

Costs and benefits of biological control of invasive alien plants: case studies from South Africa

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Invasive alien species can have significant negative environmental and economic impacts. Such species are often controlled biologically by means of introducing host-specific insects or pathogens that can reduce the species' invasive potential. In many cases, plants are brought under complete control. In this paper, we describe an attempt to estimate the costs and benefits of the biocontrol of six weed species in South Africa. We estimated the costs of biological control research that was conducted on the plants, the rate at which each of these species spreads in the absence of biological control, and the degree to which spread has been arrested or reversed by biological control. This, in turn, was used to estimate the extent to which the species would have spread had biological control not been introduced. We then estimated the most likely levels of consequences associated with uncontrolled spread. The effects were expressed in the form of three categories of benefits associated with the prevention of invasion: the loss of water due to excessive transpiration by invasive plants; reductions in the values of land that became invaded; and reductions in value added by biodiversity to ecosystem services. We compared these benefits with the costs of biological control research in order to derive cost:benefit ratios. The economic benefits of preventing invasion ranged from R300 ha⁻¹ yr⁻¹ for jointed cactus (*Opuntia aurantiaca*) to R3600 ha⁻¹ yr⁻¹ for golden wattle (*Acacia longifolia*) (values are discounted to the year 2000). The economic value of water accounted for 70% of the combined benefits. Benefit:cost ratios for the historical analysis (from the release of the biocontrol agent to the year 2000) ranged from 8:1 for lantana (*Lantana camara*) to 709:1 for jointed cactus. When future estimates of benefits were considered, benefit:cost ratios were greater, and ranged from 34:1 for lantana to 4333:1 for golden wattle. These large differences can be attributed to the length of time that the biocontrol agents have been released (this ranged from 13 to 65 years for different weed species) as well as to the 30-fold differences in the potential area that different weed species would eventually invade. A sensitivity analysis revealed that the model was sensitive to changes in the estimated rate of spread. The sensitivity analysis also showed that the returns on investment in biological control research generally remain positive with some variations between species.

Introduction

Invasive alien species are a significant and growing threat to all of the world's ecosystems. They can spread at alarming rates, displace native vegetation, disrupt important ecosystem processes, and have serious environmental impacts.^{1,2} Land managers are becoming increasingly concerned about the phenomenon, and are seeking cost-effective ways of combating the spread

of invasive species. One of the remarkable characteristics of invasive alien plants is that few, if any, of them are invasive in their countries of origin — their ability to grow vigorously and produce copious amounts of seeds is kept in check by a host of co-evolved invertebrates and pathogens. Some of these plant species, when transported to a new continent without the attendant enemies, exhibit 'ecological release'. This phenomenon allows the introduced species to multiply rapidly in the absence of a host of attendant invertebrates and diseases, with associated tendencies to spread rapidly and to out-compete native species. Biological control (or biocontrol) involves the deliberate introduction of invertebrates or diseases, and is aimed at reducing the effects of ecological release, and arriving at a situation where the plant is returned to the status of a non-invasive naturalized alien (an alien plant that is able to survive, and even reproduce, but does not invade aggressively in its new habitat). Biocontrol is potentially very cost-effective, and environmentally benign. Despite concerns to the contrary,³ the modern practice of using carefully screened and host-specific biocontrol agents is safe, and 'host shifts' (where non-target plants are attacked by the introduced agent) have not occurred in the over 350 recorded cases where weed biocontrol agents have been used worldwide.⁴

In South Africa, biocontrol has been practised since 1910, and, to date, 103 biocontrol agents (including invertebrates and pathogens) have been released against 47 weed species,⁵ making South Africa the third most active country in biological control after the U.S.A. and Australia. South Africa's biocontrol scientists form a relatively small, united and committed community. They have conducted collaborative research over the past 30 years, and have an impressive track record,^{5,6} with many weeds having been effectively brought under control.

Cost-benefit studies of biocontrol programmes generally indicate positive returns on investment. McConnachie *et al.*⁷ reviewed nine studies that had taken place between 1939 and 2000, all of which indicated positive benefit:cost ratios ranging from 1.9:1 to 53:1, with a mean of 18:1. In Australia, a benefit:cost ratio of 14:1 in 2015 (rising to 47:1 in 2050) was estimated for research into, and release of, biocontrol agents on Patterson's curse (*Echium* species).⁸ Patterson's curse causes severe losses in the productive potential of grazing lands. Another Australian study⁹ estimated the benefit:cost ratio for biocontrol of bitou bush (*Chrysanthemoides monilifera*) to be 20.7:1, arising from savings in control costs, and increased amenity and biodiversity values.

Intuitively, we would expect similar positive returns in the case of such programmes in South Africa. However, limited resources have meant that scientists have concentrated their efforts on the identification, screening, release and establishment of agents, and once established, further monitoring of the effects on a large scale were not carried out. Cost-benefit studies therefore tend to be rare exceptions rather than the norm.

In this paper, we attempt to estimate the costs and benefits of the biocontrol of six weed species in South Africa. The study

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Table 1. Invasive alien plant species in South Africa used as a basis for an analysis of the costs and benefits of biological control. The degree of damage done to the weed species by different biological control agents that have established on the weed is shown. Data are from Olckers and Hill.⁵

Invasive alien plant species and date of introduction	Growth form of weed species	Biological control agent and date of introduction	Main feeding guild	Damage to weed*
Jointed cactus (<i>Opuntia aurantiaca</i> , 1840s)	Low spinescent succulent shrub	<i>Cactoblastis cactorum</i> (?)	Stem borer	Moderate
		<i>Dactylopius austrinus</i> (1935)	Sap sucker	Extensive
Red sesbania (<i>Sesbania punicea</i> , 1850)	Medium shrub to tree	<i>Neodiplogrammus quadrivittatus</i> (1984)	Stem borer	Extensive
		<i>Rhyssomatus marginatus</i> (1984)	Seed feeder	Extensive
		<i>Trichapion lativentre</i> (1970s)	Flowerbud feeder	Extensive
Lantana (<i>Lantana camara</i> , 1880s)	Low to tall shrub	<i>Calycomyza lantanae</i> (1982)	Leaf miner	Moderate
		<i>Hypena laceratalis</i> (native)	Leaf chewer	Trivial
		<i>Octotoma scabripennis</i> (1971–75)	Leaf miner	Considerable
		<i>Ophiomyia lantanae</i> (before 1961)	Seed feeder	Moderate
		<i>Teleonemia scrupulosa</i> (1961–1989)	Sap sucker	Considerable
		<i>Uroplata girardi</i> (1974, 1983)	Leaf miner	Considerable
Long-leaved wattle (<i>Acacia longifolia</i> , 1827)	Tree	<i>Melanterius ventralis</i> (1985)	Seed feeder	Extensive
		<i>Trichilogaster acacialongifoliae</i> (1982)	Bud galler	Extensive
Golden wattle (<i>Acacia pycnantha</i> , 1835)	Tree	<i>Trichilogaster</i> sp. (1987)	Bud galler	Extensive
Silky hakea (<i>Hakea sericea</i> , 1830s)	Tall shrub	<i>Carposina autologa</i> (1970, 1982)	Seed feeder	Considerable
		<i>Cyclonema binotata</i> (1979)	Leaf and shoot borer	Trivial
		<i>Erytenna consputa</i> (1970, 1974)	Seed feeder	Extensive
		<i>Colletotricum gleosporioides</i> (native)	Causes gummosis of all tissue	Considerable

*Damage categories are: Extensive – very high levels of damage, and very few plants survive, or almost no seeds are produced; Considerable – high levels of damage, and some plants survive or seed production reduced by more than 50%; Moderate – perceivable damage, but most plants survive or seed production reduced by less than 50%; Trivial – some damage, but survival and seed production almost normal.

was identified as a priority by research managers, based on the threats facing the biocontrol research community and the benefits that they deliver, and the lack of any attempt to quantify these benefits to major funding agencies and stakeholders.

Methods

General approach

We set out to estimate the benefits of biological control at a national scale in South Africa. This is a key aspect that needs to be assessed in order to make informed policy decisions, but it is one that requires an interdisciplinary approach at a scale that is seldom attempted. Our study required us to make estimates of the impacts of biological control at a national scale, in the absence of detailed data on the extent of invasions, on the effects of biological control agents on populations rather than individual plants, and on the economic consequences of invasion. It was thus necessary to make various assumptions in the absence of data, and we consulted leading experts and practitioners in the field when formulating many of these assumptions. Where assumptions were made, these are explicitly shown. Our approach involved estimating the costs of biological control research that was conducted on six invasive alien weed species in South Africa. We attempted to estimate the rate at which each of these species spreads in the absence of biological control, and the degree to which spread has been arrested or reversed by biological control for each of these species. This, in turn, was used to estimate the extent to which the species would have spread had biological control not been introduced. Finally, we attempted to estimate the most likely levels of impact associated with uncontrolled spread, and compared this to the costs of biological control research in order to derive cost:benefit ratios.

Selection of species

We selected six species (Table 1) as examples of invasive alien weeds that had been subjected to biological control in South Africa. The species were chosen to illustrate a range of outcomes with respect to the degree of control achieved (Table 2). They included those that had become major problems before the start

of biological control, as well as species that were known to have invasive potential (such as *Acacia pycnantha*), but that had not yet spread to any significant extent. In some cases, a number of biological control agents for the six selected species were released but failed to establish — Table 1 shows only the agents that have established, together with the degree of damage each agent currently inflicts on the target weed. The combined effect of the agents on populations of all weed species except *Lantana* is either substantial or complete (Table 2).

Estimating the rate of spread of invasive species

The spread of an invading organism generally follows a sigmoid curve over time.^{10–12} The initial expansion is slow as the founder colony becomes established, and increases rapidly as the colony expands and starts new colonies, decreasing again as the potential habitat (invadable area) becomes fully occupied. The logistic model represents this process, and we used it in a discrete form with annual time steps as follows:

$$N_t = N_{t-1} + r(1 - N_{t-1}/K)N_{t-1} \quad (1)$$

where N is the number of spatial units occupied; t is the current time step, $t - 1$ is the previous time step; r is the intrinsic rate of increase, and K is the potentially invadable area. In order to estimate r values, we fitted an exponential relationship:

$$A_t = B e^{r \cdot n} \quad (2)$$

to the data on the historical extent of invasions using regression analysis. In Equation (2), A_t is the area in year t , n is the number of years after introduction, r is the intrinsic (maximum) rate of increase, e is the base of natural logarithms, and B is a constant. Equation (2) was used to estimate initial r values, assuming that the species were still in the exponential phase of their invasions, well short of the potentially invadable area.

For each species, the date of introduction provides the first data point, where population size was effectively zero. Additional estimates of the size of populations at various stages were obtained from the literature, where available. Values of r estimated from Equation (2) were later used in Equation (1) for further calculation.

Table 2. Modes of dispersal and focus and effectiveness of biological control on seven invasive alien plant species in South Africa. Estimates of overall control are from Olckers and Hill.⁹

Invasive alien plant species	Mode of dispersal	Focus of biological control	Degree of overall control achieved*
Jointed cactus	Succulent collectors and gardeners disperse to new localities. Reproduces vegetatively. Animals disperse pieces of the plant that adhere to fur and wool.	Sap suckers do extensive damage to plants. Natural dispersal moderately effective, and populations severely reduced.	Substantial
Red sesbania	Produces large numbers of hard-coated seeds that are dispersed by water and in soil.	Combination of seed-feeders to reduce seed production and stem borers to kill plants. Dispersal of agents poor and need to be introduced to new outbreaks of the weed.	Complete
Lantana	Spread initially by planting as an ornamental. Produces copious seeds which are eaten by birds and dispersed to new sites.	A combination of herbivorous insects to reduce photosynthetic tissue, and direct reduction of seed production using seed-feeders.	Negligible
Long-leaved wattle	Produces large numbers of hard-coated seeds that are dispersed by water and in soil.	Massive reductions in seed production, effectively preventing spread.	Substantial (complete?)
Golden wattle	Produces large numbers of hard-coated seeds that are dispersed by water and in soil.	Massive reductions in seed production, effectively preventing spread.	Substantial (complete?)
Silky hakea	Spreads after fires when large numbers of winged seeds are released from serotinous capsules. Wind dispersal spreads seeds many kilometres.	Large reductions in seed production caused by seed and cone-feeding insects reduces potential to spread. Fungal infections kill plants.	Substantial

* Degree of control as follows : Negligible – control of the weed reliant on other control methods; Substantial – other control methods still needed, but at lower levels; Complete – no other control methods needed to reduce the weed to acceptable levels

Estimating the potentially invadable area

To estimate the potential area that each of the species would invade, we asked experts to provide us with an estimate, in their opinion, of the percentage of each of South Africa's major vegetation types¹³ that would become invaded by the species in question, under a scenario of no control. These authorities had each spent more than 25 years conducting field studies on the weeds concerned. We deducted the areas of each of the vegetation types that had been transformed from the original extent of natural vegetation (vegetation types and transformation are both available on GIS^{13,14}). This provided an area of each vegetation type available for invasion, and this was in turn reduced by the expert assessment of percentages at risk from invasion to obtain a target invadable area. In the case of red sesbania (which invades only riparian areas), the total length of perennial rivers was buffered by 40 m to obtain a potential invadable area (this was based on observation that this species tends to invade, on average, 20 m each side of a river).

Impact of biocontrol on area and density of invasions

We used the results of the above analyses to compare the extent of invasions currently (which reflect the effects of biocontrol) with the situation that would have prevailed if no biocontrol (or other control) had taken place. Essentially, this amounts to the difference between predicted area, estimated using Equation (1) with the value of K set at the estimate of potentially invadable area, and the predicted area with the value of K set at the current extent of invasion. The current extent of invasion (point 5 in Fig. 1) reflects the outcome of biological control, and was obtained from a national estimate made in 1998.¹⁵ The time required for each species to completely invade its potential habitat was also estimated using Equation (1) (point 2 in Fig. 1).

In the absence of data with which to model the future impacts of biological control, we assumed that populations of invasive alien species would remain at current levels, reflecting the effect of biocontrol on stopping future spread to new areas. Except for the case of *Lantana*, and possibly *silky hakea*, this is a conservative assumption, as populations are being reduced.

There are no data available for modelling the density of invasive plants within the invaded area. While invasions should in all likelihood reach a cover of 100% in target areas, that may be

reached only some time after the area is occupied by the weeds. Because cover affects the extent of impacts, we used a conservative estimate of the mean percentage cover for each species from the most extensive survey available¹⁵ in order to estimate impacts.

Quantification of the costs of biocontrol research and implementation.

We used historical records to estimate the costs of the biological control research projects for each species. Data for expenditure on human resources, overheads and running costs incurred in the research were obtained from the Plant Protection Research Institute (A. Gordon, M.P. Hill, H.G. Zimmerman, pers. comm., 2001) and the University of Cape Town (J.H. Hoffmann, pers. comm., 2001). In the cases of *Hakea sericea*, *Acacia longifolia*, *Opuntia aurantiaca* and *Lantana camara*, incomplete records were supplemented by estimates, based on the number of staff involved on the project, average salary levels for the grades of staff employed, and average overhead and running costs. Annual production price indices for the duration of the research were used to convert total costs to 2000 rand values, to avoid the over-inflation of cost:benefit ratios in the case of research

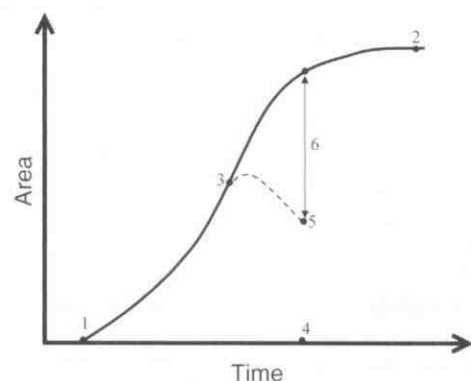


Fig. 1. Generalized model showing the approach adopted to estimate the difference between actual area invaded by a weed species, and the area that potentially would have been invaded in the absence of biocontrol. The solid line shows the estimated expansion in the absence of biocontrol, and the dotted line the actual expansion after biocontrol was introduced. The numbers refer to (1) the date of introduction of the weed; (2) the point at which the weed will have reached all available habitat; (3) the point at which biocontrol was introduced; (4) the current date; (5) the estimated area currently occupied by the weed; and (6) the estimated difference between actual and potential infestation.

Table 3. Impacts associated with seven invasive alien plant species in South Africa.

Invasive alien plant species	Biomes invaded	Major negative impacts
Jointed cactus	Thicket at greatest risk; savanna and grassland at risk but fires limit invasions to some extent. Karoo at risk along water courses.	Grazing capacity reduced by up to 90%. Overgrazing and erosion in remaining uninvaded areas. Injury to animals and damage to skin and wool products. Negative effects on biodiversity.
Red sesbania	Invades the banks of all perennial rivers and streams throughout South Africa.	Increases evapotranspiration and reduces water resources. Reduces access to rivers, and destabilizes banks, causing erosion. Impacts negatively on biodiversity.
Lantana	Most savanna areas, and moist coastal areas.	Toxic to livestock, causing substantial stock losses. Grazing capacity and access to invaded areas reduced. Negative effects on biodiversity.
Long-leaved wattle	Fynbos, and renosterveld bushveld, and grasslands in coastal areas.	Increases evapotranspiration and reduces water resources. Increases fire intensity and the costs of fire control. Negative effects on biodiversity.
Golden wattle	Fynbos, and renosterveld bushveld, and grasslands in coastal areas.	Increases evapotranspiration and reduces water resources. Increases fire intensity and the costs of fire control. Negative effects on biodiversity.
Silky hakea	Fire-prone mountain fynbos	Increases evapotranspiration and reduces water resources. Increases fire intensity and the costs of fire control. Negative effects on biodiversity.

projects that were concluded earlier than 2000. When estimating future costs associated with maintenance of the biocontrol effort, we assumed that annual maintenance costs would be 20% of the mean annual historical cost of research.

Quantification of the benefits of preventing invasion

The impacts associated with invasions by each species were identified during interviews with experts (Table 3). Wherever possible, we also assembled literature and unpublished reports of studies where attempts had been made to quantify the magnitude and value of impacts. On completion of this process, we identified three major influences that could be used to support an economic analysis. These were:

- Impacts on land values (all species).
- Effects on water yield from invaded catchment areas (long-leaved and golden wattles, hakea and sesbania).
- Influence on biodiversity values (all species).

Benefits were calculated according to the following equation:

$$B_j = \sum_{i=1}^{i=3} \sum_{t=1}^{t=N} (Q_{ij} \times (AV \times I)_{ij}) \quad (3)$$

where B is the total economic benefits from preventing invasion for each of the six species as represented by j , Q is the difference in the condensed area of invasion with and without biocontrol, AV is the average economic value, I is the proportion of AV that is realized, i represents three categories of impact (land, water and biodiversity), while t represents the one-year time steps from inception of biocontrol until the modelled time where weeds would occupy all available habitat (N) in the absence of biocontrol.

Benefits in terms of water

Reductions in streamflow associated with long-leaved and golden wattles, silky hakea and red sesbania were estimated as 1881, 1860, 1034 and 758 $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$, respectively. These values were obtained from the relationships between biomass of typical invasive plants and streamflow reductions.¹⁶ The magnitude of streamflow reductions was estimated by multiplying the streamflow reduction estimates by the difference between predicted area, estimated using Equation (1) and the estimated extent of invasion with biocontrol (Fig. 1), corrected for cover (Table 4).

The economic value of streamflow loss was estimated using recently developed methods¹⁷ and updated data on water use in South Africa. Water use per economic sector was estimated in each province.¹⁸ Water used by households, evaporation from dams, river losses, and incremental water use by alien vegetation, dryland agriculture, sugar cane and forestry for 1991–98

were taken into account in addition to water use by traditional economic sectors. Provincial estimates of gross geographical product (GGP in 1994)¹⁹ were used to estimate the value added (VAD) to the provincial economy per m^3 of water used. As the provincial economies vary considerably, weighted VAD per m^3 for each province for 1994 was linearly adjusted for 1991–98 by using the rate of growth in water use for the provinces. In order to overlap with the time horizon of rate of spread models, the average increase in water use over economic growth was estimated, and uniformly extrapolated beyond 1991–98. For 1992–98, this ratio was 0.34, implying that for every 1% growth in the economy, water use for all economic activities increased by 0.34%. The economic value of water was estimated using weighted provincial estimates of value added per m^3 of water used.

It cannot be assumed that increased streamflow, downstream of alien invasions, will find immediate productive use in all sectors of the economy. Such use might be found in water-intensive sectors such as irrigation or industry (where limits are placed on absolute water availability), but not necessarily in sectors such as trade and services. Even in a case of absolute water scarcity, technological change (increasing efficiency in using water, thus reducing demand) or careful management could ease the demand for water. VAD calculations also include the values of other primary factors such as labour and capital,²⁰ so that the economic value of water based on VAD calculations would significantly overestimate marginal prices for water. To correct for this, we assumed that the term I in Equation (3) was 5%, meaning that only 5% of additional streamflow would have economic significance.¹⁷

Benefits in terms of land value

We used market values for land to estimate the impacts of invasion, as the market value of land should equate to its ability to generate income, and follows the widely accepted assumption that land prices will reflect the average productivity of land over multiple years. South Africa's land values followed an almost parallel pattern to current real returns between the 1950s and the 1990s.²¹ This approach does not account for the value of improvements,²² but we assumed that every hectare of land that became 100% invaded would lose 2% of its value [I in Equation (3)], due to lost production potential.

We collected data from the Deeds Office on the value of farms in three provinces — the Western and Eastern Cape, and Mpumalanga (Table 5). Within each province, magisterial districts that overlapped with the known distribution of the six invasive species^{15, 23} were selected. The data set consisted of

Table 4. Results of estimates of the extent of invasion (rounded to the nearest 1000 ha) of seven invasive alien plant species in South Africa with and without biological control. The difference between current and predicted areas was reduced to allow for canopy cover in order to estimate an area that would be 100% covered by alien plants.

Species	Pre-biocontrol rate of expansion (%)	Estimated current (2000) extent of invasion (km ²)	Potential extent of invasion (km ²)	Estimated year in which 100% of area invaded without biocontrol	Mean canopy cover (%) in invaded area (2000)	Predicted current (2000) extent of invasion in the absence of biocontrol (km ²)	Difference between the current and predicted extent in 2000 (km ²)	Difference between current and predicted extent in 2000, reduced for cover (km ²)
Jointed cactus	0.137	19 000	295 000	2047	4	284 000	265 000	11 000
Red sesbania	0.09	2 000	9 000	2109	2	3 000	1 000	20
Lantana	0.109	18 000	45 000	2095	3	30 000	12 000	360
Long-leaved wattle	0.074	1 500	78 000	2164	10	2 000	500	50
Golden wattle	0.074	100	78 000	2174	5	3 000	2 900	145
Silky hakea	0.088	6 000	25 000	2108	9	13 000	7 000	630

selling prices of all rural (non-urban) land parcels or farms that changed hands between 1983 and 2000. Farms where the selling value exceeded R500 000 per ha were excluded as outliers. Where alien species occurred in only one province, the impact of that species on land values was taken as the average price of land in all magisterial districts in that province. Where a species occurred in more than one province, the average price for both provinces was used. We used the 1983 land values for the calculation of impacts of alien plants on land values prior to 1983, while the average land values over the 18 years were used in the assessment of impacts after 2000.

Benefits in terms of biodiversity

The value of biodiversity is not captured in market prices, and few data were available to support our analysis in this regard. Many components have no market value (for example, the subsistence use of wildlife products and the indirect use, option and existence values of natural areas), and they are difficult to assess in developing countries, yet the few studies that have been undertaken suggest that these values are considerable.²⁴ We were only able to find direct consumptive use values, where estimates were available for biological resources that are transformed into revenue through harvesting, for shrubland^{25,26} and savanna²⁷ ecosystems. This approach will not provide a true value for biodiversity, but does give an indication of the kinds of value derived from indigenous and uninvaded ecosystems. The estimates covered harvested wildflowers, food and medicinal plants, and thatch for shrublands, and thatch, poles, meat and herbs for savanna ecosystems. Firewood was excluded as it was assumed that invasive species, especially long-leaved and golden wattles, would supply that need where they replaced native plants. Benefits from grasslands were assumed to be the same as for savannas. In the case of shrubland ecosystems, the relative contribution (in terms of area) of different vegetation types was used to weight the values where benefits arose from certain vegetation types only. For savannas, where data were in the form of estimates of the numbers of people utilizing biodiversity and the value added per person, we estimated a value per hectare based on the area of woodlands used by a known number of people. Where a species occurred in more than one ecosystem (shrubland, savanna or grassland), an average value for the ecosystems where it occurred (weighted by the relative distribution of the invasive species between ecosystems) was used.

Economic analysis

The total economic benefits were compared with the total costs of biocontrol over the period from which research on biocontrol was begun up to the year 2000, in order to estimate a historical cost:benefit ratio. In addition, we estimated a cost:benefit ratio that took both historical and estimated future costs and benefits into account. This was based on the predicted continued spread in the absence of biocontrol on the one hand, and a scenario where the levels of infestation remained constant at 2000 levels into the future on the other. The date at which the invasive species would infest 100% of the potential invadable area was taken as the limit of the study. We used a discount rate of 8% in our economic analysis.

Sensitivity analysis

We measured the robustness of the economic analysis by modelling the effect of changes in key assumptions on the predicted benefit:cost ratios. The assumptions on various inputs were varied for this purpose. For rate of spread, we examined

Table 5. The land value of farms (rounded to the nearest R1000) in selected magisterial districts in three provinces, showing the occurrence of invasive alien plant species used to calculate impacts on land values.

Province	Magisterial districts	Invasive alien plant species	Land value (R ha ⁻¹ , year 2000 values)
Mpumalanga	Lydenburg	Lantana	35 000
	Nelspruit	Red sesbania	
	Pilgrims Rest		
	Waterval Boven		
Eastern Cape	Albany	Long-leaved wattle	14 000
	Alexandria	Silky hakea	
	Bathurst	Jointed cactus	
Western Cape	Bredasdorp	Long-leaved wattle	38 000
	Caledon	Golden wattle	
	Paarl	Silky hakea	
	Swellendam		
	Worcester		

the effect of increasing or decreasing the r values (Table 4). For example, an increase of 2% in the spread rate for silky hakea would increase r from 0.088 to 0.108. The effect of invasions on the value of land (assumed to be 2% in the base model), were tested for values of 1, 3, 4 and 5%. The effect of the percentage of water that would find economic use (assumed to be 5% in the base model) were tested for values of 4, 3, 2 and 1%.

Results

Estimating the rate of spread of invasive species

Very few estimates for the historical extent of invasions exist, and where available they are usually not very accurate. However, we were able to estimate r values for the six study species (Table 4), as described below.

Jointed cactus spreads in two ways. First, it is introduced to a new area, normally by collectors. Once established in an area, it spreads by means of vegetative propagation.

Cladodes break off and adhere to the skin and fur of animals, and when rubbed off, they take root and start a new colony. The invaded area reached 400 ha in 1892, increasing to around 200 000 ha in 1934, and to 1 000 000 ha in 1974.²⁸ This provided sufficient data for fitting a regression to estimate the rate of expansion (r) as 0.137.

Red sesbania was first recorded in 1850 in the botanical gardens in Cape Town.²⁹ It invades rivers and stream courses, where it produces copious numbers of hard-coated seeds that are spread downstream. In 1984 the total extent of the invasion was estimated to be 10% of all perennial rivers (J.H. Hoffmann, pers. comm., 2001). The 1:50 000 scale database on rivers provides an estimate of 231 961 km of perennial rivers in South Africa. Assuming an invaded riparian strip of 40 m, 92 784 ha would have been invaded. In 1997 the total area invaded was estimated at 1.4 million ha,¹⁵ after the introduction of successful biocontrol. This total was inflated by incorrect mapping of low-density invasions, and we estimate that the 1997 invasions were between 140 000 and 200 000 ha. We used an estimate of 200 000 ha in 1997, based on comparisons of the extent of invasions in 1984 and 1997. There were too few data points reliably to estimate the rate of expansion (r), so it was conservatively set at 0.09.

Lantana was introduced in 1883 from Mauritius and again in 1885 from Europe.³⁰ Invasion in KwaZulu-Natal increased 3-fold between 1962 and 1976, and 5-fold between 1962 and 1976 in the former Transvaal.³⁰ These figures are equivalent to expansion rates (r) of 0.096 and 0.122, respectively. We used the mean of the last two estimates (0.109) in our calculations.

Long-leaved wattle was introduced in 1827²⁹ and covered an estimated 200 160 ha in 1997,¹⁵ well after the introduction of effective biocontrol. In 1984 the area of all invasive Australian *Acacia* (wattle) species in the former Cape Province was 896 200 ha.³¹ In 1997 the area invaded by long-leaved wattle was about 9.2% of the total area invaded by all wattle species in the Western Cape.¹⁵ Assuming that the percentage for each species is roughly constant, this gave an area of about 82 536 ha invaded by this species in 1984. According to Stirton's map,³² long-leaved wattle occurred in 37 quarter-degree squares in the Cape Province. Each quarter-degree cell is equivalent to about 67 700 ha. In 1997 long-leaved wattle was recorded in 80 quarter-degree squares (SAPIA database).³³ Converting this to hectares and dividing by the invaded estimated area in 1998¹⁵ gives a mean of 3.7% of each square invaded. If this percentage was similar in 1978, then 92 574 ha would have been invaded in 1978. Using the date of introduction and the crude estimates above, r was estimated to be 0.074.

Golden wattle was probably introduced in 1835,²⁹ and little is known about the extent of invasions by this species. It is very similar to Port Jackson wattle (*Acacia saligna*) and most previous estimates had overlooked it. It was only when the fungal biocontrol of Port Jackson trees began to be effective that the true extent of invasion by golden wattle became apparent (M.J. Morris, pers. comm., 1996). The only estimates of the extent of invasions were made in 1998: 7601 ha¹⁵ and 902 ha (J. Hoffman, pers. comm., 2000). These values differ but the larger¹⁵ is an underestimate (M.J. Morris, pers. comm., 1996). Stirton³² showed it to be present in 18 quarter-degree squares and it was recorded in 24 squares in 1997,³³ which is well after the introduction of biocontrol. Owing to the lack of data we used the rate (r) estimated for long-leaved wattle.

Silky hakea was introduced in 1835. Plants are spread by means of wind-blown seeds, released in copious numbers after fires. The estimated extent of invasions was 9000, 111 345 and 279 200 ha in 1939, 1969 and 1974, respectively.³⁴ These data gave an estimated expansion rate (r) of 0.088.

Estimating the potentially invadable area

Jointed cactus had the highest potentially invadable area (more than double that of the next nearest species, Table 4), followed by the two wattle species, lantana and silky hakea. Our estimates do not account for the possibility that suitable area may be invaded by competing weed species. For example, the invadable area for both long-leaved and golden wattle is the same (Table 4) as both species would occupy similar habitats.

Table 6. The costs of research (rounded to the nearest R100 000) into the biological control of seven invasive alien weed species in South Africa.

Invasive alien weed species	Years in which active research was conducted	Estimated cost of research (2000 rand values)
Jointed cactus	1932–1939; 1970–1985	8 600 000
Red sesbania	1978–1997	3 000 000
Lantana	1969–2001	17 300 000
Long-leaved wattle	1981–1991	2 300 000
Golden wattle	1985–2001	700 000
Silky hakea	1965–2000	9 200 000
Total		41 100 000

Impact of biocontrol on extent of invasions

Biological control has had the largest impact in the case of jointed cactus, where estimates indicate that almost 300 000 km² would have been invaded had biocontrol not been in place (Table 4). This is in part because biocontrol of this species has been practised for much longer than for other species (Table 1). Substantial savings appear to have been made in the case of lantana, hakea, golden wattle, and red sesbania as well (Table 4). These effects will increase with time, assuming that growth in the invasive alien species would have been at an exponential phase, but is now static under the effects of biocontrol. Because the invasive alien plants do not cover 100% of the areas where they occur, we reduced the estimates of area saved by the estimates for mean canopy cover (Table 4) to arrive at 'condensed' areas (the equivalent area that would be occupied by invasive alien plants at 100% cover).

Costs of research programmes

The total historical cost (in 2000 rand values) for the research programme was R41.1 million (Table 6). Of this, 42% (R17.3 million) was spent on one species — lantana. A further 43% was spent on jointed cactus (R8.6 million) and silky hakea (R9.2 million). Only 15% of the budget was spent on the remaining three species (red sesbania, long-leaved wattle and golden wattle).

Benefits of preventing invasion

The economic losses that would be suffered if an uninhabited area became invaded ranged from R300 ha⁻¹ yr⁻¹ for jointed cactus to R3600 ha⁻¹ yr⁻¹ for golden wattle (values are for the year 2000, Table 7). The values for lantana and jointed cactus were

substantially lower than for the other species, as these species were not considered as excessive water users, thus restricting their impacts in our study to land values and biodiversity alone. The contribution of land values and the value of water to the overall benefits accounted for 99% of the estimates of combined benefits, with the bulk of the effect (70%) accounted for by water. The contribution of biodiversity to the estimates was only 1%, and this probably reflects an inability on our part to estimate the true benefits, which were almost certainly underestimated.

Economic analysis

Benefit:cost ratios ranged from 709:1 for jointed cactus to 8:1 for red sesbania (Table 8). When future estimates of benefits were considered, benefit:cost ratios ranged from 4333:1 for golden wattle to 34:1 for lantana (Table 9). These large differences can be attributed to the length of time that the biocontrol agents have been released, as well as to differences in the estimated potential area that different weed species would eventually invade. Biocontrol agents were released on jointed cactus in 1935 (Table 1), and thus benefits have already accrued over 65 years in our estimates. The potential area that a weed would eventually invade varied 30-fold, from under 10 000 km² in the case of red sesbania to almost 300 000 km² for jointed cactus. This obviously contributed significantly to the differences in the ratios as well.

Sensitivity analysis

The model proved to be very sensitive to the estimated rates of spread, and sensitive also to the value of land lost due to invasive species and the productive value of additional downstream water use. A one per cent change (increase or decrease) in the rate of spread leads to slightly more than three times the change

Table 7. Potential economic loss that would arise if an uninhabited area became invaded by seven alien species in South Africa. Losses are expressed in terms of economic use of water and biodiversity, and preservation of the value of land. Data are in R ha⁻¹ yr⁻¹ for the year 2000 (rounded to the nearest R10).

Species	Economic use of water	Economic value of land	Economic use of biodiversity	Total value
Jointed cactus	0	280	30	310
Red sesbania	1160	680	30	1870
Lantana	0	680	30	710
Long-leaved wattle	2880	520	10	3410
Golden wattle	2810	780	10	3600
Silky hakea	1680	520	10	2410

Table 8. Economic benefits and costs of biocontrol between the initiation of research on biocontrol up to the year 2000. Estimates are expressed in R million, discounted to the year 2000.

Species	Benefit due to streamflow	Benefit due to land value	Benefit due to biodiversity	Cost of biocontrol research	Benefit:cost ratio
Jointed cactus	0	5479	634	8.62	709:1
Red sesbania	12	10	0.32	3.04	8:1
Lantana	0	375	15	17.33	22:1
Long-leaved wattle	200	39	1.43	2.32	104:1
Golden wattle	349	100	1.55	0.68	665:1
Silky hakea	1742	550	13.32	9.19	251:1

Table 9. Economic benefits and costs of biocontrol between the initiation of research until the estimated date at which weed populations would cover all available habitat. Estimates are in R million, discounted to the year 2000.

Species	Benefit due to streamflow	Benefit due to land	Benefit due to biodiversity	Cost of biocontrol research	Benefit:cost ratio
Jointed cactus	0	9246	1023	8.9	1154:1
Red sesbania	101	49	2	3.38	45:1
Lantana	0	609	23	18.64	34:1
Long-leaved wattle	3422	406	15	2.62	1465:1
Golden wattle	2796	560	9	0.78	4333:1
Silky hakea	4680	1292	31	9.83	611:1

in benefits (Fig. 2). In the case of a one per cent decrease in the rate of spread, the benefit:cost ratio of long-leaved wattle falls from 104:1 in the baseline model to 6:1. Sesbania and silky hakea become economically unviable to control, whereas lantana is the only species that was not sensitive to such a scenario. A change in the productive value of water used downstream has the most impacts on the benefits of controlling long-leaved and golden wattle, followed by hakea and sesbania (Fig. 3). If the estimated loss in land value increases, this has significant impacts on the benefit:cost ratios of especially jointed cactus and lantana (Fig. 4).

Discussion

Validity of assumptions underlying benefit:cost ratios

The benefit:cost ratios reported here are relatively high compared to other studies that have examined the control of invasive alien plants. This may be interpreted as being a result of unrealistic assumptions about the magnitude of benefits, but we chose conservative assumptions wherever possible. In the case of rates of spread, our estimated *r* values (Table 4) ranged from 0.074 to 0.137. Values for *r* reported in the literature^{35,36} range from 0.01 to 0.65, with values of between 0.1 and 0.3 being regarded as reasonable for aggressive weed species, such as those considered in this study.¹⁵ The assumption that only 5% of additional water reclaimed by clearing will find economic use is also conservative, given the inability of most of South Africa's rivers to meet water demands. Likewise, a reduction in the value

of land of only 2% following full invasion of previously pristine natural vegetation is very small, but data on the differential paid for uninvasioned land are not available. Finally, the value of biodiversity (accounting for only 1% of the benefits of preventing invasion) is probably an underestimate. The comparatively high benefit:cost ratios are more likely due to the relatively inexpensive nature of biocontrol research (the cost) rather than to the disproportionate magnitude of the benefits. Our sensitivity analysis (Figs 2–4) shows that the returns on investment in biological control research generally remain positive, even under scenarios with more conservative assumptions, with some variations between species. The control of jointed cactus was viable under all scenarios tested, while both long-leaved and golden wattle had positive benefit:cost ratios for all scenarios, although only marginally so for a decrease of 2 percentage points in the assumed rate of spread. The control of sesbania has the lowest benefit:cost ratios, and the benefit:cost ratio for both sesbania and hakea become negative under a scenario of decreased rates of spread. However, as explained above, these lower rates of spread are probably unrealistic. Given the sensitivity of the models to assumptions on rates of spread, this aspect of our model warrants further research.

We have tested key assumptions through the sensitivity analysis, but several implicit assumptions could not be tested. For example, we assumed a situation where a single weed will invade all the area available, and that if it is brought under control, then that area will be spared from invasion. In reality, there is more than one weed species, and bringing one

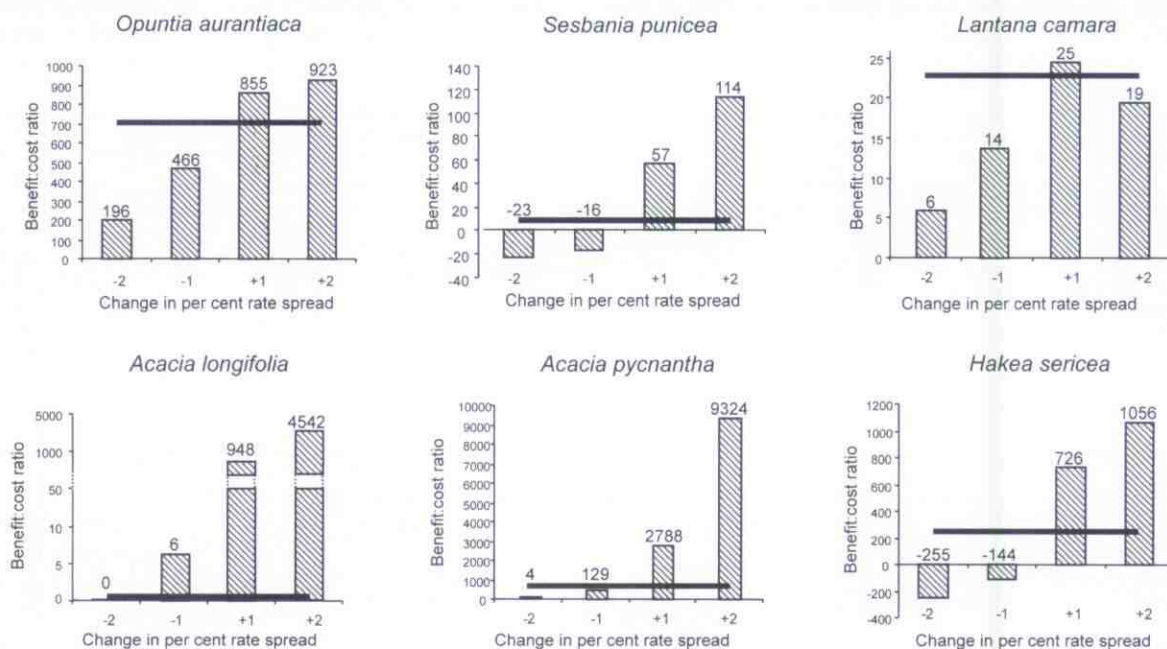


Fig. 2. Changes in the estimates of benefit:cost ratios associated with the biological control of six weed species in South Africa, resulting from changing the estimated rate of spread of weed populations. The solid line shows the baseline benefit:cost ratio (see Table 8). Note the break in scale for *Acacia longifolia*, and that the scales for benefit:cost ratios differ.

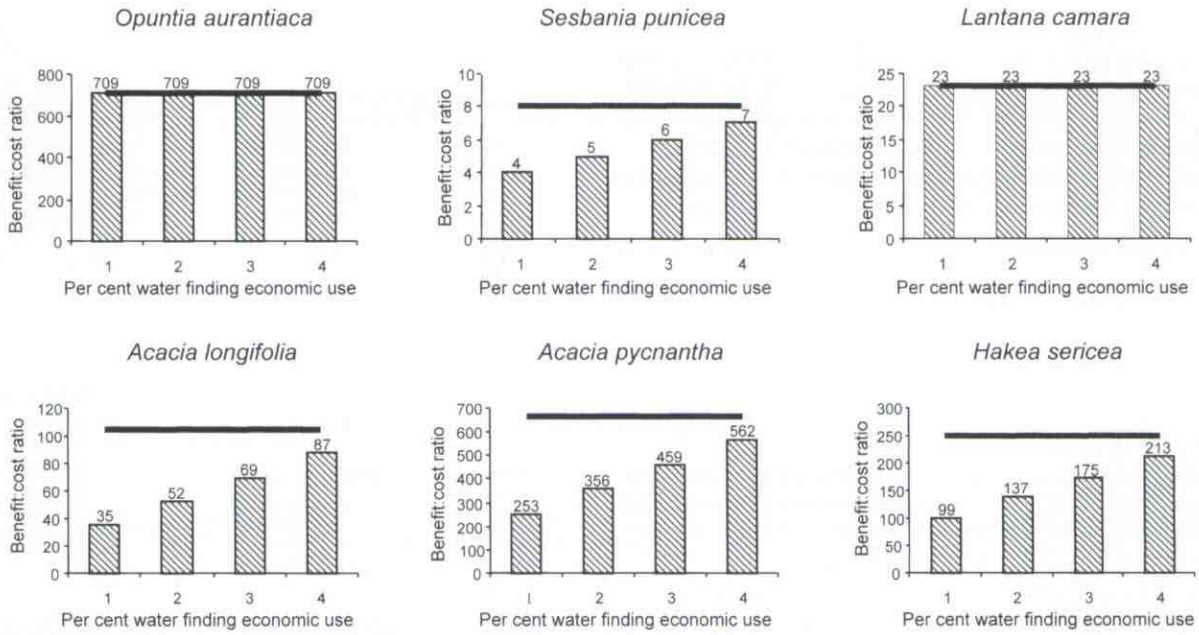


Fig. 3. Changes in the estimates of benefit:cost ratios associated with the biological control of six weed species in South Africa, resulting from changing the percentage of water that will find economic use. The solid line shows the baseline benefit:cost ratio (see Table 8). Note that the scales for benefit:cost ratios differ.

under control may simply leave the area open to invasion by the next weed. We were also unable to consider competition between invasive species. This will obviously have an effect on the modelled rate of spread, which could lead to reduced impacts from a single species. In many cases areas that have been spared invasion (because the threatening species is under biocontrol) have escaped invasion by another weed species to date, but this does not preclude new weed species entering the equation in future. We argue that this underlines the importance of sustained effort to finding solutions for emerging weed species.

Distribution of costs

Despite positive benefit:cost ratios under most scenarios, private landowners often do not have appropriate incentives to control alien invasive species, as many of the benefits accrue to

external parties (such as water users downstream), and the private cost of control is not compensated by direct, short-term private benefits. For a sustainable programme on the control of alien species, incentives for control by private landowners should be seriously investigated, without becoming a tax burden on the country's scarce resources.

The value of biological control

The contribution of biological control to preventing substantial losses to the economy of South Africa (and elsewhere, presumably) is significant, but it does not produce an immediately visible or vibrant economic enterprise. Rather, it prevents the loss of ecosystem services that contribute to human well-being. People tend to notice a problem only when it has manifested itself, and its absence is a difficult concept to convey to politicians, voters and funders. This study has indicated that invest-

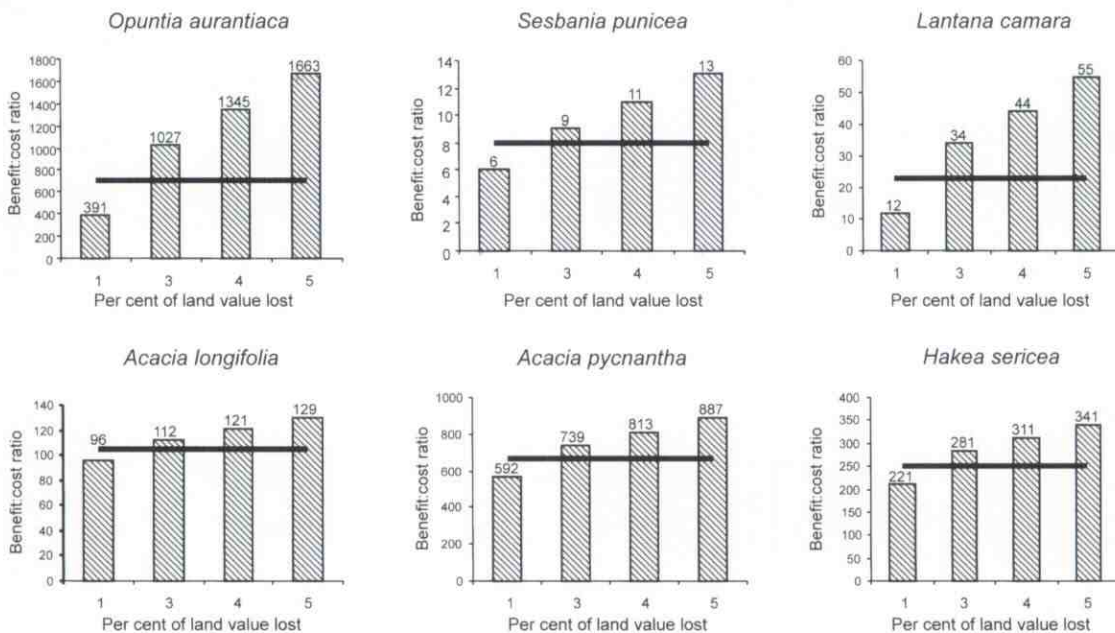


Fig. 4. Changes in the estimates of benefit:cost ratios associated with the biological control of six weed species in South Africa, resulting from changing the percentage of the land value lost due to invasion. The solid line shows the baseline benefit:cost ratio (see Table 8). Note that the scales for benefit:cost ratios differ.

ing in research into biological control, and maintaining the capacity (in the form of trained people and infrastructure) will under most scenarios deliver positive and even considerable returns on investment. The challenge for ecologists is to show how valuable this approach can be. The analysis described in this paper may provide enough information on which to base convincing arguments for investment in biological control.

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- Bright C. (1998). *Life Out of Bounds — Bioinvasion in a borderless world*. Norton, New York.
- Kaiser J. (1999). Stemming the tide of invasive species. *Science* **285**, 1836-1841.
- Louda S.M., Kendall D., Conner J. and Simberloff D. (1997). Ecological effects of an insect introduced for the biological control of weeds. *Science* **277**, 1088-1090.
- Waterhouse D.F. and Norris K.R. (1987). *Biological Control: Pacific prospects*. Inkata Press, Melbourne.
- Olckers T. and Hill M.P. (1999). Biological control of weeds in South Africa (1990-1998). *African Entomology Memoir* **1**.
- Hoffmann J.H. (1991). Biological control of weeds in South Africa. *Agric. Ecosyst. Environ.* **37**, 1-255.
- McConnachie A.J., Hill M.P., Byrne M.J. and de Wit M.P. (2003). Economic evaluation of the successful biological control of *Azolla filiculoides* in South Africa. *Biol. Con.* **28**, 25-32.
- Nordblum T., Smyth M., Swirepik A., Sheppard A. and Briese D. (2001). Benefit-cost analysis for biological control of *Echium* weed species (Patterson's curse/salvation Jane). In *The Co-Operative Research Centre (CRC) for Weed Management Systems: An impact assessment*, pp. 35-43. CRC for Weed Management Systems Technical Series No. 6, Adelaide.
- CRC (2001). Control of bitou bush: a benefit-cost analysis. In *The Co-Operative Research Centre (CRC) for Weed Management Systems: An impact assessment*, pp. 27-34. CRC for Weed Management Systems Technical Series No. 6, Adelaide.
- Harper J.L. (1977). *Population Biology of Plants*. Academic Press, London.
- Mack R.N. (1985). Invading plants: their potential contribution to population biology. In *Studies on Plant Demography: A festschrift for John L. Harper*, ed. J. White, pp. 127-142. Academic Press, London.
- Birks H.J.B. (1989). Holocene isochrone maps and patterns of tree-spreading in the British Isles. *J. Biogeog.* **16**, 503-540.
- Low A.B. and Rebelo A.G. (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.
- Fairbanks D.H.K., Thompson M.W., Vink D.E., Newby T., van den Berg H.M. and Everard D.A. (2000). The South African land-cover characteristics database: a synopsis of the landscape. *S. Afr. J. Sci.* **96**, 69-86.
- Versfeld D.B., le Maitre D.C. and Chapman R.A. (1998). Alien invading plants and water resources in South Africa: a preliminary assessment. Report No. TT99/98, Water Research Commission, Pretoria.
- Le Maitre D.C., van Wilgen B.W., Chapman R.A. and McKelly D.H. (1996). Invasive plants and water resources in the western Cape Province, South Africa: modelling the consequences of a lack of management. *J. appl. Ecol.* **33**, 161-172.
- De Wit M.P., Crookes D.J. and van Wilgen B.W. (2002). Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. *Biological Invasions* **3**, 167-178.
- Crafford J.G., King N.A., Malubane T.G., Anderson H.J. and de Wit M.P. (2001). Water Resource Accounts for South Africa (1991-1998). Report ENV-P-C2001-050, Division of Water, Environment and Forestry Technology, CSIR, Pretoria.
- Statistics South Africa (1995). *Statistical release P0401*, 16 November. Pretoria.
- De Wit M.P., Crookes D.J. and Geach B.G.S. (2000). The costs and benefits of black wattle in South Africa. CSIR report ENV-P-C 2000-023, Pretoria.
- van Schalkwyk H. (1995). Factors influencing land values. *Farmer's Weekly*, 3 March, 17-18.
- Theunissen P. (1998). What if land prices deflate? *Farmer's Weekly*, 17 July, 20-21.
- Henderson L. (2001). *Alien Weeds and Invasive Plants*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria.
- Swanson M.S. and Babier E.B. (1992). *Economics for the Wilds*. Earthscan Publications, London.
- Turpie J.K., Heydenrych B.J. and Lamberth S.J. (2003). Economic value of terrestrial and marine biodiversity in the Cape Floristic Region: implications for defining effective and socially optimal conservation strategies. *Biol. Cons.* **112**, 233-251.
- Turpie J.K. and Heydenrych B.J. (2000). Economic consequences of alien infestation of the Cape Floral Kingdom's Fynbos vegetation. In *The Economics of Biological Invasions*, eds C. Perrings, M. Williamson and S. Dalmazzone, pp. 152-182. Edward Elgar, Cheltenham, Glos.
- Shackleton C.M., Netshiluvhi T.R., Shackleton S.E., Geach B.S., Balance A. and Fairbanks D.E.K. (1999). *Direct use values of woodland resources from three rural villages*. CSIR report ENV-P-1 98210, Pretoria.
- Moran V.C. and Anneke D.P. (1979). Critical reviews of biological pest control in South Africa. 3. The jointed cactus, *Opuntia aurantiaca* Lindley. *J. Ent. Soc. S. Afr.* **42**, 299-329.
- Shaughnessy G.L. (1986). A case study of some woody plant introductions to the Cape Town area. In *The Ecology and Management of Biological Invasions in Southern Africa*, eds I.A.W. Macdonald, F.J. Kruger and A.A. Ferrar, pp. 37-43. Oxford University Press, Cape Town.
- Cilliers C.J. and Naser S. (1991). Biological control of *Lantana camara* (Verbenaceae) in South Africa. *Agric. Ecosyst. Environ.* **37**, 57-75.
- Macdonald I.A.W. and Jarman M.L. (1985). Invasive alien plants in terrestrial ecosystems of Natal, South Africa. *S. Afr. Natl Sci. Prog. Rep.* **118**. CSIR, Pretoria.
- Stirton C.H. (1978). *Plant Invaders. Beautiful, but Dangerous. A guide to the identification of twenty-six plant invaders of the Province of the Cape of Good Hope*. Cape Nature Conservation, Cape Town.
- Henderson L. (1998). Southern African Plant Invaders Atlas (SAPIA). *Appl. Plant Sci.* **12**, 31 - 32.
- Kluge R.L. and Naser S. (1991). Biological control of *Hakea sericea* (Proteaceae) in South Africa. *Agric. Ecosyst. Environ.* **37**, 91-113.
- Richardson D.M. and Brown P.J. (1986). Invasion of mesic mountain fynbos by *Pinus radiata*. *S. Afr. For. J.* **56**, 529-536.
- Lonsdale W.M. (1993). Rates of spread of an invading species — *Mimosa pigra* in northern Australia. *J. Ecol.* **81**, 513-521.

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