A decision-making framework for restoring riparian zones degraded by invasive alien plants in South Africa

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Riparian habitats in many parts of South Africa are severely degraded by invasive alien plants, especially trees. These invasions reduce water yields from catchments and affect riverine functioning and biodiversity. Initiatives are under way countrywide to clear alien plants from watercourses and surrounding catchments. Current understanding of key processes that regulate riparian functioning and define options for restoration is rudimentary. We review the impacts of riparian invasions and identify factors limiting the recovery of natural vegetation following alien clearance. We propose a framework of strategic interventions for optimizing restoration success. The framework identifies abiotic and biotic barriers to restoration at the scales of catchments and local reaches. In highly transformed catchments, interventions at the reach scale may fail if important barriers at the catchment scale are not addressed. The extent to which propagule supply and microsite conditions inhibit vegetation recovery is unknown. We also know little of the relative importance of dispersing vegetative propagules, dispersing seeds and soil-stored seed banks in vegetation dynamics, particularly after severe disturbances such as dense invasion by alien plants. The importance of geomorphological and hydrological factors in mediating recovery of riparian vegetation has not been adequately explored for all climatic areas in South Africa. More research is needed to determine the influence of different alien species and clearing treatments on the recovery of riparian vegetation. The literature strongly suggests that in highly alien-transformed catchments, the re-introduction of riparian species is required to promote recovery and suppress re-invasion. However, such interventions are unlikely to be widely implemented unless the cost: benefit ratios are favourable.

Introduction

Early interventions in riparian ecosystems to combat invasive alien plants tended to be *ad hoc* and focused on localized alien control, with little consideration of restoration in the context of the whole catchment. We aim to provide new insights into riparian restoration within this broader context. We review the impact of alien plant invasions in riparian zones and identify factors that limit natural vegetation recovery after alien clearing operations. Following this analysis, we present a framework of strategic interventions to optimize restoration success, using some typical examples of invasion, and identify aspects that require further research.

Riparian zones form the interface between aquatic and terrestrial ecosystems[1] and, except in broad floodplains, are relatively narrow, linear features across the landscape. Riparian zones support distinctive vegetation that differs in structure and function from adjacent aquatic and terrestrial ecosystems.[2] Riparian vegetation is shaped by disturbance regimes of the surrounding landscape, by wind and fire for example, and by disturbances associated with aquatic systems, such as flooding, debris flows and sedimentation processes.[3] The distribution of riparian vegetation types is primarily determined by gradients of available moisture and oxygen, and plant communities can be stratified by height above the river channel.[4,5] Variations also exist owing to the post-disturbance successional phase of the vegetation.[6]

Rivers are dynamic ecosystems and while active channels generally are hostile to vegetation establishment, the adjacent riparian zones are colonized by specialized disturbance-adapted species.[2] Riparian plants are adapted to fluctuations in the water-table, as river levels alternate between low base flows and floods. Riparian vegetation provides habitat, stabilizes riverbanks and filters sediments and nutrients from the surrounding catchment.[7] These ecosystems may be considered 'critical transition zones' as they process substantial fluxes of materials from closely connected, adjacent ecosystems.[8]

Riparian zones worldwide have been the focus of human habitation and development for many centuries,[9] resulting in direct and indirect degradation of their ecological integrity. Direct degradation includes vegetation clearance for agriculture,[10,11] grazing and trampling by livestock,[12] pollution from the surrounding catchment[9,10] and the planting of alien species.[4,13–15] The widespread damming of rivers has greatly altered hydrological regimes and indirectly impacted on the functioning of aquatic and riparian ecosystems in many of the world's rivers.[16–18]

River ecosystems are highly prone to invasion by alien plants because of their dynamic hydrology and opportunities for recruitment following floods.[19,20] Efficient dispersal of alien propagules in water and continuous access to water resources facilitates alien plant invasions.[21,22,24–26] Many alien invaders of riparian habitats in South Africa are tall trees with higher water consumption than the indigenous vegetation.[27,28] As much of South Africa is semi-arid,[29] invasive alien trees impact negatively on the country's scarce water resources by reducing run-off. Research in higher rainfall areas indicates that tall invasive alien trees may reduce the mean annual run-off by up to 300 mm/yr.[30] The influence of alien trees on water resources increases with proximity to water courses.[30] For this reason, invaded riparian zones and their immediate subcatchments are targeted for alien clearance by the national Working for Water programme (WfW).[31] Invasion by aquatic alien plant species, such as water hyacinth (*Eichornia crassipes*), is also widespread, particularly in lowland rivers,[32] but will not be addressed here.

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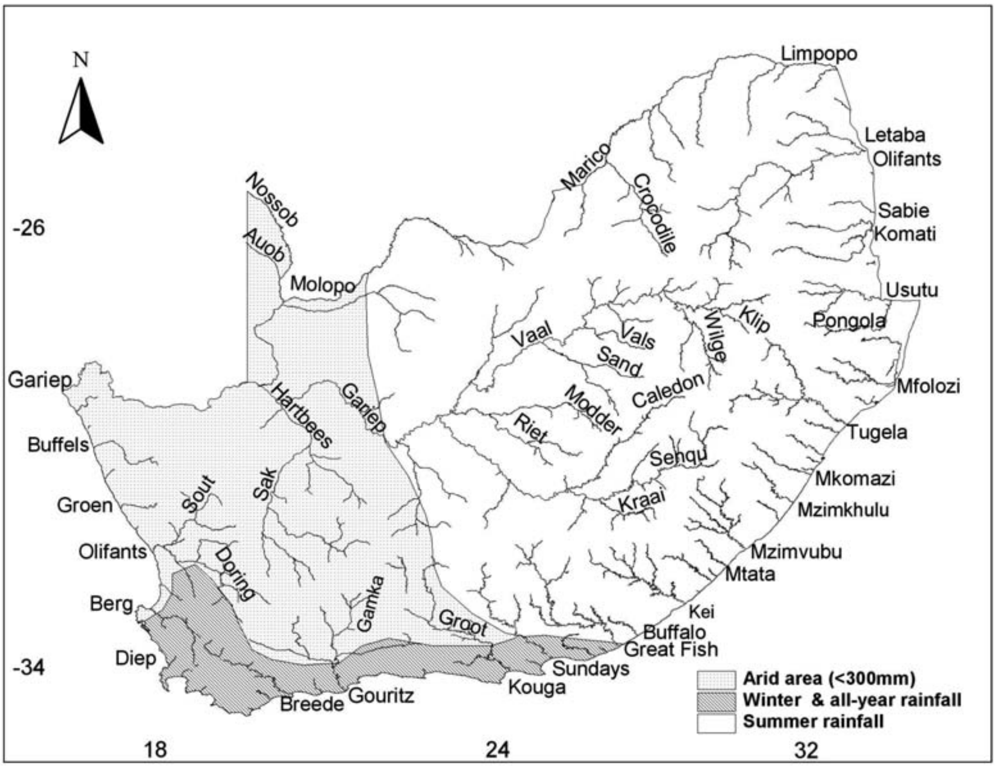

Fig. 1. Broad climatic regions and major rivers in South Africa.

Riparian vegetation in South Africa

South Africa is an ecologically diverse region, encompassing eight terrestrial biomes,[33] with an extremely rich flora and high levels of endemism.[34] In relation to river systems, and riparian zones in particular, the various biogeographical entities may be simplified into three separate areas: those with predominantly winter or all-year rainfall, predominantly summer rainfall, or low rainfall (Fig. 1).

The winter or all-year rainfall area comprises mainly the fynbos biome; the summer rainfall area encompasses the grassland and savanna biomes; and the arid area comprises primarily the succulent and Nama Karoo biomes. The thicket and forest biomes are present in landscape patches that are protected from fires throughout the non-arid areas of South Africa, including some riparian zones.

All regions of South Africa experience at least partially seasonal rainfall, with periodic droughts that reduce water tables and flow rates, and floods that inundate stream channels. In relatively high-rainfall areas, an annual cycle of floods and low-flow periods occurs, whereas in arid areas most rivers have intermittent, occasional flows [except the Gariep (also known as the Orange) River, which has perennial sources]. Longer cycles of dry and wet periods of about 18 years have occurred over the past few centuries.[35] Many of the flood-producing rains in South Africa are associated with cut-off low pressure systems, most frequent in spring and autumn.[35]

Extreme flood events may coincide with tropical cyclones moving inland from the east coast.[35] These factors translate into highly variable river flow regimes, with the coefficient of variation of mean annual runoff at 78% being the highest for any country.[36] During the past 60 years, there have been four flood events in the Sabie River that exceeded mean flow by more than two standard deviations.[37] Furthermore, there were seven droughts during this period (flows below 1 standard deviation of the mean) and in 1992 the flow on the Sabie dried up on the Mozambique border.[38] These rivers are also highly complex due to the interaction between spatially and temporally variable sediment supply from the catchment, highly variable hydrology, a complex long profile, and complex hydraulics generated by a heterogeneous bedrock template.[39] This geomorphological complexity leads to a correspondingly high level of diversity in vegetation structure and composition.[40]

Global climate change is predicted to imply an increase in extreme events in the future,[41] with floods and droughts of increasing amplitude resulting in disruptions to riparian vegetation and increasing susceptibility to alien invasions.

Determinants of riparian vegetation structure and composition

Fluvial, including hydrological, processes are the chief determinants of plant community structure and composition in riparian zones.[19,42,43] Hydrology influences the vegetation via floods, droughts and water-table fluctuations, whereas sediment deposition provides new habitat for plant colonization. Prolonged drought or flow reductions due to impoundments can lead to a lowering of riparian water tables and mortality in riparian trees.[44] Simultaneously, greater channel bar exposure may result in their colonization by riparian trees.[45]

Plant species attributes are important in determining which riparian lateral zones they occupy and hence the structure and composition of different riparian communities. Species closer to the channel are able to survive the physical stress of frequent flooding, whereas those at higher elevations tend to be intolerant of flooding, but require access to the water table.[2,46]

Life-history strategies are important in determining where and when a riparian plant species may colonize a site, but in many regions the relative importance of seed versus vegetative recruitment is poorly known. In one northern European study, floating vegetative propagules outnumbered seeds 9:1, with a dispersal period in the former of eight months, demonstrating the importance of vegetative propagules for long-distance dispersal in the riparian environment.[47] Most opportunities for recruitment occur after floods when the availability of establishment sites is greatly increased and dispersal of propagules in water may have a major role in structuring the flora.[48,49] The final location of water-dispersed propagules depends on the hydrological regime during propagule release and transport, and the channel morphology and hydraulics.[50] Species with specialized establishment requirements will be most sensitive to these factors. Dispersal of plant propagules by animals and wind is also important in riparian systems.[49,51] Further recruitment opportunities may occur following fire. However, the structural characteristics of many riparian communities render them less flammable than surrounding vegetation, and fire may be excluded, particularly in summer rainfall areas. Riparian plant species have adaptations to fluvial disturbances, such as resprouting ability or seed storage, which confer resilience and facilitate regeneration after fire.[52]

Many riparian plant species require bare, wet surfaces for establishment, as may be generated by large floods, point bar migration, channel abandonment and riverbank erosion.[6,53] In contrast, Galatowitsch and Richardson[54] noted the recruitment of woody riparian seedlings only in stable, protected sites in fynbos headwater systems. It is thus likely that different regions and components of the vegetation will have different recruitment requirements. Flood-coupled recruitment in humid regions depends on the maintenance of low water levels during the seedling establishment phase[55] whereas in semi-arid areas establishment sites are often abundant, but water availability and rate of decline in the water table are factors limiting successful establishment.[56]

Winter rainfall areas

The winter or all-year rainfall area is dominated by the Cape Fold Belt mountains that rise steeply to an elevation of 2000 metres, and greatly influence river geomorphology. These mountains comprise mainly sandstones that yield nutrient-poor substrata.[57] From the steep mountainous terrain the rivers flow through a short foothill zone onto the coastal plains, the latter mostly comprising shale substrata. The downstream coastal plain has lower gradients, finer sediments and less confined channels, and the dominant geomorphological process is deposition, in contrast to the mountain stream zone where it is erosion.[58]

Riparian vegetation is usually distinct from the surrounding fire-prone fynbos vegetation, although it occurs under similar macroclimatic conditions.[59] It has been variously named 'closed scrub fynbos',[60–62] 'hygrophilous mountain fynbos'[63] and 'broad sclerophyllous closed scrub'.[64] This vegetation (Fig. 2A) is described as being similar to forest and thicket in its relatively high cover of broad-leaved woody plants, but dissimilar in its high cover of fynbos elements, such as Restionaceae and Ericaceae.[61] Other structural types, from tall herbland to forest, may also occur in the riparian zone.[64] Afromontane Forest develops in areas of steep topography, such as ravines, and on riparian boulder fields that afford protection from regular fires, but in the southern Cape it covers more extensive areas. Common riparian scrub species include *Metrosideros angustifolia, Brachylaena neriifolia, Brabejum stellatifolium* and *Diospyros glabra.*[65]

Riparian vegetation in downstream systems of the coastal forelands is largely transformed by agriculture and few rivers remain undisturbed between the foothills and the sea.[66] Thus reference ecosystems are lacking for lowland riparian corridors. It is likely that the interplay between soil texture, climate and fire frequency determined whether fynbos or renosterveld shrublands, *Acacia karroo* thicket, or forest vegetation types predominated.

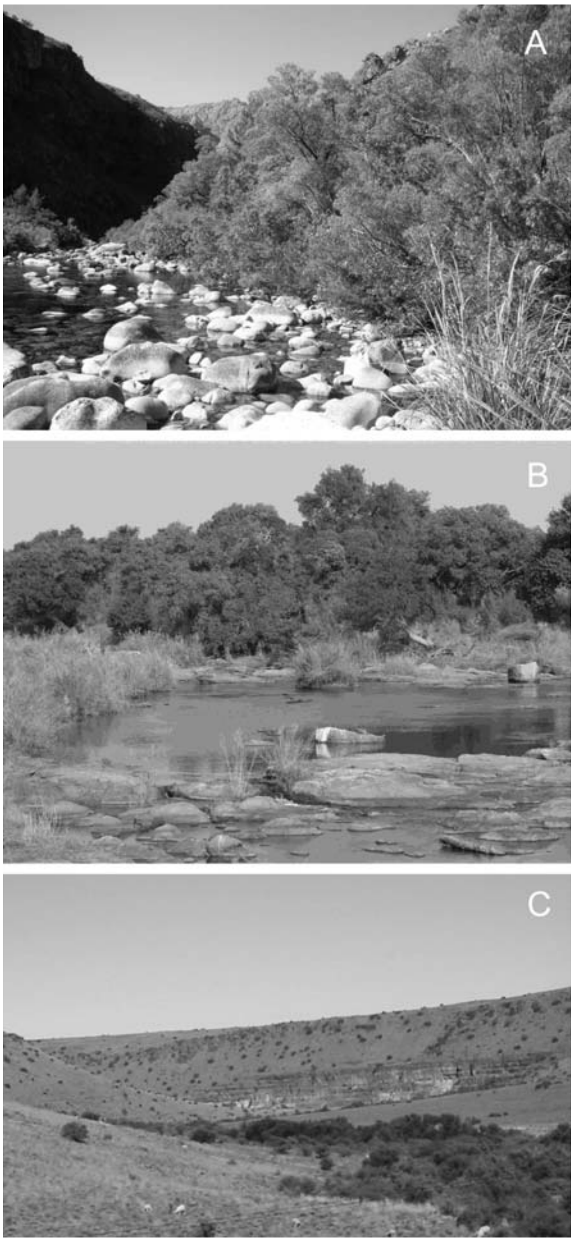

Fig. 2. Examples of indigenous riparian vegetation in three broad climatic areas of South Africa: **A**, closed-scrub fynbos vegetation in the winter to all-year rainfall area (Elands River: photograph P.M. Holmes); **B**, woodland riparian vegetation in the summer rainfall area (Sabie River: photograph L.C. Foxcroft); **C**, *Acacia karroo* riparian vegetation in the arid interior (near Three Sisters: photograph S.J. Milton).

Summer rainfall areas

Most research on riparian vegetation in the summer rainfall area has concentrated on the rivers entering the Kruger National Park (KNP) in the northeast of the country. These rivers originate in the Drakensberg Mountains in grassland vegetation, then flow through various savanna vegetation types.[15,67] Extraction of upstream water for agriculture, forestry and human settlements greatly reduces the mean annual flow of the rivers.[15,68,69] Rivers in the KNP occupy large, deeply incised, mixed bedrock–alluvial macro-channels with a steep bank on either side of the channel floor.[68,70] One or more active channels carry water throughout the year along the river corridor (Fig. 2B). Reduced flows resulting from catchment developments upstream lead to marked changes in the structure of riverbeds,[45] with prolonged low flows and decreased frequencies of high flows, resulting in a significant accumulation of sediments that have become colonized by vegetation.[71]

Table 1. Number of invasive alien plant species of different growth forms in the riparian zones of South Africa's major biomes. Alien species with over 30 records in the SAPIA[†] database were included in the analysis; of these, species with over 20 records in a biome were selected for that biome.

Biome	Riparian specialist aliens					Riparian and terrestrial aliens						
	G	H	S	ST	TT	G	H	C	S	SS	ST	TT
Fynbos	1	0	2	1	5	1	0	0	6	0	6	8
Karoo*	1	0	2	2	4	0	0	0	3	0	2	4
Grassland	1	1	3	1	10	0	8	2	10	0	7	11
Savanna	3	1	5	1	8	0	4	2	13	2	5	12
Forest	0	1	0	0	0	0	0	1	3	0	2	6

[†] Southern African Plant Invaders Atlas.
*Succulent and Nama karoo combined.
G = grass, H = herb, C = climber, S = shrub, SS = succulent shrub, ST = short tree (<10 m), TT = tall tree.

The later successional riparian woodland is dominated by a variety of indigenous tree species, including several *Acacia* species, *Combretum erythrophyllum, Ficus sycomorus, Lonchocarpus capassa, Syzigium guineense* and *Kigelia africana.*[68] *Phragmites australis* reed beds are also common features within the main and secondary river channels in lowveld savannas.[72]

Arid areas

Riparian woodlands occupy the main drainage lines of the arid interior. These habitats are naturally unstable and are subject to unpredictable flooding events, with consequent high levels of disturbance and soil movement.[73] The resultant destruction of vegetation and deposition of silt makes them vulnerable to invasion by alien plants.[74] Taxa from many different plant communities occur in the drainage lines, with the taller woody species, such as *Acacia karroo,* being most prominent (Fig. 2C). The deep sandy alluvium provides a suitable environment for many annual taxa.[73] In the succulent karoo there is an abrupt change in vegetation structure from dwarf succulent shrubland to riverine woodland on the banks of large drainage lines,[75] with *Tamarix usneoides* often the dominant indigenous riparian tree species present.[76]

Degradation in South African riparian vegetation

Impacts of physical and hydrological changes

Riparian zones in South African rivers have undergone much degradation as a result of human activities.[77,78] In common with most other developed or developing regions of the world, extensive dam construction in the upper rivers and abstraction of water for irrigation has reduced flows and altered the riparian habitat.[16,17,79]

The recent national spatial biodiversity assessment of mainstem rivers (including riparian zones) revealed that Gauteng province has no intact mainstem rivers remaining and very few mainstem rivers survive intact in the Western Cape, Eastern Cape and Free State provinces. The results reflect the present state and demand for water in these provinces, where most or all of the major rivers are impounded.[81] Impoundments affect riparian vegetation via reductions in flows and alterations to the flow variability. These changes alter erosion and deposition processes and impact on the widths of channels and riparian corridors.[16,17] In arid regions an increase in soil salinity in the floodplains may result from irrigation practices.[79]

In common with many regions of the world, agricultural development has occurred along alluvial floodplains in South Africa, with the removal of riparian vegetation to maximize the area of high productivity under cultivation.[11,78,82] Cultivation is likely to increase soil erosion rates in the catchment area, leading to sediment accumulation or movement in the riparian zones, thus further degrading riparian ecosystems. Other impacts on riparian vegetation recorded elsewhere, such as grazing and trampling by livestock[12,83–85] also take place in South African river ecosystems,[78] as livestock tend to congregate there during the dry season.[86] Additional human-related disturbances that have occurred in some river systems include eutrophication or pollution resulting from adjacent land-use[9,82,87] and the planting of exotic forestry species.[13,88]

Human-related disturbances further exacerbate the natural susceptibility of riparian ecosystems to invasion by alien plants, for example, through the provision of transformed habitat for colonization, the creation of unsuitable conditions for indigenous riparian species and the provision of alien propagules from gardens adjacent to riverbanks.[89]

Impacts of invasive alien plants

South Africa has a long history of problems, rating amongst the worst in the world, associated with invasion by alien plants.[90] Although the full extent of invasion by alien plants in riparian zones countrywide has not been documented, regional information indicates that the proportion of rivers invaded is likely very high as riparian zones are among the most densely invaded habitats in all biomes (Fig. 3) and many alien species spread along watercourses.[91,92] In the summer rainfall area riparian zones are extensively invaded, with 50% of all woody alien species being recorded along river corridors, despite their relatively small land surface area.[93] Hood and Naiman[15] compared the invasibility of riparian plant communities high on riverbanks with those on the channel floors of four rivers in the Kruger National Park. They found that three times more alien species occupied the floors than the banks of the river. The more frequently disturbed riparian habitats appear to offer more opportunities for invasion by alien plant species. In the arid area, naturally disturbed drainage line, river bank and floodplain habitats generally support more aliens than undisturbed terrestrial habitats.[74]

An analysis of the South African Plant Invaders Atlas database (SAPIA)[25] indicates that alien invaders of riparian zones are mostly woody species (Table 1). The most prominent riparian specialist alien invaders are usually tall (>10 m) trees, whereas aliens that invade both riparian zones and the surrounding landscape may be shrubs or short and tall trees (Table 1). Of the ten most frequent alien invaders of riparian zones, five are tall trees and only one is non-woody: the giant reed *Arundo donax* (Table 2, Fig. 3D). *Melia azedarach* has the widest distribution, followed by *Salix babylonica* and *Ricinis communis,* but *Salix* and *Acacia mearnsii* are the most frequently recorded species (Table 2).

Invasion by alien trees and shrubs has had a large negative effect on riparian vegetation throughout the country.[91] In the winter and all-year rainfall area, species of Australian *Acacia* (e.g. *Acacia mearnsii, A. longifolia* and *A. saligna*) and *Eucalyptus* (especially *E. camaldulensis*)[94] transform riparian vegetation, altering riparian ecosystem functioning. The principal alien invaders in riparian zones of the summer rainfall region are trees, such as *Acacia* species (especially *A. mearnsii* and *A. dealbata*), *Salix babylonica* and *Melia azedarach,* and shrubs, including *Ricinus communis, Sesbania punicea, Solanum mauritianum, Lantana camara* and *Chromolaena odorata* (Table 2).[95] In arid riparian areas, *Nicotiana glauca* and *Prosopis glandulosa* are the most frequently recorded invaders, but other common species include the trees *Schinus molle, Acacia* species, *Populus X canescens* and *Tamarix* species, the shrub *Atriplex nummularia* and the reed *Arundo donax.*[25] Although biological control agents have been successfully established on some alien species, thus potentially reducing future spread,[96] extensive areas remain invaded.

The effects of alien species in riparian zones include suppression and replacement of indigenous vegetation[91] and increased transpiration and reduction in flows owing to the larger biomass of the alien compared to the indigenous vegetation.[28,90,97,98] Changes to local vegetation structure and composition following invasion alters litter quantity and quality and nutrient cycling regimes.[91,99,100] Local soil erosion increases in areas densely invaded by alien trees,[101] as the ground cover that provides surface stability is excluded by the alien canopy. A further consequence may be a change to the natural fire regime; for example, a decrease in frequency following invasion by less flammable alien species or an increase in intensity caused by flammable aliens altering the vertical fuel structure (e.g *Chromolaena odorata* and *Arundo donax*).[52,102–104]

Invasive alien trees impact on catchment hydrology and sediment yield and thus may affect river geomorphology indirectly via runoff as well as directly where they invade river banks and channels. Sediment yield from a catchment may be particularly high following fires through dense alien stands or plantations,[105–108] with implications for downstream geomorphology.

The degree of erosion or deposition in a watercourse depends on the balance between the erosive force of flow and the erodibility of substrata.[14] Dense stands of tall aliens in the catchment reduce runoff and hence the erosive force of flow, which can shift the system towards one of sediment deposition. Dense stands of alien trees in the catchment may also increase the sediment supply through their influence on fire regime and soil stability as discussed above, thus further exacerbating the impacts on river geomorphology.

Within the flood-prone width of the river, dense alien stands increase flow resistance, dampen turbulence and aid sediment deposition.[5,14] Changes to channel shape may then follow, with the type of change related to the particular geomorphological reach in which the invasion occurs. In some cases, usually in lowland rivers, channels deepen and banks steepen.[4] In less entrenched foothill rivers, alien trees have a damming effect on flow, leading to a widening of the watercourse and the conversion of well-defined rivers into diffuse systems of shallow channels.[5,14] Once the flood waters subside, these channels may be further colonized by alien plants.[109] Isolated alien trees or groups of trees in the channel form obstructions that increase flow vortices around them and may cause local scour of river banks during floods.[14] A risk associated with the development of higher depositional banks under aliens is that rooting depth is less likely to extend below the failure plane of the bank, resulting in more frequent bank slumping.[14,110] In headwater streams, invasion by alien trees may increase the amount of woody debris entering the stream, causing debris dams that potentially may lead to local channel widening.[14] This effect would likely have the highest impact on aquatic ecosystems when short riparian

Fig. 3. Examples of alien plant invasions in riparian zones in South Africa: **A**, dense invasion by *Acacia mearnsii* along a foothill section of the Riviersonderend River in the winter to all-year rainfall area (photograph: D.M. Richardson); **B**, *Salix babylonica* invasion along the Vaal River in the summer rainfall area (photograph: H. Klein); **C**, dense *Prosopis* species invasion along a watercourse in the arid interior (photograph: M. Anderson); **D**, dense invasion by the alien reed *Arundo donax* along the Huis River in the arid interior (photograph: S.J. Milton).

Table 2. The top ten alien invaders of riparian zones in South Africa, in order of decreasing frequency of occurrence in the SAPIA database.

Alien species	Growth form	Predominant distribution (biome/area)	Distribution (No. QDS)*
Salix babylonica L.	Tall tree	Grassland/summer rainfall	475
Acacia mearnsii De Wild.	Tall tree	Grassland and fynbos/summer and winter rainfall	432
Populus X *canescens* (Ait.) J. E. Sm.	Tall tree	Grassland and fynbos/summer and winter rainfall	372
Melia azedarach L.	Tall tree	Savanna/summer rainfall	558
Ricinus communis L.	Shrub	Savanna/summer rainfall	471
Arundo donax L.	Grass	Savanna & karoo/summer rainfall; arid area	377
Acacia dealbata Link.	Tall tree	Grassland/summer rainfall	256
Sesbania punicea (Cav.) Benth.	Shrub	Savanna/summer rainfall	325
Nicotiana glauca R. C. Grah.	Shrub	Karoo/arid area	396
Prosopis glandulosa var *torreyana*/*velutina*	Small tree	Karoo/arid area	412

*Recorded distribution by number of quarter-degree squares occupied.

vegetation, such as grassland or shrubland, is replaced by an alien tree stand.

The global invasion literature indicates that the most damaging alien species transform ecosystems by altering the flow, availability or quality of nutrient resources, and by modifying trophic or physical resources.[92] Many of the alien species that invade South African rivers exert some or all of these influences and thus qualify as 'transformer species'.[92] However, research is needed to understand fully the consequences of many of the alien species that invade riparian zones, especially in regions outside the fynbos biome,[90] as well as potential emerging invader species (e.g. *Casuarina cunninghamiana*) that remain to be studied.

Restoration prospects for alien-invaded riparian zones

While our focus here is to review information pertaining to the restoration of alien-invaded riparian zones and to identify knowledge gaps, it is important to state that river systems are part of the broader landscape and are influenced by the land uses and management operating in the catchment area.[78] Full riparian restoration depends on the management of upland ecosystems throughout the catchment area and successful restoration projects have recognized the importance of re-establishing stream flow regimes.[111] Numerous factors operating in the catchment may limit or even counteract restoration actions in specific reaches. For example, loss of native vegetation in upslope riparian and terrestrial areas limits recolonization by natural dispersal, and may alter stream hydrology and the extent to which historical riparian plant assemblages may be restored.[111]

In larger river floodplain restorations, quantitative hydrological requirements, reference conditions and interdisciplinary partnerships are important.[112] At a catchment scale, modifications to hydrology required to facilitate restoration, such as water releases from impoundments to coincide with the dispersal phenology of key riparian species,[47] needs cooperative interdisciplinary partnerships, as would any required changes to land-use practices. Socio-economic factors place severe limitations on the extent to which a natural flow regime can be regained and large river restoration becomes a compromise.[112,113] Effective restoration requires clear ecological and physical objectives, baseline data on reference conditions and the functional attributes of biotic refugia. Also needed is a commitment to long-term planning, implementation and monitoring, and a thorough understanding of past natural and human-induced changes to the hydrological and geomorphological regimes.[69,114,115] The breadth of disciplines essential to the restoration of stream corridors is daunting, with many associated areas of fundamental research.[113]

The impacts of alien clearing on geomorphology and riparian vegetation recovery

WfW has been operating in South Africa since 1995 to conduct and coordinate alien plant management so as to safeguard water production and quality.[31,90] Control has been implemented using appropriate mechanical, chemical and biological methods. Despite ten years of implementation, no research has been published on the consequences of mechanical and chemical alien control methods on vegetation recovery, and little monitoring has been done to indicate whether post-clearance restoration actions are required to accelerate recovery. Furthermore, no studies have tested the potentially negative effects of herbicides on amphibians and other fauna.[115] Historically, all alien trees and shrubs were felled and stumps of coppicing species treated with herbicide. Felled material was either removed from the river corridor or burnt in slash stacks. Larger trees (>200 mm basal diameter) are now killed by frilling or ring-barking as felling and timber removal is too expensive (Working for Water managers, pers. comm.). The biophysical impacts of standing dead trees, and later fallen trees, in the riparian zones have not yet been assessed.

The longer-term success of alien clearing operations depends to a large extent on the degree of recovery of indigenous vegetation. Without good vegetation recovery, ecosystems are prone to re-invasion by the same alien or secondary alien species.[116,117] Alien species quickly colonize after a disturbance to dominate the early succession and alter the establishment conditions.[118] Conversely, promoting indigenous species, through increased propagule pressure, may constrain invasion by alien plants.[119] Thus riparian sites must often be revegetated after alien control to avoid reinfestation or invasion by other alien species.[120]

At sites where alien species have formed closed stands and the indigenous vegetation has been eliminated, natural recovery depends to a large degree on propagule establishment, either from local soil-stored seed banks or by dispersal into the area from intact vegetation patches in the catchment area. If natural recruitment potential is to be maximized, it is imperative that the initial and follow-up clearing treatments do not counteract it. For instance, indigenous seedlings should be protected from drift of foliar herbicide targeting alien seedlings and coppice. If river banks are artificially raised owing to the influence of an alien stand on river geomorphology, the indigenous seed banks are likely to be buried underneath the accumulated sediments and will not germinate until the sediments have been eroded away in floods. At such sites it may be appropriate to fell and burn the alien material *in situ* in order to remove any alien surface roots and facilitate the erosion process.

In the control of alien acacias and other aliens that accumulate large stores of hard-coated seeds in the soil, burning is a useful method for reducing their seed bank via triggering mass germination and mortality.[121,122] However, a burn treatment, which avoids the initial expense of felling, may not be successful as coppicing may occur, making follow-up control more difficult.[123] A study that compared different methods of integrated alien control suggested that some herbicide application methods are more harmful to the recovery of indigenous vegetation than others. However, it is often difficult to separate the effects of previous land use, the impacts of the invaders themselves and the control methods on vegetation recovery.[124]

Factors limiting the restoration of riparian zones and potential interventions

Restoring plant species diversity to degraded riparian ecosystems hinges on an understanding of the processes influencing diversity levels and the pathways by which plant species colonize sites.[125] Downstream dispersal of vegetative propagules or seeds by water from intact riparian vegetation patches is one important pathway.[47] However, seed dispersal by wind or animal vectors along the riparian corridor and from adjacent terrestrial vegetation also plays a role,[49] as may *in situ* soil-stored seed banks. Propagule pressure from dispersal will be low in highly transformed catchments where few natural refugia remain; to counter this, propagules should be supplied, or else nodes of riparian species established to promote future dissemination of propagules.

Many processes serve to bury seeds in riparian soils: flood waters disperse seeds across floodplains and bury them under sediments.[125] Additional processes, such as animal burrowing and seed-burial, soil drying and cracking, may bury seeds. Many buried seeds have long viability and may remain dormant until suitable germination conditions develop.[126] However, little is known about the importance of soil seed banks in South African riparian ecosystems, as is the case for riparian ecosystems worldwide.[127] Soil-stored seed banks are an important source of regeneration in vegetation subject to frequent disturbances, such as fires, and are likely to play a role in riparian vegetation dynamics. For example, Richter and Stromberg[125] found a viable native seed bank in riparian areas dominated by the alien *Vinca major.* In fire-prone fynbos vegetation, soil seed banks confer restoration potential following several decades of dense alien invasion.[128,129] On the other hand, many of the most problematic invader species have persistent seed banks, hindering restoration efforts; for example, *Acacia mearnsii,*[123] *Solanum mauritianum*[67] and *Chromolaena odorata.*[130]

The flood disturbance process is responsible for maintaining high biodiversity by creating spatial and temporal heterogeneity and allowing co-existence of plants with a variety of life-history strategies.[125] Indigenous riparian species that recruit episodically following a flooding event, such as cottonwood in North America, may be restored to an area only if water releases from impoundments mimic these events.[18] This may be done in high rainfall years to minimize the impacts on other water users. Currently, there is no information on the hydrological regimes required for establishment by South African riparian species.

Poor recruitment of riparian species following alien plant clearing may relate to unsuitable germination or establishment conditions. Rowntree[14] noted that vegetation may establish only in areas with a stable or accreting bed. Thus a more natural river geomorphology may have to re-establish before riparian vegetation can colonize. Local site conditions are unlikely to be optimal for the establishment of all species and it may be necessary to apply proactive management to increase the survival of seedlings.[131]

Transformer alien species (e.g. *Acacia mearnsii*) alter soil chemistry and may promote the colonization of uncharacteristic indigenous species or secondary alien species. Where soil nitrogen levels are increased following *Acacia* invasion, grasses have an enhanced competitive advantage and may become dominant after alien clearance.[100]

A recent study in headwater streams of the fynbos winter rainfall area, found that in riparian zones cleared of dense alien thickets, regeneration by indigenous riparian trees and shrubs was poor compared with alien species, suggesting that the recovery phase may be protracted.[54] Similar results were found post-clearance in savanna and grassland reaches on the Sabie River, where new dominant invasive species (e.g. *Solanum mauritianum*) replaced the previous dominants (*Eucalyptus grandis*).[67]

Propagule supply may limit recruitment of some indigenous species, whereas for others the post-clearance environment may not be suitable for germination or establishment. Increased survivorship of indigenous species can be achieved where aliens are controlled, for example by careful herbicide application[132] or manual clearing. Seed regeneration of fynbos closed scrub species was found not to be disturbance-triggered, as established seedlings were found mostly on stable banks and rock fractures.[54] More recently, it was noted that these species germinate along the channel margins during low base flows (P.M. Holmes, pers. obs., 2005), suggesting that germination is not a limiting factor, but that safe establishment sites might be. In degraded winter and all-year rainfall riparian zones, re-introducing indigenous pioneer woody and herbaceous species may facilitate recovery of fynbos closed scrub vegetation. In summer rainfall grassland areas, the sowing of grasses following alien tree control promoted riparian vegetation recovery.[13]

Information gaps requiring further research

Future studies should investigate further the effects of different alien clearing methods on riparian vegetation recovery, particularly in relation to the riparian vegetation type and river hydrology and geomorphology. For instance, are the higher costs of felling and removing large trees from the riparian zone justified in terms of better long-term recovery in riparian ecosystems? Does a slash burning treatment facilitate or retard the re-establishment of indigenous riparian species? Fire is one of the important drivers of plant community structure, yet our understanding of its effects on different riparian ecosystems is poor.

A better understanding of dispersal, seed bank dynamics and recruitment in riparian species would greatly facilitate the planning and execution of restoration activities. How important are seeds compared with vegetative propagules in the colonization of disturbed riparian sites in the different climatic areas of South Africa? In relation to the contribution from seeds, how does seed fall interact with the flow regime, and to what extent does the timing and magnitude of extreme events result in preferential propagule input, transport and establishment?[127] Do any key riparian species require high flows for dispersal and establishment? How important are riparian soil-stored seed banks in vegetation dynamics, and does the depth distribution of seed banks change in different geomorphological situations?

In headwater systems, the focus for restoration may be on local conditions for the establishment of riparian species establishment. However, in foothill or floodplain systems where most rivers are affected by dams and water abstractions, changes to the flow regimes and fluvial dynamics also will need to be considered,[111] and possibly manipulated to facilitate the establishment of key riparian species.

Table 3. Descriptions of hypothetical case study sites.

Case study number and climatic area	River segment	Reference vegetation	Assessment of riparian vegetation and catchment condition			
			Case study reach	Upstream reaches	Downstream reaches	Catchment area
Winter to all-year rainfall	Foothill	Fynbos closed scrub	Closed canopy (>75% cover) alien tree stand of *Acacia mearnsii*; very sparse fynbos scrub understorey (Fig. 3a)	Fynbos closed scrub with light (<25% cover) alien presence	Various levels of alien *Acacia* invasion; some patches of fynbos closed scrub	Largely uninvaded; some light *Pinus* and *Hakea* invasion
Winter to all-year rainfall	Foothill	Fynbos closed scrub	Closed canopy mixed alien stand of *Acacia* & *Eucalyptus* species; no indigenous perennials	Dense (>50% cover) to closed alien stands; sparse occurrence of indigenous species	Closed canopy mixed alien stands; no indigenous perennials	Largely transformed catchment area comprising cultivated lands, forestry & dense mixed alien stands
Summer rainfall	Lowland	Mixed riparian woodland	Dense alien tree stand (*Melia* & *Acacia* species) with some indigenous tall trees and dense mixed alien-understorey; sparse indigenous understorey (Fig. 3b)	Various levels of alien tree & shrub invasion; some patches of intact riparian woodland	Various levels of alien tree & shrub invasion; some patches of intact riparian woodland	Adjacent savanna vegetation largely uninvaded; some alien shrub invasion higher up in catchment area; water abstraction in upper catchment
Summer rainfall	Mountain stream	Grassland	Closed canopy mixed alien stand of *Acacia*, *Salix* and *Populus* species; sparse indigenous understorey (Fig. 3c)	Various levels of alien tree invasion; some patches of intact riparian grassland	Closed canopy mixed alien stand of *Acacia, Salix* and *Populus* species; sparse indigenous understorey	Largely transformed catchment area comprising *Pinus* and *Eucalyptus* plantations & dense mixed alien stands
Arid area	Lowland	*Acacia karroo* woodland	Dense canopy alien tree stand of *Prosopis* species with a moderate (25–50% cover) *Nicotiana* understorey (Fig. 3d)	Dense canopy alien tree stand of *Prosopis* species with a moderate (25–50% cover) *Nicotiana* understorey	Dense canopy alien tree stand of *Prosopis* species with a moderate (25–50% cover) *Nicotiana* understorey	Extensive alien tree and shrub invasion along the floodplain and drainage lines; widespread ground water abstraction
Arid area	Foothill	*Acacia karroo* woodland	Closed canopy stand of the alien reed *Arundo donax*; sparse indigenous perennial species (Fig. 3e)	Largely indigenous *Acacia* woodland	Various levels of alien reed and shrub invasion; some patches of intact riparian woodland	Largely untransformed catchment area; light to moderate invasion by alien shrubs and trees; some ground water abstraction

Hypothetical case studies

The strategic restoration of alien-invaded riparian zones requires an understanding of the factors that increase susceptibility to invasion as well as the potential barriers to natural recovery (from reach to catchment scales). In selecting six hypothetical examples of typical invasion scenarios from different climatic areas in South Africa (Table 3), we consider these factors and suggest strategies for restoration based on the information currently available (Table 4).

Winter and all-year rainfall areas

The two hypothetical case studies (1 & 2; Tables 3, 4) contrast local reach invasion in a relatively pristine catchment area with that in a highly alien-transformed catchment area. Strategic interventions for case study 1 relate mainly to actions at the reach level, whereas those for case study 2 also require catchment-level interventions if restoration is to be optimized (Table 4). In relatively pristine catchment areas, interventions that facilitate recovery of native species generally should be sufficient. However, in highly transformed rivers and catchment areas, native riparian species should be actively re-introduced, both to suppress alien re-invasion and to promote recovery of fynbos closed scrub vegetation.

Summer rainfall areas

The hydrological regimes of most summer rainfall rivers have been altered by impoundments and water abstraction both in mountain and lowland segments. As demand for water is unlikely to fall, riparian restoration must operate within these limitations (Table 4: case study 3). Alien trees also have a large effect in reducing flows, particularly in the higher altitude grassland vegetation (case study 4). The reduced flows in both examples result in increased sediment deposition along river channels. This cannot easily be remedied in lowland savanna rivers, but in the mountain streams removal of alien trees should promote the development of a more natural geomorphology. To facilitate vegetation recovery at highly degraded grassland riparian sites, the area should be sown with indigenous grasses once alien cover has been significantly reduced. This action will help to prevent re-invasion by alien species. Nodes of key riparian species should be re-established in degraded catchments to facilitate future propagule dissemination.

Arid areas

The potential for riparian restoration will be limited by the extent to which land uses in the catchment area have altered the natural hydrological regime. Removal and control of alien trees along watercourses and drainage lines should make a beneficial difference to the hydrological regime and allow some recovery of indigenous vegetation. Removal of livestock from riparian zones will also be necessary to facilitate its recovery. In extensively invaded catchments (Table 4: case study 5), as for all climatic areas, clearing should be planned from upstream to downstream segments in order to minimize re-invasion potential. Where indigenous propagule pressure is anticipated to be low, nodes of key riparian species should be established to speed up the rate of riparian vegetation recovery. Where the alien reed, *Arundo donax,* invades, changes to local geomorphology and vegetation flammability may occur (case study 6). The original characteristics may only be reinstated after the removal and control of this vigorous alien species.

Table 4. Strategic interventions required for restoration using case study examples (see Table 3).

Case study	Barriers to restoration at the catchment scale	Barriers to restoration at the reach scale	Interventions required
1.	*Hydrological*: none *Geomorphological*: none *Biological*: potential future alien expansion	*Hydrological*: increase in local water usage by vegetation *Geomorphological*: local accumulation of sediments under alien stand *Biological*: dominance of alien species; local depletion of native propagules & abundance of alien propagules	• Clear alien stand • Poison stumps to kill alien trees; burn slash on soil surface to loosen roots & accumulated sediments to facilitate natural erosion • Burn slash to flush (kill & germinate) alien seed bank • Promote native species establishment from seed bank & adjacent sources by removing alien recruits • Control alien species in the broader catchment area & introduce biological control agents where not present
2.	*Hydrological*: runoff reduction owing to high water usage plantations & alien stands *Geomorphological*: increased erosion and sediment transport into rivers from cultivated lands *Biological*: dominance of alien species & reduced native propagule sources	*Hydrological*: increase in local water usage exacerbates effect of reduced flows from catchment *Geomorphological*: local accumulation of sediments under alien stands exacerbated by reduced flows & increased sediment transport; heightened banks & more confined channel *Biological*: dominance of alien species & propagules; widespread depletion of native propagules	• Clear local & adjacent alien stands • Clear aliens in the broader catchment area & maintain follow-up control • Phase out all high-water using land-uses with marginal economic benefits • Improve cultivation practices in the catchment area to minimize soil loss • In riparian zones, poison stumps to kill alien trees; burn slash on soil surface to loosen roots & accumulated sediments & thus facilitate natural erosion • Clear local & adjacent alien stands; kill larger trees standing • Re-introduce pioneer riparian scrub species by seed once alien cover has been significantly reduced • Establish nodes of climax riparian scrub species using cuttings, or other suitable methods, to act as sources for future propagule dissemination • Protect any native species recruits & maintain follow-up control of alien recruits • Control alien species in the broader catchment area (from top of catchment down) & introduce biological control agents where not already present
3.	*Hydrological*: reduced flows owing to water abstraction *Geomorphological*: reduced erosive force of water and increased deposition *Biological*: potential future alien expansion	*Hydrological*: reduced flows *Geomorphological*: increased sediment deposition along channel floors owing to reduced flows *Biological*: dominance of alien species; local reduction in native propagules & high abundance of alien propagules	• Amending reduced flows is beyond the scope of restoration intervention as demand for water is unlikely to fall • Release periodic, synchronized large flows from dams in high rainfall years to partially restore geomorphology • Kill large alien trees standing & clear alien understorey shrubs without damaging surviving indigenous species • Maintain regular alien follow-up control to prevent re-invasion • Control alien species in the broader catchment area & introduce biological control agents where not present
4.	*Hydrological*: reduced flows owing to high water usage plantations & alien stands *Geomorphological*: reduced erosive force of water & increased deposition *Biological*: dominance of alien species & reduced native propagule sources	*Hydrological*: increase in local water usage by aliens exacerbates effect of reduced flows from catchment *Geomorphological*: potential narrowing of channel & increased sediment deposition under aliens *Biological*: dominance of alien species & propagules; widespread depletion of native propagules	• Clear local & adjacent alien stands • Clear aliens in the broader catchment area & maintain follow-up control • Phase out all high-water using land-uses with marginal economic benefits • Promote erosion of sediments deposited under alien trees by burning alien slash in zones of accumulation • Clear local & adjacent alien stands; kill larger trees standing • Sow indigenous grasses once alien cover has been significantly reduced • Establish nodes of key grassland riparian species using cuttings, or other suitable methods, to act as sources for future propagule dissemination • Protect any native species recruits & maintain follow-up control of alien recruits • Control alien species in the broader catchment area & introduce biological control agents where not yet present
5.	*Hydrological*: reduced frequency, duration & volume of surface water flows *Geomorphological*: increased sediment deposition *Biological*: dominance of alien species & reduced native propagule sources	*Hydrological*: increase in local water usage by aliens exacerbates effect of reduced flows from catchment *Geomorphological*: local accumulation of sediments under aliens; widening of water course *Biological*: dominance of alien species & propagules; widespread depletion of native propagules	• Clear local & adjacent alien stands • Clear aliens in the broader catchment area & maintain follow-up control • Rationalize the extent of ground water abstraction to prevent wastage & promote ecologically sound land-use practices • Promote erosion of sediments deposited under alien trees by burning non-utilizable alien slash in zones of sediment accumulation • Clear local & adjacent alien stands • Establish nodes of key arid riparian species using cuttings, or other suitable methods, to act as sources for future propagule dissemination • Protect any native species recruits & maintain follow-up control of alien recruits • Control alien species in the broader catchment area & introduce biological control agents where not present
6.	*Hydrological*: reduced flows owing to ground water abstraction *Geomorphological*: increased sediment deposition *Biological*: potential future alien expansion	*Hydrological*: reduced flows *Geomorphological*: slowing of flow, local accumulation of sediments & widening of channel around *Arundo* *Biological*: Local exclusion of indigenous species by *Arundo*; increased flammability	• Rationalize the extent of ground water abstraction to prevent wastage & promote ecologically sound land-use practices • Clear *Arundo* to promote erosion of accumulated sediments • Remove or burn flammable alien material off site • Protect any native species recruits & maintain follow-up control of alien recruits • Control alien species in the broader catchment area & introduce biological control agents where not present

Conclusions

We have outlined a framework of strategic interventions to promote the recovery of riparian vegetation following several alien plant invasion scenarios. These are largely untested and based on the best available information. The recommended framework is hierarchical, as it identifies barriers to restoration at the broader catchment and local reach scales. These barriers include abiotic (hydrological and geomorphological) and biotic factors. It is important to acknowledge that interventions at the reach scale may have limited success if potential barriers at the catchment scale cannot be addressed.

Much research remains to be done to inform better the restoration framework presented here. We need to explore further the relative importance of propagule supply and establishment conditions in mediating vegetation recovery. In particular, we need to know the importance of dispersing vegetative propagules relative to seeds in recruitment and the potential of residual soil-stored seed banks for initiating vegetation recovery in the different riparian ecosystems. The role of abiotic factors in riparian vegetation recovery has also not been fully explored for all the climatic areas in South Africa.

On a practical level, more research is needed on the impacts of different alien species and clearing treatments on riparian vegetation recovery. Experience suggests that in highly transformed catchments, the re-introduction of riparian species is required to promote recovery and prevent re-invasion. However, such interventions are unlikely to be widely implemented unless the cost: benefit ratios are deemed acceptable.

Thanks are due to Lesley Henderson for access to the South African Plant Invaders Atlas database, Tony Rebelo for commenting on the manuscript and Mao Angua for producing the map. Patricia Holmes was supported by the National Working for Water Project. Patricia Holmes, Karen Esler and David Richardson acknowledge support from the DST-NRF Centre of Excellence for Invasion Biology, University of Stellenbosch.

Received 12 September. Accepted 18 November 2005

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