

Tree-grass coexistence in a flood-disturbed, semi-arid savanna system

Matthew F. Child · Sue J. Milton · Richard W. J. Dean · Marisa K. Lipsey · James Puttick · Tessa N. Hempson · Gareth K. Mann · Hassan Babiker · Jamshed Chaudrey · Glynis Humphrey · Grant Joseph · Nicola C. Okes · Reda Potts · Thuli Wistebaar

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Abstract The coexistence of trees and grasses in savanna ecosystems is a contentious phenomenon. Fire and herbivory disturbances are often cited as major structuring forces that create a sustainable tree–grass relationship. However, periodic flooding of savanna patches may also enable coexistence. The aim of this study was to investigate the effects of flood-disturbance on the recruitment patterns of *Acacia karroo* trees in a semi-arid savanna system in South Africa. We analysed the spatial coincidence of *A. karroo* seedlings with tussocks of the tall spiny grass *Stipagrostis namaquensis* in the riverbed and related herbivory intensity to spatial position. The data showed that *A. karroo* seedlings were significantly positively associated with *S. namaquensis* (Chi-square

test, $\chi^2_1 = 45.20$, $n = 118$, $P < 0.001$); *A. karroo* seedlings growing inside of tussocks experienced less browsing pressure than those growing in the floodplain (Kruskal–Wallis test, $H = 11.90$, $n = 118$, $P < 0.01$); and recruitment success of *A. karroo* trees was spatially discrete (K–S test, $D = 0.78$, $n = 196$, $P < 0.01$). We suggest that floods create an enemy-free zone, which *S. namaquensis* colonises and then facilitates successful *A. karroo* establishment. High levels of *A. karroo* recruitment in the riverbed may replenish the woodlands fringing the river, which appear to be sink areas for *A. karroo* seedlings. Thus, the interaction between disturbances at different spatial and temporal scales (flooding versus herbivory) seems to maintain the inherently unstable coexistence of tree and grass species in this ecosystem. These findings also suggested that flood disturbances alter the tree–grass relationship.

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M. F. Child · S. J. Milton · R. W. J. Dean · M. K. Lipsey · J. Puttick · T. N. Hempson · G. K. Mann · H. Babiker · J. Chaudrey · G. Humphrey · G. Joseph · N. C. Okes · R. Potts · T. Wistebaar
DST/NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

M. F. Child (✉)
Conservation science group, Department of Zoology,
University of Cambridge, Downing Street, Cambridge
CB2 3EJ, UK
e-mail: mattychild@gmail.com

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Introduction

Savanna vegetation types are characterised by the coexistence of grasses and woody vegetation (Higgins et al. 2000). The conundrum of this co-existence is an issue that has received much attention from ecologists (Jeltsch et al. 2000; Scholes and Archer

1997; Higgins et al. 2000; House et al. 2003). Grasses and trees are often in direct competition for light, nutrients and water, which raises debate over the ecological mechanisms allowing their somewhat paradoxical coexistence in savannas. Some authors have argued that coexistence results from a differentiation of rooting depths (e.g. Walter 1971; Jurena and Archer 2003), whereas others suggest that natural disturbances maintain a mix of grass and woody vegetation in savannas by reducing the strength of competitive interactions and creating shifting mosaics of habitat types (Wu and Loucks 1995; Naiman and Decamps 1997). For example, Higgins et al. (2000) argue that while mortality of adult trees in savannas is relatively low, fires create fluctuations in tree recruitment rates, thereby allowing the persistence of grasses in the landscape.

Several authors also argue for the importance of fire–herbivore interactions (e.g. van Langevelde et al. 2003; Archibald et al. 2005). Thus, although mean annual precipitation determines the maximum cover of woody biomass (Sankaran et al. 2005), fire intensity and frequency interacting with herbivory appears to control savanna structure below the maximum. Further, savanna patterns shape the cross-scale processes (Gillson 2004): fire regimes depend on available grass biomass, which is in turn determined by water and nutrient availability and the intensity of herbivory on the landscape. Herbivory at high intensities can upset the tree–grass balance by causing bush encroachment, which leads to positive feedback as fire intensities are reduced (Archer 1989; Archibald et al. 2005). Further, spatial modelling and empirical evidence support the contention that savanna systems are characterised by local disequilibrium and broad-scale stability determined through a hierarchy of disturbances (for example, Wu and Levin 1994; Wu and Loucks 1995; Gillson 2004; Briske et al. 2005). Thus, it is clear that disturbance plays a key role in limiting the effects of competition and allowing both grasses and trees to persist in savannas. However, there are few examples in the literature of broad-scale disturbances other than fire maintaining coexistence and local patch heterogeneity in savanna systems.

Flooding rates are acknowledged as an important variable in riparian areas, and flood events can cause mortality and damage to vegetation at comparable magnitudes to those caused by fires (Naiman and

Decamps 1997). Tree species may use extreme flood events as recruitment opportunities (Duncan 1993), and tree seedling establishment appears to be associated with a ‘flush’ germination at high water levels (Medina and Silva 1990). Flooding in riparian systems may thus induce vegetation state changes in savanna systems whenever floods pulse through the linear riparian corridor (Gregory et al. 1991). Yet there has been little investigation of flooding as a mechanism for tree–grass coexistence. Grass fuel in fire-prone savannas affects the intensity of fire, and has an impact on the survival and recruitment rates of savanna trees (Scholes and Archer 1997). Conversely, in a system where flooding is the dominant disturbance, the opposite may be true: grass may slow the rate of flood water flow, thereby preventing seeds or seedlings from being swept away, as well as providing ideal microhabitat conditions for tree seed germination (Pettit and Naiman 2006). Further, piles of woody debris serve as collection points for nutrients as well as seeds swept away by floods and can facilitate establishment of riparian plants (Pettit and Naiman 2006). If herbaceous vegetation acts in a similar fashion at smaller spatial scales, we might expect establishment of woody species to be associated with herbaceous cover in frequently-flooded systems. Additionally, in areas of high herbivore density, herbivory on seeds or seedlings might be reduced for trees establishing under herbaceous cover in comparison to those establishing in open areas. Thus, flood disturbances may add another source of heterogeneity to savanna systems. Further, the woodland patches formed in the course of the riverbed may provide a refuge from fires in systems where fire disturbances are common, thereby providing a valuable sourcepool of tree propagules that enhance the regional resilience of woodland ecosystems.

This aim of this study was to test whether flooding disturbances can maintain the coexistence of trees and grasses in the course of an ephemeral river in an arid ecosystem. This system experiences both periodic flood events and high rates of herbivory, providing an ideal opportunity to study the effects of hierarchical disturbances on savanna patch dynamics. To test the hypothesis that herbaceous cover could facilitate woody plant establishment following flooding in a riparian savanna system, we examined whether seedlings of *Acacia karroo* in the disturbed river channel were associated with the dominant

grass, *Stipagrostis namaquensis*. A fence that prevented sheep from entering the riparian zone was present along the downstream stretches of the study area, allowing us to consider how browsing intensity affects the relationship between *A. karroo* seedlings and *S. namaquensis*. To investigate how coexistence patterns change with time since flooding, adjacent *A. karroo* woodland habitats, which occupy previous river courses, were compared to the river channel patterns in terms of *S. namaquensis* basal cover and *A. karroo* frequency distributions. The evidence emerging from these data were then synthesised into a preliminary conceptual model of tree–grass coexistence in a flood-disturbed, semi-arid savanna.

Methods

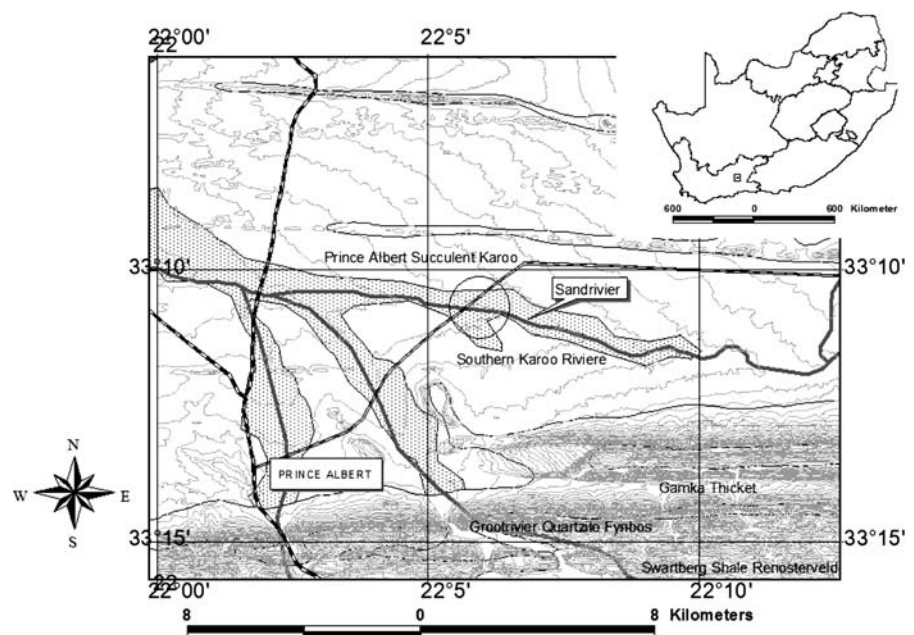
Site description

The study site was located in the channel of the Sand River, about 2 km North-East of Prince Albert, in the Western Cape Province of South Africa (S33°10'798"; E22°05'599", Fig. 1). The river drains an arid, shrub-dominated environment, receiving a long-term mean annual rainfall of about 167 mm (Milton et al. 1992, S1, suppl.). The river flows westwards in a shallow valley that supports a sparse, dwarf vegetation type

known as Prince Albert Succulent Karoo (Mucina et al. 2006, S2, suppl.), while vegetation in and around the channel is classified as Southern Karoo Riviere, an Inland Saline vegetation type (Mucina et al. 2006, S3, suppl.). This vegetation sheds water rapidly after summer thunderstorms, resulting in periodic flows. The dry river bed varies from 50 m to 200 m in width and comprises freely drained structureless alluvial sand and gravel overlying Beaufort-series sedimentary rock. The river course is braided with bare soil or grass in active channels, and woodland on islands in disused channels and on the river banks (S3, suppl.). Minor flows occur on average once annually and last less than one day. Larger floods also occur periodically, usually following major summer thunderstorms and the flow may continue for two to four days. Three such large flooding events (1989, 1996 and 2001) took place in the last 20 years (SJM personal observation). The most recent flooding event prior to sampling was in early May of 2007. No fires have occurred in the last several decades in the vicinity of the study site and fire disturbance was assumed to have a negligible impact on the ecology of this savanna.

The riparian zone ranges in width but is on average about 100–200 m across. The river is dominated by a savanna-like mix of the grass *S. namaquensis* and stands of *A.karroo*. *Stipagrostis namaquensis* is a perennial grass native to southern Africa, often found

Fig. 1 Map of the Sand River study area (encircled) in the Prince Albert region of South Africa. The study area falls within the Southern Karoo Riviere vegetation and is characterised by alluvial sand and gravel overlying Beaufort-series sedimentary rock



in dry rivers and riparian zones in arid areas. It forms dense tussocks up to 2 m in height and the hard narrow leaves are spine-tipped (Rubin and Palmer 1996). The grass is unpalatable to herbivores except when culms are actively-growing. *Acacia karroo* is one of the most common southern African trees. It has many variations in growth form and can reach heights of up to 15 m. It has a relatively short lifespan, flowers from two or three years of age (Archibald and Bond 2003), and maintains a seedling bank rather than a seed bank. *Acacia karroo* seeds only remain viable for approximately a year, but seedlings are able to establish themselves within grass tussocks as they are tolerant of low irradiance and interference (O'Connor 1995). *Acacia karroo* leaves are palatable to many browsing herbivores and the tree is physically-defended through the growth of long, sharp spines.

The dominant browsing species in this area are kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), hares (*Lepus capensis*), and domestic sheep and goats. A livestock fence bisects the study area. This is the boundary of a sheep ranch on the west (downstream) stretch of the river. The fence was damaged in the recent flooding of May 2007, but probably remains a significant barrier to foraging sheep. Thus, we expected browsing by domestic livestock to be greater both historically and currently on the western half of the study area, downstream of the fence.

Data collection

We collected field data between the 3rd and 5th June 2007. In order to understand the association between *A. karroo* and *S. Namaquensis* in the riverbed a total of 32 50 m line transects were laid perpendicularly (North–South) across the riverbed which runs from east to west. The transects started at the southern bank of the riverbed, and were laid parallel to each other at 50 m intervals, resulting in a study area stretching for 1.55 km of the Sandrivier's course. Nineteen transects were laid to the east of where the Zeekoegat road from Prince Albert crosses the river, and thirteen to the west. The total grass cover along each transect was measured as the basal area of *S. namaquensis* directly beneath the transect line. All *A. karroo* individuals located within five metres of the transect line were recorded, and their position in

relation to the grass tussocks noted as either 'in' (surrounded by grass), 'out' (surrounded by bare ground) or 'edge' (on the edge of a grass tussock). To test whether *S. Namaquensis* tussocks act as *A. karroo* seed capturers during a flood pulse, it was noted whether the tree was located upstream (east) or downstream (west) of the tussock.

The browsing intensity experienced by *A. karroo* in the river channel was quantified by recording three variables related to herbivory. Firstly, because multi-stemmedness is often a response to herbivory (Rooke et al. 2004), we counted the number of stems on each seedling that were above the height of 10 cm from the soil surface (stems of seedlings inside grass tussocks were not visible or accessible below this level). Secondly, we quantified the proportion of branch-tips on each seedling that had been damaged by herbivores. For this measure, we chose a branch on the north edge of the tree and examined a series of 10 random tips on the chosen branch. A tip was considered "browsed" if it had obvious scarring and absence of leaves or shoots at its outermost point. We also recorded the height of each branch from the soil surface. Finally, we measured the length of thorns on all *A. karroo* found in river transects (Milewski and Madden 2006). On each branch tip examined for browsing we measured the first non-pliable thorn from base to point. Non-pliable thorns were used because they have already reached their maximum length, whereas soft thorns near branch tips are commonly assumed to still be growing. We measured one thorn per branch tip (a total of 10 thorns per tree) for all trees in river channel transects. Thorn length has been shown to be a good indicator of herbivory pressure (Young 1987; Grubb 1992; Milewski and Madden 2006) and is presumably a more reliable and temporally integrated ecological indicator than immediate browsing damage.

To assess how later successional habitats (areas that have not been flood-disturbed recently) affect the association between *A. karroo* and *S. namaquensis*, we measured vegetative cover using 12 line transects through the woodland bordering the active river channel. There were fewer transects in the woodland areas because woodland areas occupied less space in the study area (S2, S3, suppl.). Data were collected in the same way as in the riverbed—i.e. 50 m long transects spaced 50 m apart, perpendicular to river flow (running North–South). Transects were taken

from a point at least 1 m from the edge of the channel, which was usually well defined (S2, S3, suppl.). We quantified both *A. karroo* canopy cover and *S. namaquensis* basal area in terms of linear metres of each type of cover intersected by each transect. Overlap between tree canopies and grass cover was measured, as canopy cover did not always exclude grass or shrub cover. To construct a size-class distribution in the woodland, we counted the number of *A. karroo* trees in rectangular transects 5 m to either side of line transects and recorded their heights (50 × 10 m total).

Statistical analyses

Before analyses were performed, the data were checked for normality and homogeneity of variances using the Kolmogorov–Smirnov (K–S) test for normality and the Levene’s test for homoscedasticity. All percentage data were arcsine transformed to increase the normality of distribution. All analyses were performed in *Statistica 7* (Statsoft Inc. 2004).

We assessed the association between *A. karroo* and grass tussocks and the frequency of growth on upstream versus downstream edges of tussocks using Chi-square goodness-of-fit tests. Upstream *A. karroo* seedlings were those found on the eastern edge of a clump, while downstream individuals were located on the western edge. We performed this analysis to ascertain the degree to which seedling position co-occurred with grass tussocks. We tested the hypothesis that the association is primarily caused by *A. karroo* seed pods being caught in grass tussocks during floods by using a chi-square test on the ‘upstream’ or ‘downstream’ distinction of ‘edge’ *A. karroo*, and excluding those individuals that were either well inside or totally outside *S. namaquensis* tussocks. Three tests were performed to ensure that the results were not spurious: one without ‘edge’ *A. karroo*, one with ‘edge’ and ‘out’ *A. karroo* pooled, and lastly with ‘edge’ and ‘in’ *A. karroo* pooled. The null hypothesis was that allocation of *A. karroo* to these two positions should be random and thus roughly equal in incidence, while the alternative hypothesis proposed that ‘downstream’ positions should be advantageous to seedlings so as this would reduce the damage potentially caused by flood torrents.

We assessed the effect of tree position on multi-stemmedness and proportion of tips browsed using a Kruskal–Wallis test, as only the variable ‘thorn length’ was normally distributed (but see S4, suppl.). Post-hoc Tukey tests were used to make pair-wise comparisons among tree positions. The analysis of potential differential herbivory between ‘in’, ‘out’ or ‘edge’ seedling positions was more complicated. The active hypothesis proposed that herbivory pressure should be less intense for young *A. karroo* within tussocks. Although we collected the proportion of branch tips browsed data, this is snapshot image and cannot inform us of longer term browsing history on the individual. Thus, in order to detect any true herbivory signal within the context of allometry, we had to isolate the variation in thorn length caused by herbivory alone. Although Darlington and Smulders (2001) decry the use of residual analysis, the assumptions of both ANCOVA and GLM were violated by non-normality and heteroscedasticity of the data, as well as the interdependence of the categorical predictor (tree position ‘effect’) with the covariates. Using a residual analysis allowed us to circumvent these problems. The analysis was also re-run using both ANCOVA and GLM and the significance of the results did not change. The residuals of the regression between thorn length and branch height were collected, checked for normality and entered into a one-way ANOVA. Additionally, differences in herbivory below the former sheep fence (‘downstream’) and above the sheep fence (‘upstream’) were assessed through Student’s *t*-tests. To test whether population structure of the trees changes through time since a flood disturbance, by using woodland position relative to the active river bed as an indicator of elapsed time, the size-class distributions of *A. karroo* were compared between the riverbed the woodland using a K–S test. Correlations were also performed in order to assess the assumption that trees competitively exclude grasses in areas of a prolonged disturbance hiatus.

Results

Acacia karroo seedlings are significantly positively associated with tussocks of *S. namaquensis* in the riverbed, with the pattern remaining strong even when trees found on the edge of tussocks are included in the ‘out’ group for analysis (Table 1). There was no

Table 1 Results of the chi-squared tests of the association of *A. karroo* with tussocks of *S. namaquensis* in the riverbed of the Sand River in the semi-arid southern Karoo

	Chi-squared value (χ^2)	<i>n</i>	<i>P</i> -value
In vs. Out	104.4 (d.f. = 1)	78	<0.001
In + Edge vs. Out	284.2 (d.f. = 1)	118	<0.001
In vs. Edge + Out	45.2 (d.f. = 1)	118	<0.001

The first test includes only those trees located within tussocks and those in bare areas, the second includes individuals located on the edge of tussocks in the 'in' group, and the last includes them in the 'out' group

discernable downstream or upstream difference in establishment for those *A. karroo* seedlings on the edge of the tussock (chi square test, $\chi_1^2 = 0.40$, $n = 40$, $P = 0.53$). The mean basal cover of grass in the riverbed was 14.4% with the remainder (85.6%) being bare ground. A total of 45 *A. karroo* trees were counted inside grass tussocks, 40 were counted on the edge of grass tussocks, and 33 were outside of grass tussocks.

Tree position had a marked effect on multi-stemmedness in *A. karroo* (Kruskal–Wallis test, $H = 52.25$, $n = 118$, $P < 0.01$). Individuals growing outside of grass tussocks had significantly more stems than those growing on the edges of, or inside of tussocks (Tukey test, $H = 52.25$, $n = 118$, both $P < 0.001$, Fig. 2). The 'branch tips browsed' variable differed significantly only for *A. karroo* inside of tussocks compared to those completely outside of tussocks (Tukey test, $H = 11.90$, $n = 118$, $P < 0.01$, Fig. 2), where individuals inside tussocks were less browsed than those on the edge or outside ($52 \pm 37\%$ compared to $73 \pm 32\%$ and $80 \pm 30\%$ respectively). The regression between thorn length and branch height was highly significant (ANOVA, $F = 7.90$, $n = 118$, $P < 0.01$). A post-hoc Tukey test revealed that *A. karroo* seedlings within tussocks had

significantly shorter thorns than those on the 'edge' or 'outside' tussocks (20.7 mm compared to 22.9 and 28.2 mm respectively, both $P < 0.01$). Thorn length did not differ significantly between trees living on the edge or outside of tussocks ($P = 0.35$).

The effect of the livestock fence on indices of browsing was investigated. Sheep are contained downstream of the fence, but excluded upstream of the fence. All browsing variables were analysed for differences in downstream and upstream values using *t*-tests. All variables, except 'number of stems' (although this variable did exhibit a negative relationship with distance upstream but was insignificant, Spearman rank correlation, $r_s = -0.11$, $P = 0.15$), tended to be significantly higher in value downstream (Table 2). Thus, in the upstream reaches of the riverbed where sheep were excluded *A. karroo* had lower branch heights, shorter thorn lengths and fewer branch tips browsed. This relationship was particularly strong for 'thorn length' (Table 2).

Recruitment patterns between the mature woodland adjacent the riverbed and those from within the riverbed were analysed. A K–S frequency distribution test revealed that the population structure of the two areas was highly significantly different ($D = 0.78$, $n = 196$, $P < 0.01$, Fig. 3): the woodland areas contained far taller trees than the riverbed habitat (3.36 ± 2.05 m compared to 0.79 ± 0.55 m for the woodland and riverbed trees respectively). The majority (76%) of the trees in the recently disturbed river channel were less than 1 m tall. Tree density, however, was roughly comparable across habitats, as the K–S failed to reject the null hypothesis of similar density distributions ($D = 0.48$, $n = 44$, $P = 0.10$). Interestingly, shrub coverage was positively, although also non-significantly, associated with tree abundance ($r = 0.42$, $n = 12$, $P = 0.23$).

Fig. 2 Plot of (a) mean number of stems and (b) mean proportion of tips browsed on a branch within 1 m of the ground per individual for *A. karroo* found in *S. namaquensis* tussocks (in), on the edge of tussocks (edge) and in bare areas (out) in the riverbed. Error bars indicate 95% confidence interval

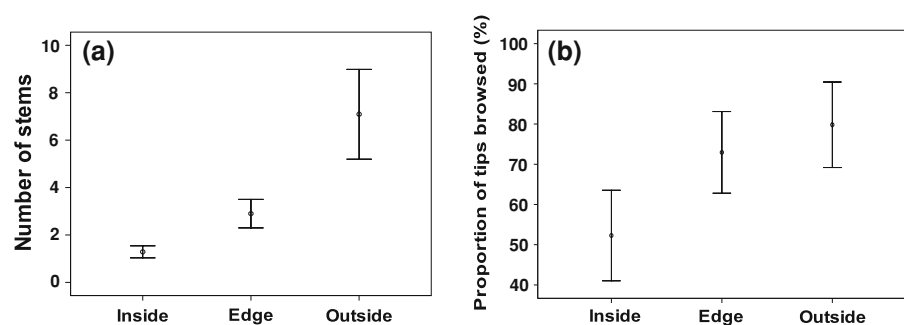
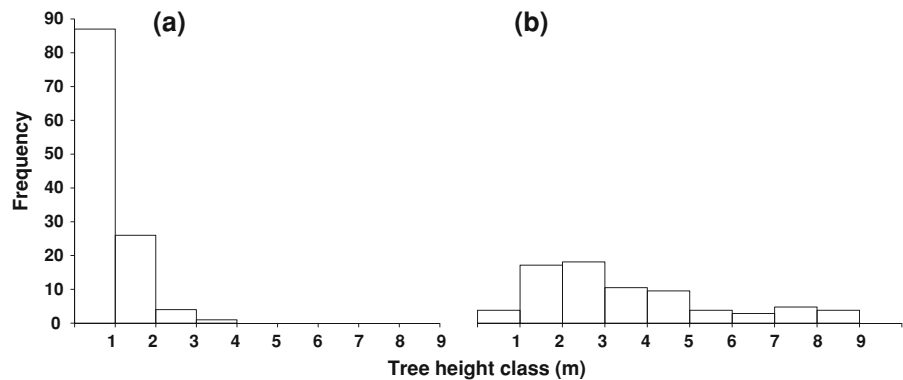


Table 2 The difference in mean values of different traits associated with herbivory between downstream ($n = 13$ transects) and upstream ($n = 19$ transects) trees sampled

Variable	t/Z value	P-value	Downstream mean \pm SD	Upstream mean \pm SD
Thorn length (mm)	3.80	<0.01	27.8 \pm 12.7	18.9 \pm 12.3
Tree height (cm)	3.50	<0.01	1.0 \pm 0.6	0.7 \pm 0.5
Tips browsed (%)	2.46	<0.01	78.1 \pm 29.7	61.1 \pm 36.9
Branch height (cm)	2.12	<0.05	0.8 \pm 0.5	0.7 \pm 0.4
Number of stems	1.82	0.06	4.4 \pm 4.5	2.9 \pm 3.4

Every variable except the number of stems ($P = 0.06$), were significantly lower upstream (all $P < 0.05$)

Fig. 3 The frequency distribution of tree height for (a) the riparian woodland and b) riverbed habitats. These distributions were significantly different in shape ($D = 0.78$, $n = 196$, $P < 0.01$) indicating that the demographic and ecological dynamics of the two habitats differ substantially



Discussion

Blurring the line between competitor and companion

Acacia karroo seedlings were significantly associated with the occurrence of *S. namaquensis* tussocks, despite there being far less grass cover than bare ground in the riverbed. Further, *A. karroo* seedlings were mostly found inside of the grass tussocks and are relatively less browsed than seedlings growing on bare ground. These results are a surprising inversion of the traditional tree–grass relationship: whereas many previous studies have documented the positive effects of trees and their canopies on the survival of smaller perennial and ephemeral species (for example Shreve 1931; Tewksbury and Lloyd 2001), few have demonstrated the positive effects of a grass species on a tree species. Shrubs are known to facilitate tree species on occasion (Holl 2002), but mainly because the shrubs manage to suppress competition by grass (Chhin and Wang 2002). Generally, trees and grasses have been viewed as competitors in savanna ecosystems (Van Auken 2000; Smit 2005 but see Scholes

and Archer 1997). However, our data suggest that *S. namaquensis* may initially aid tree establishment in the riverbed. The spiny perennial grass *S. namaquensis* can form thick, impenetrable tussocks up to 2 m high, which appear to function as shrubs in protecting tree seedlings from herbivory. Evolution of a shrub-like form in this *Stipagrostis* species may thus have changed its interaction with *A. karroo* from that of competitor to that of facilitator in an ecosystem shaped by flooding and herbivory. Thus, even though broader scale disturbances and environmental conditions constrain the distribution and density of trees at regional scales, this study further demonstrates that unique and idiosyncratic plant–plant interactions determine a diverse local-scale patch composition (sensu Gillson 2004).

It can be argued that *A. karroo* seedlings may be providing benefits to the grass tussocks by fixing atmospheric nitrogen from the soil, thereby confounding our results. However if *A. karroo* were facilitating the *S. namaquensis* tussocks one would expect to see a far more patterned network of grass tussocks (sensu Gagnon et al. 2007), as tussocks spread out radially from their point of association

with trees. Yet our data show that there were almost as many *A. karroo* seedlings on the edge of tussocks as they were inside of tussocks (Table 1). Furthermore, as nitrogen levels are generally higher in floodplains than they are in the surrounding terrestrial matrix (Pinay et al. 1995), it is unlikely that the grass tussocks are nitrogen limited. Instead, it seems more plausible that *S. namaquensis* tussocks are providing a refuge from periodic flooding disturbances. Although there was no preference for upstream versus downstream positions on the edge of tussocks, which could mean that flood events are too infrequent for downstream positions to be of adaptive advantage, the tussocks probably provide a ‘safety net’ during flood events that enables the initial establishment of the *A. karroo* seedlings. This association then appears to be enforced by a second phase disturbance, herbivory.

Herbivory as a potential driver of the association

The thorns of *A. karroo* were longer on saplings on the edge and outside of *S. namaquensis* tussocks than on those inside them. This corroborates the finding that browsed branch tips were significantly fewer in number on trees inside of tussocks. Herbivory has a palpable cost on the reproductive fitness of damaged plants in terms of lower flowering and fruiting rates (Milewski and Madden 2006; Goheen et al. 2007). Trees outside and on the edge of tussocks were found to be bearing significantly more stems than those inside of tussocks. This multistemmed, ‘cage-like’ architecture has been interpreted as a mechanical defence against browsing (Archibald and Bond 2003; Bond et al. 2004), or as adaptive ‘overcompensation’ (*sensu* Paige 1992). Thus, we believe there is a genuine difference in browsing pressure between those trees that are inside of tussocks and those that are on the edge or outside of tussocks. This is most likely due to trees inside of the tussocks being hidden for the critical establishment phase of their lives and then, once having breached the height of the grass tussock, being more difficult to reach than other trees growing in the open. However, we must assume that all trees encountered in the riverbed, all else being equal, would experience a homogenous grazing pressure. If some trees had escaped the ‘browse zone’ then tree height would have acted as a confounding variable on the rest of the analyses,

and not simply a covariate. This assumption is likely to hold in this case because the proportion of branch tips browsed was not significantly correlated with either tree or branch height (11 and 6% respectively, both $P > 0.20$, S4, suppl.).

Analyses of the longitudinal profile of the riverbed revealed further evidence of herbivory as the driving force between the unusual tree–grass interactions found in this system. The impact of sheep grazing in the downstream reaches of the study area resulted in the serendipitous ‘treatment’ of increased herbivory pressure in the downstream transects, which was found to be significantly different from those upstream (Table 2). Sheep grazing has been previously documented to hinder plant regeneration (Tiver and Andrew 1997), which may explain the occurrence of relatively more browsed, longer-thorned trees downstream.

Is one acacia in the riverbed worth two in the woodland?

Patch dynamics have an important bearing on the demography of a species (Cipollini et al. 1994), with different parts of the landscape acting as various source and sink areas for populations (Pulliam 1988). This study has found that there is a large discrepancy in the height class distribution, and therefore age distribution (Sweet 1980), of *A. karroo* trees occurring in the riverbed compared with those occurring in the woodland fringes. This is not an artefact of there simply being less trees in the woodland because the density of trees between the woodland and the riverbed was approximately equal. Thus, it would seem there is a spatial separation of age classes in this system, with adult trees mainly occurring in the woodland and seedlings in the riverbed. This pattern is expected in systems where disturbance leads to infrequent recruitment (Young and Lindsay 1988, Bond et al. 2000). It is likely that, as a riverbed develops into woodland (in the time between flood disturbances), fewer and fewer grass tussocks are available for tree seedlings to establish within. Simultaneously, there could be an increase in herbivory pressure due to the shade conferred by mature trees with spreading canopies (Dean et al. 1999). Thus, even those tree seedlings that do manage to establish without the protection of grass tussocks may be more heavily browsed at a young age. This

would most likely retard their progression into taller, more reproductively active age classes (Milewski and Madden 2006), which indicates that recruitment and population turnover in the woodland may not be as effective as within the course of the river.

However, when a flood pulses through that self-same woodland it uproots and washes away old trees and moribund vegetation. The ‘enemy free space’ (sensu Jeffries and Lawton 1984) formed in this way allows grass tussocks to establish free from the constraints of inter- and intra-specific competition. Previous observations of the post-flood system suggest this removal of established trees can be highly effective (SJM, pers. obs.). This process would free the previously suppressed grass species to colonise the nutrient-rich floodplain and, subsequently, allow *A. karroo* seedlings to colonise the grass tussocks. Dispersal of tree seedlings would presumably not be a problem because, firstly, the unidirectional flow of the flood pulse makes passive seedpod transportation highly effective and, secondly, woodlands on opposite banks of the flood pulse could provide an ample source pool for colonisation (Duncan 1993; Cipollini et al. 1994). Once the flood waters recede it would probably be those *A. karroo* seedlings that co-develop with grass tussocks that progress into mature trees, as seedlings growing in the open are exposed to increased herbivory pressure. Thus, floods may provide the occasional crucial disturbance that prevents *A. karroo* recruitment failure in undisturbed habitats and maintains a shifting spatial balance of *A. karroo* cohorts.

Ecosystem implications

The coexistence of trees and grasses is the result of competition and facilitation interacting in complex ways over various spatial and temporal scales (Scholes and Archer 1997). However, House et al. (2003) ask how woody and herbaceous vegetation coexist without one becoming dominant. The results of this study suggest that flood disturbances can create local-scale patches in the riverbed that allow periodic recruitment of woody plant components, which parallels the findings of Bond et al. (2000) who demonstrated that frequent disturbance by fires and herbivory leads to spatially clumped recruitment patterns in tree populations. Interestingly, many of the previously documented interactions and

mechanisms of savanna systems have been found to be qualitatively inverted in this system. For example, whereas Simmons et al. (2007) found that trees in the temperate ecosystem of northern Texas responded positively to the removal of grass, our results suggest that *A. karroo* seedlings have a highly beneficial association with the grass species *S. namaquensis*. Scholes and Archer (1997) have previously described a scenario where young and small trees experience a net facilitation, rather than competitive outcome, with grasses. In other words, facilitation is initially a stronger force than competition. As trees become older and larger, competition may overshadow facilitation and adversely affect grass productivity (Scholes and Archer 1997). This implies that the two types of interaction are constantly at work and merely change in magnitude through time. This system seems to indicate a complete qualitative shift in interaction between grasses and trees: herbivory pressure interacts with flood disturbances to ‘repel’ *A. karroo* seedlings into grass tussocks, which highlights Hobbs and Huenneke’s (1992) supposition that it is often the interaction between different disturbances that has the largest effect. This finding also supports Fukami’s (2001) hypothesis that the sequence of disturbance events determines the structure of ecological communities. Further, the local patchiness within this riparian corridor may endow the overall savanna system with metastability (Wu and Loucks 1995): a shifting patch mosaic of local woodland and grassland habitats, organised through the hierarchical, interactive flood and herbivory disturbances, might continually renew the woodland and grassland elements in the system (sensu Levin and Paine 1974). Presumably, the spatial pattern of these dynamic woodland patches will then go on to periodically affect the course of flood pulses through the landscape, thereby enhancing environmental asymmetry and heterogeneity at broader spatial scales (sensu Gillson 2004, Cumming et al. 2008). The fascinating question then arises as to whether the different geometries of flood versus fire disturbances (linear versus radial) create different patterns of heterogeneity and whether the results of their interaction in space and time create unique patch hierarchies.

We speculate that without the initial establishment of *A. karroo* seedlings in grass tussocks, few seedlings would escape the browse zone and survive into

adulthood, thereby trapping the system in a semi-permanent grassland ecosystem. Although our analyses lack the experimental manipulations that could test the effect of herbivore removals, previous studies have convincingly demonstrated decreased seedling survival when large herbivores are present as compared to when they are not (e.g. Goheen et al. 2004; Goheen et al. 2007; Fornara and Du Toit 2008). Thus, we believe our data present a compelling pattern for a unique effect of herbivory on savanna systems. Our results are interesting as they contrast with wetter savanna systems where browsing indirectly stimulates grass growth and thereby enhances the negative effect of fire on trees (Scholes and Archer 1997, van Langevelde et al. 2003). Further, given that the Sand River experiences a fairly wide range in intensity, duration and frequency of flood events (S1, suppl.), it leaves open the question as to whether both small and large scale disturbances produce qualitatively similar or divergent ecosystem effects.

Conclusions

Acacia karroo seedlings are significantly positively associated with *S. namaquensis* tussocks and they experience less browsing damage inside rather than outside the tussocks. This is shown by longer thorn lengths, more ramified branching patterns and more extensive browsing damage exhibited by trees growing in the open patches of the riverbed. In the mature woodlands there is less grass cover and far fewer *A. karroo* seedlings, which may indicate that *A. karroo* recruitment is not as effective in the riparian zone as in the riverbed. Flood disturbances, however, ‘reset the playing fields’ by allowing *S. namaquensis* tussocks to occupy the open riverbed and form thick tussocks that assume the functions of shrubs. Grass tussock microhabitats then appear to facilitate *A. karroo* seedling establishment after a flood event; and the subsequent association is reinforced by tussocks protecting the seedlings from herbivory. We suggest that flood pulses and herbivory maintain a dynamic temporal and spatial interaction of trees and grasses, which demonstrates how patches of woodland and grassland can coexist at local spatial scales when organised by hierarchical disturbances (Wu and Loucks 1995; Gillson 2004). Thus, floods produce similar landscape patterns to fires by creating

heterogeneous patches at local scales. Interestingly, however, flood disturbances appear to cause different ecological innovation in local-scale interactions, as demonstrated by the unusual relationship between *A. karroo* and *S. namaquensis* in this system.

Although our data lack experimental manipulation we provide empirical evidence for the demographic-bottleneck model of savanna trees, which emphasises periodic opportunities for recruitment rather than continuous competition with grasses (Higgins et al. 2000). The results also support the contention that savanna systems are inherently unstable and are maintained by interactive disturbances across scales. Thus, this study is congruent with the hierarchical patch dynamics paradigm that characterises complex adaptive systems.

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References

- Statsoft Inc. (2004) Statistica (data analysis software system), version 7. www.statsoft.com
- Archer S (1989) Have southern Texas savannas been converted to woodlands in recent history? *Am Nat* 134:545–561
- Archibald S, Bond WJ (2003) Growing tall vs. growing wide: tree architecture and allometry of *A. karroo* in forest, savanna and arid environments. *Oikos* 102:3–14
- Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire-grazer interactions in an African savanna. *Ecol Appl* 15:96–109
- Bond WJ, Midgley GF, Woodward FI (2000) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Glob Chang Biol* 9:973–982
- Bond WJ, Lee WG, Craine JM (2004) Plant structural defence against browsing birds: a legacy of New Zealand’s extinct moas. *Oikos* 104:500–508
- Briske DD, Fuhlendorf SD, Smeins FE (2005) State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecol Manag* 58:1–10
- Chhin S, Wang GG (2002) Spatial and temporal pattern of white spruce regeneration within mixed-grass prairie in the Spruce Woods Provincial Park of Manitoba. *J Biogeogr* 23:903–912
- Cipollini HL, Wallace-Senft DA, Whigham DF (1994) A model of patch-dynamics, seed dispersal, and sex ration in the dioecious shrub *Lendera benzoin* (Lauraceae). *J Ecol* 82:621–633

- Cumming GS, Barnes G, Southworth J (2008) Environmental asymmetries. In: Norberg J, Cumming GS (eds) Complexity theory for a sustainable future. Columbia University Press, New York, pp 15–46
- Darlington RB, Smulders TV (2001) Problems with residual analysis. *Anim Behav* 62:599–602
- Dean WRJ, Milton SJ, Jeltsch F (1999) Large trees, fertile islands, and birds in arid savannah. *J Arid Environ* 41: 61–78
- Duncan RP (1993) Flood disturbance and the coexistence of species in a lowland podocarp forest, South Westland, New Zealand. *J Ecol* 81:403–416
- Fornara DA, Du Toit JT (2008) Responses of woody sapling exposed to chronic mammalian herbivory in an African savanna. *Ecoscience* 15:129–135
- Fukami T (2001) Sequence effects of disturbance on community structure. *Oikos* 92:215–224
- Gagnon PR, Platt WJ, Moser EB (2007) Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest. *Forest Ecol Manag* 241:288–294
- Gillson L (2004) Evidence of hierarchical patch dynamics in an east African savanna? *Landscape Ecol* 19:883–894
- Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 85:1555–1561
- Goheen JR, Young TP, Keesing F, Palmer TM (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J Ecol* 95:129–138
- Gregory SV, Swanson FJ, McKee WA, Cummins KW (1991) An ecosystem perspective of riparian zones. *Bioscience* 41:540–551
- Grubb PJ (1992) A positive distrust in simplicity: lessons from plant defence and from competition among plants and among animals. *Ecology* 80:585–610
- Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savannah. *J Ecol* 88:213–229
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity and invasion: implications for conservation. *Conserv Biol* 6:324–337
- Holl KD (2002) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *J Ecol* 90:179–187
- House JI, Archer S, Breshears DD, Scholes RJ, NCEAS Tree-Grass Interaction Participants (2003) Conundrums in mixed woody-herbaceous plant systems. *J Biogeogr* 30:1763–1777
- Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. *Biol J Linn Soc* 23:269–286
- Jeltsch F, Weber GE, Grimm V (2000) Ecological buffering mechanisms in savannahs: a unifying theory of tree-grass coexistence. *Plant Ecol* 161:161–171
- Jurena PN, Archer S (2003) Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84:907–919
- Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. *Proc Nat Acad Sci USA* 71: 2744–2747
- Medina E, Silva JF (1990) Savannahs of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. *J Biogeogr* 17:403–413
- Milewski AV, Madden D (2006) Interactions between large African browsers and thorny *Acacia* on a wildlife ranch in Kenya. *Afr J Ecol* 44:515–522
- Milton SJ, Dean WRJ, Kerley GIH (1992) Tierberg Karoo Research Centre: history, physical environment, flora and fauna. *T Roy Soc S Afr* 48:15–46
- Mucina L, Jurgens N, le Roux A, Rutherford MC, Schmiedel U, Esler KJ, Powrie LW, Desmet PG, Milton SJ (2006) Succulent Karoo Biome. In: Mucina L, Rutherford MC (eds) *The Vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19*. South African National Biodiversity Institute, Pretoria, pp 221–299
- Naiman RJ, Decamps H (1997) The ecology of interfaces: riparian zones. *Ann Rev Ecol Syst* 28:621–658
- O'Connor TG (1995) *Acacia* karoo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103:214–223
- Paige KN (1992) Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076–2085
- Pettit NE, Naiman RJ (2006) Flood-deposited wood creates regeneration niches for riparian vegetation on a semi-arid South African river. *J Veg Sci* 17:615–624
- Pinay G, Ruffinoni C, Fabre A (1995) Nitrogen cycling in two riparian forest soils under different geomorphic conditions. *Biogeochemistry* 30:9–29
- Pulliam HR (1988) Sources, sinks and population regulation. *Am Nat* 132:652–661
- Rooke T, Bergstrom R, Skarpe C, Danell K (2004) Morphological responses of woody species to simulated twig-browsing in Botswana. *J Trop Ecol* 20:281–289
- Rubin F, Palmer AR (1996) The physical environment and major plant communities of the Karoo National Park, South Africa. *Koedoe* 39:25–52
- Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Forst PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. *Nature* 438:846–849
- Scholes RJ, Archer SR (1997) Tree-grass interactions in savannahs. *Ann Rev Ecol Syst* 28:517–544
- Shreve F (1931) Physical conditions in sun and shade. *Ecology* 12:96–104
- Simmons MT, Archer SR, Ansley RJ, Teague WR (2007) Grass effects of tree (*Prosopis glandulosa*) growth in an arid savannah. *J Arid Environ* 69:212–227
- Smit GN (2005) Tree thinning as an option to increase herbaceous yield of an encroached semi-arid savannah in South Africa. *BioMed Cent Ecol* 5:4
- Sweet SS (1980) Allometric inference in biology. *Integr Comp Biol* 20:643–652
- Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425–434
- Tiver F, Andrew MH (1997) Relative effects of herbivory by sheep, rabbits, goats, and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *J Appl Ecol* 34:903–914

- Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annu Rev Ecol Syst* 31:197–215
- Van Langevelde FC, van de Vijver AD, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350
- Walter H (1971) *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh
- Wu J, Levin SA (1994) A spatial patch dynamic modelling approach to pattern and process in an annual grassland. *Ecol Monogr* 64:447–464
- Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70:439–466
- Young TP (1987) Increased thorn length in *Acacia depreanlobium*- an induced response to browsing. *Oecologia* 71:436–438
- Young TP, Lindsay WK (1988) Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *Afr J Ecol* 26:69–72