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Vulnerability of riparian zones to invasion by exotic vascular plants

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Key words: Biological invasions, Exotic species, Kruger National Park, Riparian zones, South African rivers

Abstract

We compared the invasibility of riparian plant communities high on river banks with those on floodplain floors for four South African rivers. Analyses of abundant and significant riparian species showed that the floors have 3.1 times more exotic plants than the banks. The percent exotics ranges from 5% to 11% of total species richness for the banks, and from 20% to 30% for the floors. Species richness and percent exotics are negatively correlated for the banks, but not correlated for the floors.

Despite great differences in climate, species richness, and landuse history, the percentages of exotic plants in three rivers in the Pacific Northwest of the USA and one river in southwestern France are similar to those in South Africa (24-30% vs. 20-30%, respectively). Furthermore, the high proportions of exotic species in these riparian plant communities are comparable to those reported for vascular plant communities on islands. We conclude that the macro-channel floor regions of the riparian zones of South African rivers are highly vulnerable to invasion by exotic vascular plants.

Introduction

Riparian zones associated with drainage networks are important landscape elements (Malanson 1993; Naiman & Décamps 1990, 1997). Riparian vegetation controls the flow of water, nutrients, and sediments into streams (e.g., Décamps 1993; Junk et al. 1989; Forman & Godron 1986; Peterjohn & Correll 1984); it serves as a landscape corridor facilitating the movement of organisms (DeFerrari & Naiman 1994; Pysek & Prach 1994; Baker et al. 1993; Forman & Godron 1986); and it contains a disproportionately high species richness (Murray & Stauffer 1995; Naiman et al. 1993; Carothers et al. 1974).

One explanation for the high plant species richness of riparian zones is that regular floods decrease the strength of competitive interactions, periodically return portions of the riparian community to early successional stages, and create a complex and shifting mosaic of landforms that provides a diversity of microhabitats (Pollock et al. 1998; Décamps & Tabacchi 1992; Gregory et al. 1991; Wissmar & Swanson 1990; Kalliola & Puhakka 1988).

The same factors supporting high plant species richness in riparian habitats may also increase susceptibility to invasion by exotic species (Pysek & Prach 1994; Henderson & Wells 1986). Disturbance is thought to facilitate successful invasions by exotic species for some of the same reasons that it maintains native species diversity. Anthropogenic disturbances may introduce exotic species to riparian zones, and natural disturbances may facilitate their spread throughout the drainage network. The availability of moisture and the dispersal of propagules by water may be alternative or synergistic causes of the invasibility of riparian zones.

Given this foundation for an expectation of riparian invasibility, and that exotic species have been known to have dramatic effects on ecosystem processes (Ramakrishnan & Vitousek 1989; Vitousek 1986; Graf 1978) there is cause for concern about the extent and effects of exotic invasions on riparian systems. Unfortunately, there are few comparisons of different ripar-

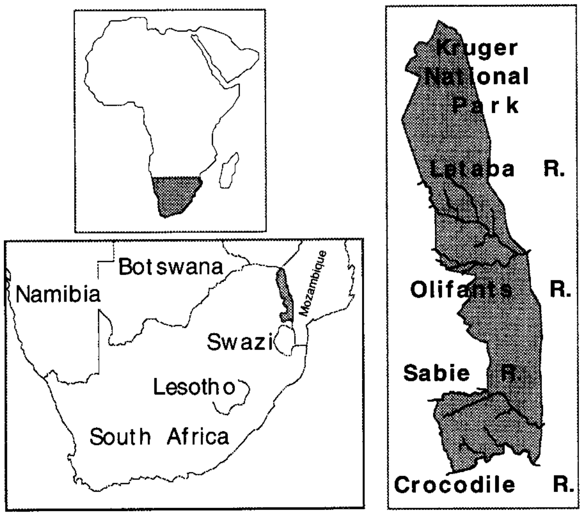

Figure 1. Location of Kruger National Park and the Letaba, Olifants, Sabie and Crocodile rivers.

ian systems or of riparian systems with upland systems to support or refute the hypothesis of high riparian invasibility. The objective of this paper is to reduce this deficiency by describing the pattern of invasibility within the riparian zones of four South African rivers. The riparian zones are stratified into two geomorphic units which differ in riverine proximity and influence, and in species richness of exotic vascular plants. The pattern of invasibility which we describe supports arguments that riparian zones are indeed highly vulnerable to invasion by exotic vegetation.

Sites and methods

South Africa

Data on South African riparian zones are from reports prepared for Kruger National Park (Bredenkamp & Van Rooyen 1993a–c; Bredenkamp et al. 1991) on the Crocodile, Letaba, Olifants, and Sabie rivers (Figure 1). These studies were designed to provide baseline data for monitoring environmental impacts on riparian vegetation and channel structure resulting from upstream water extraction by agricultural, silvicultural and industrial consumers. The reports characterized the riparian plant communities through stratified random sampling with square plots of 200 m^2. Stereo aerial photographs (1:10 000 scale) were used to stratify the study areas according to physiographic structure recognizable in the photographs. The number of survey plots ranged from 101 to 160 per river with the frequency of sample plots ranging from one per 0.5 km to one per 1.6 km of river length.

Study areas of the Sabie and Crocodile rivers consisted of the portions of the rivers which lie within Kruger National Park. These river segments were 106 and 119 km long for the Sabie and Crocodile, respectively. The rivers originate in the Drakensberg Mountains west of the park and flow eastward through malelane-mountain bushveld followed by mixed *Combretum-Acacia* veld (Sabie) or mixed *Combretum* veld (Crocodile) toward Mozambique where they join the Komati River. Rainfall is seasonal with most falling between November and March. The mean annual precipitation in the study areas ranges from 600 to 700 mm; the elevation of the study areas ranges from 400 m upstream to 200 m downstream. The major land use upstream from the park includes agriculture, forestry, and urban and dense rural settlement. Upstream water extraction substantially reduces the mean annual flow of the rivers (van Coller & Rogers 1995; Bredenkamp & Van Rooyen 1993a; Bredenkamp et al. 1991). Significant human disturbance dates only to the late 19th Century (Henderson & Wells 1986).

Study areas of the Letaba and Olifants rivers also consisted of approximately 100 km lengths which cross through Kruger National Park. They differ from the Sabie and Crocodile rivers in that they flow through red bushwillow-mopane veld and knobthorn-maroela veld. Mean annual precipitation for both rivers within the park ranges from 400 to 500 mm; elevation ranges from 300 m upstream to 200 m downstream. Landuse upstream from the Letaba and Olifants rivers, and its effects on the rivers, is similar to that of the Sabie and Crocodile rivers (Bredenkamp & Van Rooyen 1993b, c).

Rivers in Kruger National Park occupy large, deeply incised, mixed bedrock-alluvial *macro-channels* which consist of a *macro-channel bank* on either side of the *macro-channel floor* (van Coller et al. 1997; van Coller & Rogers 1995). Along the macro-channel floor are one or more active channels which carry water throughout the year, as well as seasonal channels (Figure 2). The macro-channel floor has relatively shallow slopes, an elevation less than 2 m above the channel and is frequently disturbed by seasonal floods and associated routing of alluvial sediments, and by browsing by large animals. In contrast the macro-channel bank has relatively steep slopes, ranges in elevation from about 2 to 10 m above the channel, is rarely disturbed by floods, contains no alluvium, but

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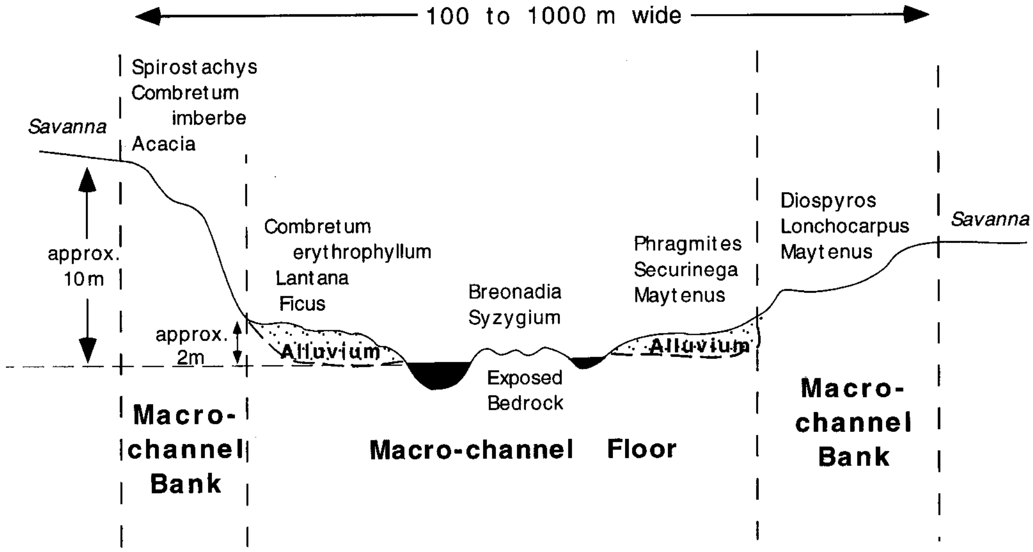

Figure 2. Generalized cross-section of rivers in Kruger National Park with dominant riparian plant species.

does receive substantial browsing (Naiman & Rogers 1997; van Coller et al. 1997). Plant species high on the macro-channel bank typically occur in the surrounding savanna vegetation but occur in greater abundance in the riparian zone. Species lower on the bank and on the macro-channel floor are found only in the riparian zone.

Plant communities in the riparian zones of the Crocodile, Letaba, Olifants, and Sabie rivers were assigned to either the macro-channel bank or the macro-channel floor riparian zones by comparing species lists of each plant community to the species associated with the diagnostic geomorphic features of the two large-scale riparian zone categories (Appendix A of van Coller & Rogers 1995). Invasive species were identified by G. Zambatis, a botanist with the Skukuza Museum of the Kruger National Park (personal communication), and by reference to various reports on the rivers of Kruger National Park (Bredenkamp & Van Rooyen 1993a–c; Bredenkamp et al. 1991), and to several floras and checklists (Macdonald & Gertenbach 1988; Mabberley 1987; Henderson & Wells 1986; Wells et al. 1986; Bond & Goldblatt 1984; Fabian & Germishuizen 1982; Compton 1976; Dyer 1975).

While the collective descriptions of plant communities are extensive, they are not comprehensive. Some plant species were omitted from community descriptions but found in appended species lists which contained all of the riparian species encountered during the vegetation surveys. These species lists did not distinguish macro-channel bank species from macro-channel floor species. Thus, our analysis of patterns of invasibility are limited to species listed in the plant community descriptions. Species listed in the community descriptions are described as ‘dominant’, ‘prominent’, ‘conspicuous’, ‘constantly present’, ‘diagnostic’, etc. Therefore, we assume that those species in the appended species lists, but omitted from the community descriptions, are uncommon and sparse. Thus, our analyses pertain only to those species which are evidently abundant and well-established, and therefore more likely to be ecologically significant. Exotic species which are abundant enough to be mentioned in the community descriptions are inferred to be relatively invasive species, since further recruitment to the local population has occurred without human intervention (Usher et al. 1988). Certainly, exotic species which are presently uncommon and sparse could become invasive in the future under changed climatic conditions or disturbance regimes; however, they could also simply go locally extinct due to the vagaries of small population size. This paper focuses on presently abundant exotics rather than potentially abundant exotics.

Patterns of species richness and exotic invasion in the South African rivers are compared to patterns previously described for several rivers located in biogeographically and historically different areas: three rivers in the Pacific Northwest of the USA and one in southwestern France (Figure 3). The studies used for comparison are DeFerrari & Naiman (1994) for the Dungeness and Hoh rivers (USA), Planty-Tabacchi

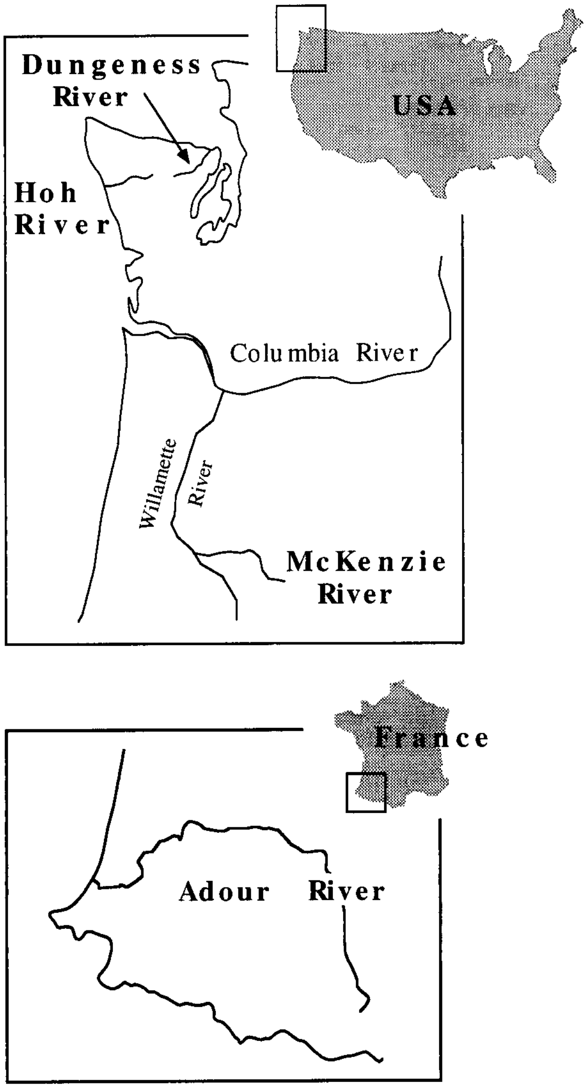

Figure 3. Location of the Adour, Hoh, Dungeness and McKenzie Rivers.

et al. (1996) for the McKenzie River (USA), and Tabacchi et al. (1990) and Planty-Tabacchi et al. (1996) for the Adour River (France).

Northwestern USA

The Dungeness and Hoh rivers are located on the Olympic Peninsula (Washington, USA). Mean annual precipitation in the Hoh watershed ranges from 2500 to over 5000 mm, while in the Dungeness watershed it ranges from 500 to 2000 mm (Henderson et al. 1989). The Hoh River flows ~ 70 km from the Olympic Mountains to the Pacific Ocean through a forested watershed dominated by *Abies amabilis* (Dougl.) Forbes, *Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong.) Carr. and *Thuja plicata* Donn. The Dungeness River flows over 40 km from the Olympic Mountains to the Strait of San Juan de Fuca through a forested watershed dominated by *Abies lasiocarpa* (Hook.) Nutt., *T. heterophylla* and *Pseudotsuga menziesii* (Mirb.) Franco. Elevation in both watersheds ranges from over 1700 m in the upper reaches to sea level at the mouths.

The McKenzie River is located in western Oregon (USA) and flows 350 km from the Cascade Mountains (1300 m elevation) to the Willamette River (200 m elevation). Mean annual precipitation in the watershed ranges from 1000 to 2000 mm. The upper reaches flow through mostly pristine riparian forests, while the lower reaches are mainly surrounded by commercial forests and agriculture. The dominant tree species are *T. heterophylla* , *P. menziesii*, *T. plicata*, *Alnus rubra* Bong., *Populus trichocarpa* T. & G. ex. Hook. and *Fraxinus latifolia* Benth. (Planty-Tabacchi et al. 1996). The primary land uses in the McKenzie, Dungeness and Hoh watersheds are wilderness protection and timber harvest. Timber harvest dates only from the late 19th Century (Felt 1985).

France

The Adour River in southwestern France flows 335 km from the Pyrénées (2200 m elevation) to the Atlantic Ocean. Mean annual precipitation in the watershed ranges from 850–2000 mm (Billen et al. 1995). The riparian vegetation is dominated by *Alnus glutinosa* (L.) Gaertner, *Salix alba* L., *S. triandra* L., *Populus nigra* L., *Acer campestre* L., *Fraxinus excelsior* L., *F. angustifolia* Vahl, *Ulmus minor* Miller and *Quercus robur* L. The natural corridor of the river is well conserved; however, the lower part of the floodplain has been managed for agriculture since the 17th century (Tabacchi et al. 1990).

Statistical analyses

Data were analyzed with the statistical package, StatView 4.01 (Abacus Concepts, Inc., Berkeley, California). When necessary, data were log-transformed after testing for assumptions of normality. Percentages were arcsin transformed (Zar 1984). Statistical tests included *t*-tests, paired sample *t*-tests and linear regression.

Results

Species richness

The riparian zones of the Sabie River contain 402 species of vascular plants; the Crocodile River 383 species; the Olifants 290 species; and the Letaba 245 species. Plant community descriptions of prominent and ecologically significant species associated with the macro-channel floor and the macro-channel bank reveal that there is no statistically significant difference in species richness of native plant species between the macro-channel banks and the floors (Figure 4: paired sample $t = 2.32$, $p < 0.10$, d.f. $= 3$). However, species richness of exotic plants is, on average, 3.1 times greater on the macro-channel floors than the banks (paired sample $t = 3.22$, $p < 0.05$, d.f. $= 3$).

Native vegetation

Vegetation of the macro-channel floor reflects that of wet and periodically flooded environments. The dominant native species are the reed, *Phragmites mauritianus* Kunth, and the trees *Breonadia salicina* (Vahl) Hepper & J. R. Wood and *Nuxia oppositifolia* (Hochst.) Benth. Other prominent species include the trees *Syzygium guineense* (Willd.) DC. and *Combretum erythrophyllum* (Burch.) Sond., and the shrub *Ficus capreifolia* Del.

The dryer and more rarely flooded macro-channel bank contains a community that is clearly intermediate between the macro-channel floor and the adjacent bushveld vegetation. Dominant native plants are various species of *Acacia* (including *A. nigrescens* Oliv., *A. schweinfurthii* Brenan & Exell, *A. tortilis* (Forsk.) Hayne and *A. welwitschii* Oliv.), other trees (including *Spirostachys africana* Sond. and *Lonchocarpus capassa* Rolfe), and various species of *Combretum* (including *C. apiculatum* Sond., *C. hereroensis* Schinz, *C. imberbe* Wawra, *C. microphyllum* Klotsch and *C. mossambicense* (Klotsch) Engl.). The dominant shrub is *Euclea divinorum* Hiern. Other prominent species include the trees *Colophospermum mopane* (Benth.) Léonard, *Croton megalobotrys* Muell. Arg. and *Terminalia pruinoides* Laws.

Native species which are prominent in both the macro-channel floor and bank include the trees *Acacia robusta* Burch., *Diospyros mespiliformis* Hochst. ex A. DC., and *Ficus sycomorus* L., and the shrubs *Maytenus senegalensis* (Lam.) Exell and *Securinega virosa* (Roxb. ex Willd) Pax & Hoffm. Forbs and grasses are present but not dominant in either area.

Exotic vegetation

The most prominent exotic species is the very successful shrub, *Lantana camara* L., which is found on both the macro-channel floor and the bank. The other prominent species which can be found on both the macro-channel floor and bank is the grass, *Cynodon dactylon* L. The native range of this grass is debatable (K. Rogers, M. Barkworth pers. commun.); it is a widely naturalized lawngrass, thought to be Eurasian in origin (Hitchcock et al. 1969).

The widespread exotics which are limited to the macro-channel floor include the forbs, *Xanthium strumarium* L., *Vinca major* L., *Ageratum conyzoides* L. and *Argemone subfusiformis* G. B. Ownb., which are found on sandy deposits in the river beds. The tree, *Melia azedarach* L., is also found on the macro-channel floor, often on *Phragmites*-dominated islands. *Eichhornia crassipes* (C. Martius) Sohms-Laub., *Polygonum lapathifolium* L. and *Pistia stratiotes* L. are widespread exotic hydrophytes. Other noteworthy macro-channel floor exotics include the forb, *Alternanthera pungens* H. B. & K., and the shrubs *Asclepias rivularis* Schltr. and *Ricinus communis* L. Exotics which are prominent on the macro-channel bank but not the floor include the cactus, *Opuntia ficus-indica* L., and the forbs, *Achyranthes aspera* L., *Bidens bipinnata* Baill. and *Tagetes minuta* L.

Invasibility – Macro-channel bank vs floor

Spatial analysis reveals a heterogeneous pattern of invasibility between the macro-channel floor and the macro-channel bank vegetation (Figure 4). The proportion of exotics on the macro-channel banks ranges from 5% to 11% of the total species richness, while the proportion of exotics on the macro-channel floor ranges from 20% to 30%. On average, the macro-channel floor is 3.1 times more invasible than the macro-channel bank. There is no relationship between species richness and percent exotics within the macro-channel floor category (Figure 5; $r^2 = 0.01$, $F_{1,2} = 0.024$, $p < 0.90$). However, within the macro-channel bank category there is a negative correlation between species richness and percent exotics (Figure 5; $r^2 = 0.91$, $F_{1,2} = 19.75$, $p < 0.05$).

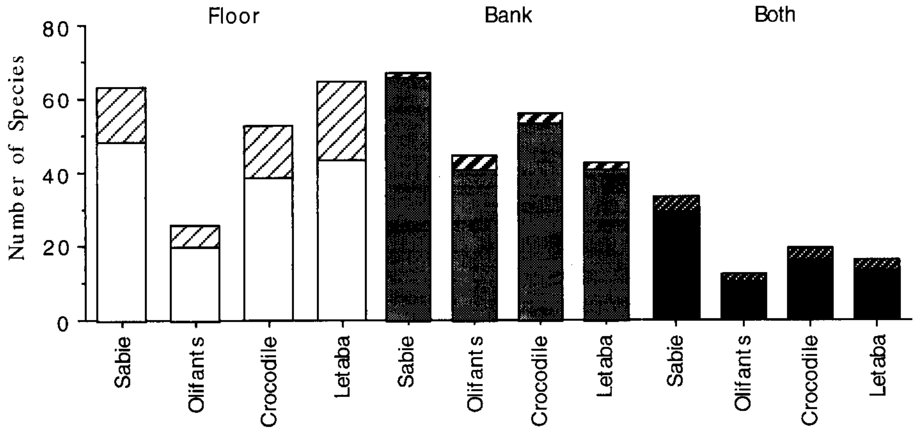

Figure 4. A comparison of the number of native and exotic vascular plant species found either on the macro-channel floor, the macro-channel bank, or in both areas. Solid bars represent native species, hatched bars represent exotic species.

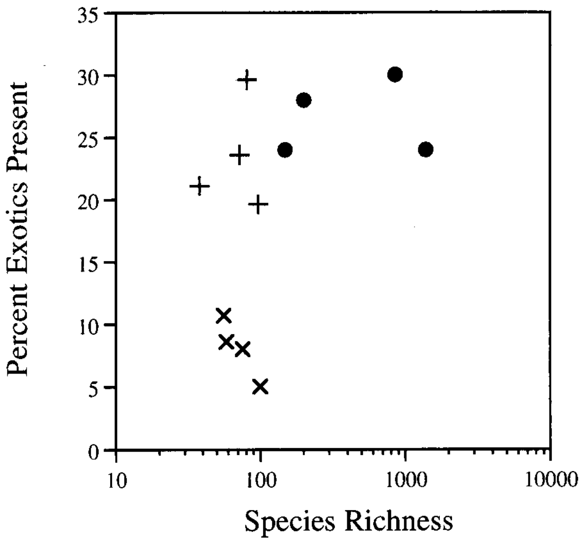

Figure 5. Relation between riparian species richness and percent exotics for the Sabie, Olifants, Crocodile, and Letaba rivers (South Africa; macro-channel floor [+] and macro-channel bank [×]) and for the French and North American rivers (•).

Invasibility – South African vs French and North American rivers

In comparison to the South African rivers, exotic species comprise 24% of the 1396 riparian species of the Adour River; 30% of the 851 riparian species of the McKenzie River; 28% of the 200 Dungeness River species; and 24% of the 148 Hoh River riparian species (Planty-Tabacchi et al. 1996). There is no relationship between species richness and percent exotics among these rivers (Figure 5; $r^2 = 0.01$, $F = 0.026$, $p < 0.90$). The percentage of exotic plants on the macro-channel floors of the South African rivers is similar to that of the northern temperate riparian zones (20–30% exotics vs. 24–30% exotics, respectively). In fact, there is no significant difference in the percentage of exotic riparian (= macro-channel floor) species between the four South African rivers and the four rivers of the northern hemisphere ($t = 1.162$, $p < 0.30$, d.f. = 6; F-test for homogeneity of variance: $F_{3,3} = 3.00$, $p < 0.50$) despite substantial regional differences in climate, landuse history, and species composition and diversity.

Discussion

Riparian vulnerability to invasion

The comparison of the percentage of exotic plant species in the macro-channel floor versus the macro-channel bank suggests that frequently flooded active channel floors are more vulnerable to invasion by exotic species than the more stable macro-channel bank. Although this comparison included only those plant species sufficiently abundant to be mentioned in the plant community descriptions, the exotic species which are abundant enough to be mentioned are successful invaders, and they are three times more common on the macro-channel floor as on the macro-channel bank.

The macro-channel bank is a zone of transition from the macro-channel floor vegetation to the upland savanna vegetation. The species composition of the vegetation of the lower portions of the macro-channel bank has considerable overlap with that of the macro-channel floor, while the higher portions of the bank have considerable overlap in species composition with the surrounding savanna (van Coller & Rogers 1995). The differences in invasibility observed between the plant communities of the macro-channel floor and the transitional macro-channel bank suggest that similar or greater differences might exist between the macro-channel floor and the savanna. Indeed, it has been observed that the savannas in the Kruger National Park are largely free of exotic plants (Macdonald & Frame 1988). In the Hluhluwe-Umfolozi Game Reserve of Natal, South Africa most introduced plants are invading along the banks of rivers. The least invaded habitats are the drier *Acacia* savannas in the south of the reserve (Macdonald & Jarman 1985). Likewise, case studies of biological invasions in four continental nature reserves in arid environments (Death Valley National Monument-USA, Canyonlands & Arches National Parks-USA, Organ Pipe Cactus National Park-USA, & Skeleton Coast Park-Namibia) reveal that vascular plant invasions have not been severe except along watercourses (Loope et al. 1988).

The preceding discussion suggests that riparian zones are more vulnerable to invasion than adjacent upland areas, at least in arid and semi-arid landscapes. Similar observations in mesic climes are uncommon (but see DeFerrari & Naiman 1994). However, a more general comparison of riparian habitats with other habitats provides a ranking of habitat invasibility. In reviewing the invasibility of nature reserves by vascular plants, Usher (1988) noted that the proportion of a community that consists of invasive exotics is 30.4% for islands; 12.3% for Mediterranean-type habitats; 5.4% for dry woodland and savanna; and 9.2% for arid lands. In comparison, the mean proportion of invasive species in the macro-channel floor zone of the Sabie, Crocodile, Olifants, and Letaba Rivers and the riparian zones of the Adour, Dungeness, Hoh, and McKenzie Rivers is 25.0%. Similarly, a survey of the vascular plants in the riparian zones of the Santa Ana and the Santa Margarita Rivers in southern California revealed that 31.8% of 311 species and 27.6% of 522 species, respectively, were exotic (Zembal 1984, cited in Faber et al. 1989). Evidently, the vulnerability of riparian zones to invasion by exotic vascular plants is similar in a wide variety of rivers and nearly comparable to that of islands. The question that naturally follows is, 'What are the characteristics of riparian zones that make them vulnerable to invasion?'

Potential causes of riparian invasibility

As the distance from the river channel increases there is a change in the native vegetation which corresponds to a gradient of declining riverine influence on the vegetation (van Coller & Rogers 1995; van Niekerk & Heritage 1993). The riverine influences which most strongly affect vegetation are: (1) the availability of river water for transport of propagules, (2) the frequency and intensity of disturbance associated with flooding (Franz & Bazzaz 1977), and (3) water availability from the water table (Bowman & McDonough 1991). Each of these riverine influences can be associated with the three steps in the invasion process: respectively, (1) dispersal to a site appropriate for germination, (2) germination and establishment with reduced competition, and (3) growth and reproduction.

Thirteen of Kruger National Park's 26 significant introduced plant species are primarily water-dispersed, 10 species are mainly animal-dispersed, and the two most abundant exotic species, *L. camara* and *M. azedarach* are dispersed by water and frugivorous birds. Native avian frugivores also eat and disperse the fruits of exotic species such as *Psidium guajava* and *Solanum mauritianum* (Macdonald & Frame 1988). Additionally, seeds can be widely dispersed while attached to the fur of mammals, or by seed-harvesting ants. Since dispersal from the macro-channel floor is possible through animal vectors, water-borne dispersal cannot be the only factor which contributes to the high invasibility of riparian zones.

Disturbance has been correlated with successful invasion by exotic species in a variety of habitats (e.g., Hobbs 1989; Mack 1989; Ewel 1986). Flooding is a common disturbance in rivers and is a fundamental force in continuously reshaping channels, banks, and floodplains through erosion and deposition of sediments (Leopold et al. 1964). Several studies of riparian invasions in northern temperate rivers have subdivided riparian zones into specific habitat types (such as cobble bars, riparian shrubs, and riparian forests), which are associated with frequency of flooding disturbance (or patch age and successional stage) and correlated with the percentage of exotics (Planty-Tabacchi et al. 1996) or the number of exotics (DeFerrari & Naiman 1994). Successionally young areas that experience frequent flood-related disturbance have a higher proportion of exotic vascular plants. These studies suggest that flooding contributes to the invasibility of riparian zones by denuding flood-prone areas, thereby reducing competition between resident native and colonizing exotic plant species.

Theoretically, the high plant species richness of riparian systems should reduce their invasibility because communities composed of many strongly interacting species are thought to limit the invasion possibilities of most similar species (Case 1990; Pimm 1989; Simberloff 1981; Elton 1958). A comparison of whole river systems for the northern temperate zone rivers shows no significant relationship between species richness and the proportion of exotic species (Figure 5). On a smaller, patch scale, Planty-Tabacchi et al. (1996) found that, contrary to theoretical predictions, species richness was positively correlated with the percentage of exotic species as one moved from the headwaters to the lower courses of both the Adour and the McKenzie rivers. Perhaps species richness is important in reducing the invasibility of undisturbed communities and not in communities experiencing frequent disturbance, such as rivers where abiotic factors often dominate over biotic interactions (Gregory et al. 1991). The correlation found by Planty-Tabacchi et al. (1996) between species richness and invasibility may be due to the basic cause for both, i.e., longitudinal variation in disturbance frequency and intensity. Since the morphology and vegetation of the macro-channel floor are much more dynamic than the relatively stable macro-channel bank due to differences in flooding frequency (van Coller et al. 1997; van Coller & Rogers 1995; van Niekerk & Heritage 1993), the absence of a correlation between species richness and percent exotics in the macro-channel floor, and the presence of a correlation on the macro-channel bank are consistent with the idea that species richness reduces invasibility in the absence of frequent disturbance.

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