & Asia.
As for *P. lanceolata* but also recorded on the western shore of Sirkelsvlei in September 1972.

**Discussion**

The naturalized alien vascular plant flora of the Cape of Good Hope Nature Reserve comprises 5 species belonging to the Gymnospermae and 68 definitely alien species belonging to the Angiospermae. An additional four angiosperms are possibly alien to the reserve. Of the 19 definitely alien monocotyledonous species seven are not known to grow in areas of natural vegetation, being confined to areas of intense human disturbance such as picnic sites. None of the monocotyledons were considered to be posing major problems in the reserve whereas one gymnosperm and six dicotyledons were. All of these were trees.

The life-form distribution of the alien flora is markedly different from that of the reserve's indigenous flora (Table 1). Even when we combined all tree and shrub categories (but not dwarf shrubs which are distinctive, being defined as species never exceeding 1 m in height), the shrub/climbers with the climbers, and the biennial and variable herbs with the annual herbs, the Chi-squared test for heterogeneity of the indigenous and alien flora distributions was highly significant ($X^2_{5,0.01} = 113, P < 0.001$).
Successful alien invaders to successfully invade fynbos within the reserve is in accord between alien and native species in fynbos communities on rocky littoral sites. The inability of low-growing alien plants such as Ammophila arenaria annuals, almost entirely restricted to sites of human disturbance. Where they are present in fynbos they are once the reserve’s alien flora. The few dwarf shrubs and perennial herbs colonized Mediterranean-type regions of the world has been attributed to the long history of human disturbance that the Mediterranean Basin. The ability of plants from this region to invade fynbos vegetation (Macdonald 1985).

The other life form which is much more frequent in the alien flora than in the indigenous flora is that of the annual herbs (Table 1). However, of the 29 definitely alien annuals, 10 are apparently confined to sites of intense human disturbance. Most of the remainder occur most commonly in such sites. These species are found in natural vegetation only where this is very open, e.g. Briza minor on stream banks, Medicago polymorpha on the edge of Sirkelsvlei, and Melilotus indica next to the sea and on the rocky hills near Ribboksdam. Raitt (1983) has shown that where fynbos is colonized Mediterranean-type regions of Australia (whence 18 of the reserve’s invasive tree and shrub species emanated) and South Africa, has identified the absence of tall trees in the fynbos as one of the important anomalies requiring explanation (Milewski & Cowling 1985). That all six of the angiosperm tree species causing major problems in the reserve are from Australia reinforces the contention that this continent has given rise to a suite of tree species especially well adapted to invading fynbos vegetation (Macdonald 1985).

Tree and tree/shrub species are much more frequent in the alien flora whereas the shrub and dwarf shrub element, which dominates the indigenous flora, is almost totally absent from the alien flora. These results are in accord with the general observation that alien trees appear to have filled an ‘empty niche’ in the fynbos (Campbell et al. 1979; Moll et al. 1980; Macdonald 1984). Comparison of ecosystems in matched environments in the Mediterranean-type regions of Australia (whence 18 of the reserve’s invasive tree and shrub species emanated) and South Africa, has identified the absence of tall trees in the fynbos as one of the important anomalies requiring explanation (Milewski & Cowling 1985). That all six of the angiosperm tree species causing major problems in the reserve are from Australia reinforces the contention that this continent has given rise to a suite of tree species especially well adapted to invading fynbos vegetation (Macdonald 1985).

Another factor that might be limiting successful invasion by plants of these growth forms is herbivory. Several herbaceous alien species have been observed to be heavily grazed by ungulates within the reserve, e.g. Avena barbata, Cortaderia selloana and Pennisetum clandentinum. The intentional introduction of forage legumes and pasture grasses to ploughed strips along the reserve’s roads in the late 1950s and 1960s failed, at least partly, as a result of excessive defoliation of the young plants (Opie 1967; Millar 1970). Grazing has been suggested to be an important selective pressure in shaping the alien flora of southern Africa (Macdonald 1984, 1985). That no geophytes have successfully invaded the reserve is possibly a further reflection of this type of selective pressure. The reserve has a high density of mole rats which feed mainly on geophytes. The large number of geophyte species in the indigenous flora presumably have adaptations that enable them to survive this predation pressure. However, geophytes from other mediterranean-type regions have not been subjected to such pressures (Milewski & Cowling 1985).

The role of ungulate herbivores in alien plant invasions in the reserve needs to be researched: on one hand, the introduction of these ungulates, most of which are alien to the reserve, is suspected to have led to the over-utilization of certain of the reserve’s indigenous plants (Macdonald et al. in press). This might favour the establishment of alien plants, particularly where over-utilization leads to an opening-up of the plant canopy. On the other hand, the observations reported above indicate that ungulates might be limiting successful invasions. The interaction is complicated by two further considerations: the first of these is that the presence of these ungulates has been the stimulus for several intentional plant introductions to the reserve. The second is that alien plants might also have been unintentionally introduced in fodder imported to supplement the nutrition of these ungulates.

Although the collection of data on the alien flora of the reserve has been intermittent it appears that at least 8 species have been recorded from the reserve for the first time in the 1980s (Bromus molliformis, Cortaderia selloana, Sesbania punicea, Vicia benghalensis, Tropaeolum majus, Callistemon rigidus, Nicotiana glauca, Orobanche ramosa). If these were all new additions to the reserve’s alien flora this would give an invasion rate of at least one species per year. On the currently observed ratio of problem species to total alien species (7:73) this rate of invasion can be expected to give rise to about one new problem species per decade.

Two important management considerations arise from the above analyses. Firstly, no more tree species should be

| Life-form categories (after Wells et al. 1986) |
|---------------------------------------------|
| Flora | Tree | Tree/ shrub | Shrub | Dwarf shrub | Shrub/ climber | Climber | Perennial herb | Biennial/ variable herb | Annual herb | Root parasite | Other parasites | Total |
|-------|------|-------------|-------|------------|----------------|--------|---------------|------------------------|------------|---------------|---------------|-------|
| Indigenous No. | 6 | 24 | 217 | 213 | 0 | 34 | 457 | 13 | 79 | 6 | 5 | 1052 |
| % | 0,4 | 2,3 | 20,6 | 20,2 | 0 | 3,2 | 43,4 | 1,2 | 7,5 | 0,6 | 0,5 | 100 |
| Alien No. | 12 | 15(?16) | 1 | 0 | 2 | 1 | 9(?10) | 3 | 29(?31) | 1 | 0 | 73 |
| % | 16,4 | 20,5 | 1,4 | 0 | 2,7 | 1,4 | 12,9 | 4,1 | 39,7 | 1,4 | 0 | 100 |
introduced to the reserve. Secondly, sites of human disturbance should be severely limited. Obviously, every effort should be made to prevent the inadvertent introduction of new alien species to the reserve, e.g. in fodder imports or during the movement of soil for roadbuilding and erosion-control purposes. A system of regular monitoring around sites of human disturbance should be initiated to enable the early detection of new invasions.

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