

Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid African savanna

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Abstract Patch dieback occurred in an almost monospecific *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard woodland in the Northern Province, South Africa, following severe droughts in 1988–1989 and 1991–1992. Discrete patches of dieback and adjacent paired areas of 'healthy' vegetation lost an average of 87 and 13% of basal area to mortality, respectively. Whole trees mostly died on 'dead' plots, while single-stem mortality prevailed on 'live' plots. Tree mortality decreased with increasing stem number per tree. Patch dieback did not occur on sandy soils. On fine-textured soils, variation in soil type, topography or slope did not affect dieback. Dieback was influenced by vegetation structure, soil surface condition and soil chemistry. Intense intertree competition, shown by self-thinning occurring prior to dieback, was a precondition for dieback. Intertree competition had heightened during the 30 years prior to dieback because of an increase in woody cover. Dieback patches had changed from functioning as sinks of water and sediment to sources of these as a result of loss of perennial herbaceous cover, decreased water retention on bared surfaces, and accelerated erosion during 50 years of livestock ranching. Vegetation had thus become increasingly drought-prone, exacerbated in places by soils with a high sodium concentration. Dieback had occurred because the water requirements of *C. mopane* could no longer be met during drought years on the dysfunctional patches.

Key words: drought, erosion, overgrazing, rill, run-off, soil water, surface water.

INTRODUCTION

The savanna biome covers one-third of South Africa. Plant-available moisture and nutrients are primary determinants of savanna structure and function, whose influence may be modified by fire and herbivory (Frost *et al.* 1986). Although the influence of these determinants on the dynamics of herbaceous vegetation has been well researched because of economic considerations (e.g. O'Connor 1985), understanding of their effect on the dynamics of woody vegetation is relatively fragmentary. The increasing demand for goods and services offered by the woody component of savannas (Shackleton 1996) demands a detailed understanding of the mechanisms driving change.

Mortality of long-lived savanna trees not only affects population dynamics but may modify biodiversity (Huston 1994) and ecosystem functioning (Solbrig *et al.* 1996). Consequently, extensive dieback may constitute a major ecological perturbation. Tree dieback has increased worldwide in magnitude and extent since the turn of the century, with unprecedented losses of mostly the dominant species (Fensham & Holman 1999) occurring in Australia, North America and Europe (Heatwole & Lowman 1986). The causes vary

in different regions and are often thought to be synergistic combinations of more than one factor (Bunyard 1986). Suggested causes of dieback are insect outbreaks (Haugen & Underdown 1990), fungal diseases (Crombie & Tippet 1990), climatic fluctuations (Watt 1987), shifts in geomorphological or hydrological gradients (Jimenez *et al.* 1985), air pollutants (Woodman 1987), salinity (Jolly *et al.* 1993), changes in land use (Trenbath *et al.* 1990), and drought (Viljoen 1995; Fensham & Holman 1999). There are, however, few reports concerning dieback in African savannas. Dieback of *Acacia xanthophloea* has been attributed to both a raised ground water table and increased soil salinity following a period of higher rainfall (Western & van Praet 1973), and to senescence of even-aged stands (Young & Lindsay 1988).

Confirmed mortality agents of African savanna trees include fire (Trollope 1982), debarking (e.g. porcupine, Thomson 1974) in conjunction with fire (Yeaton 1988), frost (Smit 1990), intensive herbivore browsing (Pellew 1983; Stuart-Hill 1992) in conjunction with fire (Trollope 1982), lightning (Spinage & Guinness 1971) and drought (Scholes 1985; O'Connor 1999). The extent of drought-induced mortality, usually of smaller individuals, depends on soil type (Scholes 1985; O'Connor 1999), density (Smit 1994) and species identity (O'Connor 1999). Mortality has not been shown, however, to occur as discrete patches admixed within healthy vegetation.

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The persistence of long-lived species requires continued availability of soil water (Tongway & Hindley 1995). The effectiveness of rainfall in supplying plant-available water is influenced by soil texture (Brady & Weil 1996), evaporative demand and topographic effects on landscape water redistribution (Coughenour & Ellis 1993). Vegetation and litter cover, topography and slope determine the amount of run-off. On bare soils, run-off occurs as sheet flow on smooth slopes (<0.5%), but high energy channels flow when the gradient is steeper, which can cause rills and gullies (Ludwig & Tongway 1997). Rills redistribute surface flow, resulting in greater plant production on run-on sinks compared with run-off source zones (Hodgkinson & Freudenberger 1997). Dysfunctional landscapes have lost the ability to capture and retain water and nutrients efficiently, and are usually characterized by denuded soil surfaces, a lack of perennial plant cover and severe soil erosion (Tongway & Ludwig 1997).

Colophospermum mopane is normally found in low altitude (400–700 m a.s.l.), low rainfall (200–800 mm per year) areas of southern Africa (Mapaure 1994), occurring usually as an almost monospecific woody component. O'Connor (1999) monitored *C. mopane* woodland in the Northern Province, South Africa between 1982 and 1997 and revealed drought-induced mortality and extensive dieback of discrete patches. This example offered an opportunity to investigate a poorly understood, infrequent and relatively recent biological phenomenon.

The specific objectives of the present study were:

1. Describe quantitatively this case of patch dieback.
2. Establish if tree density affected dieback.
3. Test the hypothesis that patch dieback is a consequence of the senescence of a cohort (Young & Lindsay 1988).
4. Assess whether soil type and drought were strong abiotic controls of dieback. If so, what landscape-level factors influenced the effect of drought

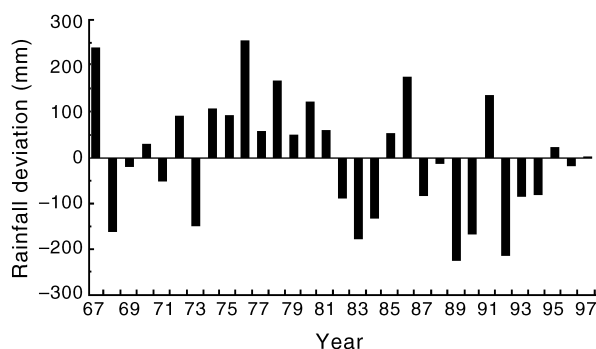


Fig. 1. Annual deviation of rainfall from the long-term mean (366 mm) at Pontdrif. Rainfall years are July to June inclusive, therefore a season is denoted by the year in which it ends (1991 is 1990–91).

such that patch dieback rather than another pattern of mortality occurred?

5. Test whether soil salinity was implicated in patch dieback.

6. Test whether dieback was a consequence of localized reductions in soil water resulting from increased soil erosion, following the establishment of livestock ranches 50 years ago (T. G. O'Connor, unpubl. data). Erosion can influence soil water availability through its effect on run-off/run-on processes and by decreased water retention because of an impaired soil surface condition (Tongway & Hindley 1995).

In the present study, patch dieback is differentiated from mortality by its localized distribution pattern within healthy vegetation and described as the synchronous mortality of neighbouring trees.

METHODS

Study area and study species

Venetia-Limpopo Nature Reserve (VLNR; 29°12'–29°23'E, 22°15'–22°30'S) is situated in the Northern Province, South Africa, approximately 30 km south of the Limpopo River, and is 34 500 ha in extent. This semi-arid region is characterized by wet, hot summers and dry, mild winters. Mean monthly minimum and maximum temperatures are, respectively, 20.3 and 32.0°C for summer (December) and 7.2 and 24.7°C for winter (June). The mean annual rainfall for Pontdrif, approximately 15 km north of the study site, is 366 mm (1967–1997). Rainfall, consisting mainly of thunder showers, falls primarily from October to March. Annual rainfall over the past few decades has been erratic (36% coefficient of variation) with extended periods of above- and below-average rainfall (Fig. 1). There were severe droughts recently in 1982–1983, 1988–1989 and 1991–1992. Mean annual evaporation (2000–2200 mm; Midgley *et al.* 1994) is sixfold greater than the mean annual rainfall.

The study area is a basin of deep (>5 m) palaeo-alluvia derived mostly from Karoo sediments with more recent alluvia occurring adjacent to current seasonal rivers. Soil forms represented are Swartland, Valsrivier, Oakleaf and Dundee (Soil Classification Working Group 1991) with an average content of 20% clay and 19% silt (Botha 1994). Sheet and rill erosion is conspicuous because of the poor perennial grass cover (O'Connor 1999).

Livestock ranching at this site commenced during the 1940s. Patterns of soil and vegetation degradation (T. G. O'Connor, unpubl. data) suggest levels of stocking were heavy, but quantitative information is not available. Livestock were removed in 1991 when the

area was consolidated as a nature reserve, after which the numbers of indigenous herbivores increased.

The study area is part of the Mopani Veld type (Acocks 1953). *Colophospermum mopane* is the dominant species of all the dryland vegetation types of VLNR (O'Connor 1992). Other common species include *Boscia foetida*, *Salvadora angustifolia* and *Lycium austrinum* (nomenclature follows Arnold and De Wet 1993).

Colophospermum mopane is a single- or multi-stemmed tree or shrub, usually <5 m in height, which occurs as in dryland situations in VLNR. The *C. mopane* woodlands of VLNR are dense, with >70% cover (O'Connor 1992). Characteristics of *C. mopane* include an affinity for heavier textured soils (Fraser *et al.* 1987), drought tolerance (Viljoen 1995; Johnson *et al.* 1996) and an ability to utilize soil water at a matric potential lower than that of herbaceous plants (Smit 1994). Severe intertree competition for water occurs in dense stands (Smit & Rethman 1998a). This species has a large root biomass and shallow root system (Smit & Rethman 1998b), and is physiologically adapted to xeric conditions (Prior 1991). Following topkill, an individual can coppice from the stem base. Hence, individual plant longevity is unknown. However, fire scars, attributed to the last recorded fire in 1948, indicate that most of the individual trees of VLNR are greater than 50 years old and thus were established prior to agricultural development (S. D. MacGregor, unpubl. data).

Data collection

A comparative approach was employed in 1998 in which 20 m × 20 m plots within 40 areas of discrete dieback (all <1 ha) were compared with adjacent paired plots, 20–150 m away (median distance 45 m), of 'healthy' vegetation on apparently similar topo-

graphy and soils. The 40 dieback patches were distributed over the topography from crest to alluvial toeslope (Fig. 2). In each plot, we measured the size structure of plants, stem and tree mortality, and soil structure and chemistry. An inherent problem of a retrospective study of an event such as dieback is obtaining measures of both vegetation and potential causal agents of tree mortality that reflect circumstances as they were at the time of dieback. Differences between paired plots for some variables could arise as a response to mortality rather than indicating causes of mortality.

All stands appeared healthy following the 1982–1983 drought, but dieback appeared by 1991 following droughts in 1988–1989 and 1991–1992 and was obvious by 1996 (T. G. O'Connor, pers. obs.). The decay of standing dead trees (lack of bark shed, amount of fine branches lost) was consistent with mortality occurring in 1991–1992.

We recorded woody vegetation species, and measured height to the uppermost living and dead part of a tree, stem circumference (20 cm above ground level) and growth state (dead or alive) of each stem per tree. Dieback per plot is expressed as the ratio of dead to total basal area. Dieback for all 'live' plots collectively or all 'dead' plots collectively is expressed as the number of trees with dead stems or the number of dead stems for each class of stem number per tree.

Averages of surface water retention capacity (SWRC), erosion severity (ES), and ecological status (Est) were calculated from the mean of the four 10 m × 10 m quadrats in each 20 m × 20 m plot (Appendix 1). Surface water retention capacity and ES were adapted from Tongway and Hindley (1995) for the present study, using a 12- and seven-point ordinal scale, respectively (Appendix I). The Est describes whether a plot functions as a net source or sink of sediment and water, taking into account geomorphic

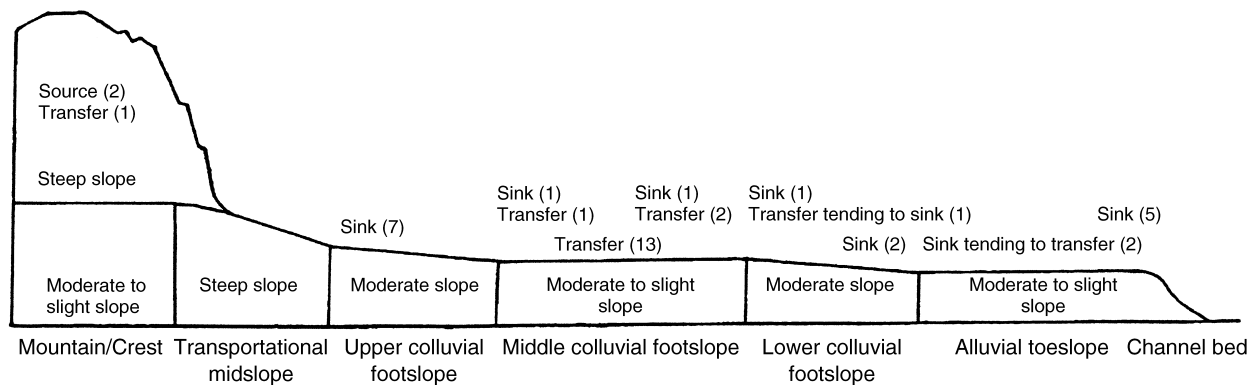


Fig. 2. Generalized valley-side cross section (catena) showing most of the topographic units (defined by slope and relative location) encountered on the Venetia-Limpopo Nature Reserve. Terms relating to source, transfer and sink denote the functioning of a site in terms of surface redistribution of water and materials that would have prevailed prior to historical erosion (past ecological status). The numbers in parentheses indicate the number of sites assigned to each rank of past ecological status.

processes and topographic position (Appendix I). Past and current ecological status were assessed using a seven-point ordinal scale, focusing on the flow of sediment and water across the plot prior to and since the advent of rill and gully erosion, respectively. Change in ecological status was the difference between past and current rankings. Aerial photography (1955–1987) revealed that gully erosion associated with the dieback sites preceded the death of trees but had occurred after 1955, that is, after the establishment of trees. An increase in SWRC occurs through the effect of litter (Kelly & Walker 1976) and from the assumed effect of sedimented rills storing water gained from upslope and transferring it to the adjacent profile, as opposed to water being shed from a compacted surface. These were included in the ranking procedure. The exposure of the surface of 'dead' plots since tree mortality may have resulted in exaggerated ranks for present Est, but this bias was consistent for change in Est.

Slope was estimated using an electronic level (Leica Wild 3000). Soil physical and chemical characteristics of both topsoil (0–200 mm) and subsoil (400–600 mm) were evaluated for each plot. Soil texture was analysed using the hydrometer method (Gee & Bauder 1986), pH (H₂O) was measured using a glass electrode pH meter (Crison micropH 2000), and the exchangeable cations (Na⁺, Ca⁺⁺, Mg⁺⁺ and K⁺) were determined by extraction with strontium (using 0.1 M strontium chloride) (Hughes & Girdlestone 1994) and expressed in meq/L⁻¹. The sodium adsorption ratio (SAR) was calculated using the equation from United States Salinity Laboratory Staff (1954) (Na/sqrt(Ca/2 + Mg/2)). The sodium adsorption ratio gives an indication of soil sodicity and thus the potential for physiologically induced drought. Total exchangeable

cations (TEC) was calculated as the sum of the concentrations of Na, Ca, Mg and K.

Data analysis

Biotic and abiotic variables in 'live' and 'dead' plots were compared using paired *t*-tests. Tree height distributions were compared using a Komolgorov–Smirnov test. Differences in variables among soil types or topographic units were examined using Kruskal–Wallis or parametric ANOVA, depending on data properties, with 'live' and 'dead' plots analysed separately. A logistic regression was performed to test whether the probability of mortality on 'dead' plots depended on stem circumference, soil type or their interaction.

To assess whether dieback had changed the nature of self-thinning (log of mean plant weight and log of plant density), the relationship between individual plant size (volume) and stem density was examined. Because of the multistemmed growth habit of *C. mopane*, density was expressed as the number of stems per unit area. An index of plant weight was calculated from the volume of a sphere, using stem radius, because heights for individual stems of multistemmed trees were not available. We used the radius of trees that had died some years earlier because direct measures had shown radial growth of live trees was minimal over this period (O'Connor 1999). A weight correction was applied by multiplying by the wood density of *C. mopane* (1.25 g cm⁻³) (Venter & Venter 1996).

The relationship between plot dieback, expressed as the percent loss of basal area (square-root transformed as indicated by a Box–Cox analysis), and those independent variables found to be significantly different between 'live' and 'dead' plots, was examined with

Table 1. Percentage of *Colophospermum mopane* trees with dead stems for each class of stem number per tree on 'live' and 'dead' plots

Plot	No. dead stems	No. stems per tree						
		1	2	3	4	5	6	7+*
'Live' plots	1	12.5	14.1	26.6	31.3	26.7	32.8	28.0
	2		9.6	2.8	11.0	10.0	29.5	20.0
	3			8.0	1.8	7.5	4.9	16.0
	4				5.5	0.8	0.0	4.0
	5					1.7	0.0	4.0
	6						1.6	0.0
	Total		12.5	23.8	37.4	49.6	46.7	68.9
'Dead' plots	1	85.7	3.5	1.3	3.7	5.4	0.0	0.0
	2		85.8	2.8	4.9	4.1	8.0	0.0
	3			88.7	1.2	5.4	8.0	0.0
	4				85.2	0.0	0.0	0.0
	5					74.3	4.0	4.0
	6						76.0	0.0
	7–10							64.0
Total		85.7	89.4	92.8	95.1	89.2	96.0	68.0

*7–11 stems for 'live' plots; 7–16 stems for 'dead' plots.

multiple linear regression. The standardized variables were mean tree height, change in ecological status, SWRC, ES, pH (subsoil), texture (topsoil), SAR (subsoil), TEC (subsoil), number of stems, basal area of *C. mopane* and basal area of *Salvadora angustifolia*. Because 66% of all fine (<5 mm) *C. mopane* roots occur in the top 400 mm of the soil profile (Smit & Rethman 1998b) in this study area, we considered cation concentrations relevant to dieback would be encountered in this layer. Thus subsoil values were included in the regression. Variables were entered one by one into the regression model according to their contribution to R^2 (adjusted) and reduction in s^2 at each step. Only main effects ($P < 0.05$) were included in the final regression as there was no evidence of interactions. One site located in riparian vegetation exerted undue leverage on the model and was excluded.

RESULTS

Patterns of dieback

Dieback of stem basal area ranged from 1 to 49% in live plots and from 55 to 100% in dead plots. Mean dieback

was $88 \pm 1.6\%$ on 'dead' plots, but only $14 \pm 1.9\%$ on 'live' plots. The three woody species on the plots other than *C. mopane* made up only 5% of woody basal area.

There were 1–16 stems per tree across all plots. One third of the trees had single stems, 50% had two or three stems, and <2% had more than six stems. On 'live' plots, 27% of trees had dead stems, and 17% of stems were dead. On 'dead' plots, 89% of trees had dead stems and 86% of stems had died. Mostly entire trees died on 'dead' plots, whereas single-stem dieback prevailed on 'live' plots. Tree mortality (death of all stems) decreased with increasing stem number per tree (Table 1).

Abiotic variables influencing dieback

There was little variation in mean dieback on the upper, mid and foot slopes on live (12–14%) or dead (86–93%) plots. Dieback did not differ among topographic units on 'live' ($P = 0.722$), 'dead' ($P = 0.449$) or all plots ($P = 0.986$). Nor did dieback differ among soil types on 'live' ($P = 0.438$), 'dead' ($P = 0.434$) or all plots ($P = 0.998$). Means of variables from 'live' and 'dead plots' are shown in Table 2. Slope did not differ between 'live' and 'dead' plots.

'Live' and 'dead' plots did not differ in past Est,

Table 2. Summary of the results from paired *t*-tests ($n = 40$) of variables describing vegetation structure and variables potentially responsible for dieback

Variable	'Live' plots mean (\pm SE)	'Dead' plot mean (\pm SE)	<i>t</i> -value	<i>P</i>
Relief				
Slope (%)	1.2 (\pm 0.09)	1.2 (\pm 0.10)	0.31	0.750
Soil condition				
Surface water retention	3.0 (\pm 0.18)	1.7 (\pm 0.11)	7.9	0.001
Erosion severity	2.3 (\pm 0.14)	2.7 (\pm 0.10)	3.1	0.010
Past ecological status	1.3 (\pm 0.28)	1.3 (\pm 0.28)	0.0	1.000
Current ecological status	0.7 (\pm 0.16)	-1.2 (\pm 0.16)	8.0	0.001
Change in ecological status	-0.7 (\pm 0.30)	-2.5 (\pm 0.32)	8.0	0.001
Soil chemistry				
pH subsoil	7.3 (\pm 0.11)	7.0 (\pm 0.1)	5.2	0.001
Texture topsoil (sand : fines)	2.7 (\pm 0.56)	2.2 (\pm 0.36)	2.2	0.050
Texture subsoil (sand : fines)	3.2 (\pm 1.19)	2.0 (\pm 0.5)	1.8	0.070
Na subsoil (me L ⁻¹)	0.2 (\pm 0.03)	0.4 (\pm 0.09)	2.3	0.050
SAR subsoil	0.06 (\pm 0.011)	0.13 (\pm 0.030)	2.3	0.030
TEC subsoil (me L ⁻¹)	13.0 (\pm 0.6)	15.0 (\pm 0.6)	2.7	0.010
Vegetation variables				
Stem basal area dieback (%)	13.0 (\pm 1.6)	87.0 (\pm 1.7)	36.72	0.000
Tree height (m)	3.7 (\pm 0.19)	3.2 (\pm 0.14)	3.4	0.001
Range for tree height (m)	5.3 (\pm 0.29)	4.3 (\pm 0.25)	4.1	0.000
Stem circumference (cm)	23.0 (\pm 1.1)	25.0 (\pm 1.0)	1.4	0.162
Range in stem circumference (cm)	65.0 (\pm 3.9)	58.0 (\pm 3.9)	1.4	0.080
Total number of stems (per plot)	164.0 (\pm 12.0)	96.0 (\pm 6.0)	6.2	0.001
Stem basal area of <i>Colophospermum mopane</i> (m ² ha ⁻¹)	19.0 (\pm 0.7)	13.0 (\pm 0.7)	8.4	0.001
Stem basal area of <i>Salvadora angustifolia</i> (m ² ha ⁻¹)	0.3 (\pm 0.10)	0.8 (\pm 0.17)	2.3	0.050
Stem basal area of <i>Boscia foetida</i> spp. (m ² ha ⁻¹)	0.5 (\pm 0.15)	0.4 (\pm 0.10)	0.7	0.520
Stem basal area of <i>Lycium austrinum</i> (m ² ha ⁻¹)	0.08 (\pm 0.029)	0.02 (\pm 0.008)	1.9	0.060

Estimates of basal area include live plus dead stems.

suggesting appropriate criteria were used for pairing of sites, but they differed markedly in current Est (Table 2). Plots were originally functioning, on average, as transfer zones with a slight tendency to act as sinks of water and sediment. The current average Est for 'live' plots was similarly positive, but 'dead' plots functioned as a transfer zone tending to a source. The change in Est reveals that both 'live' and 'dead' plots have, on average, become more dysfunctional, but the extent of change on the 'dead' plots was three times that of the 'live' plots (Table 2).

Erosion severity was greater and SWRC was lower on 'dead' than on 'live' plots (Table 2). Although negatively correlated ($r = -0.62$), the relationship between SWRC and dieback appears to be a threshold response with some very high incidence of dieback at $SWRC < 2.5$, but only low levels of dieback at $SWRC > 2.5$ (Fig. 3). The greater SWRC of 'live' plots correlated positively with current Est ($r = 0.73$). This underscores their functioning as sinks. The greater proportion of clay plus silt particles on 'dead' plots would have further reduced water availability during drought.

Differences in soil chemistry (pH, TEC) between 'live' and 'dead' plots (Table 2) were not large, possibly resulting from a change in nutrient cycling following mortality of *C. mopane* trees on 'dead' plots. The variables pH, TEC, and SAR were not correlated with textural variation. Individual cations (Ca, Mg and K) were not at significantly different concentrations in 'dead' and 'live' plots.

Role of competition

There were significant negative correlations between the log of mean stem 'weight' and the log of stem density on 'live' ($r^2 = 75.9, P < 0.001$) and 'dead'

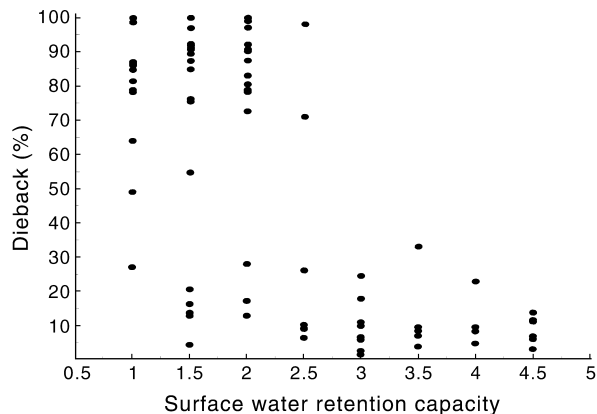


Fig. 3. Percentage dieback of *Colophospermum mopane* in relation to surface water retention capacity. The only site located within riparian vegetation is excluded.

($r^2 = 68.6, P < 0.001$) plots prior to dieback (Fig. 4a). The slopes did not differ ($P > 0.5$), suggesting consistent self-thinning. However, there was a negative correlation of percentage dieback with total basal area ($r = -0.51$) and stem density ($r = -0.47$) of *C. mopane*, and there was a greater stem density and total basal area on 'live' than on 'dead' plots (Table 2). This argues against a role of intraspecific competition in dieback. The self-thinning relationship was still evident on 'live' plots after dieback ($r^2 = 72.2, P < 0.001$) (Fig. 4b) and the slope of this relationship did not differ ($P > 0.5$) from that before mortality. In contrast, no self-thinning relationship was apparent on 'dead' plots after dieback ($r^2 = 5.9, P = 0.08$). Change in the log of mean stem 'weight' on 'live' plots ('weight' of [live plus dead

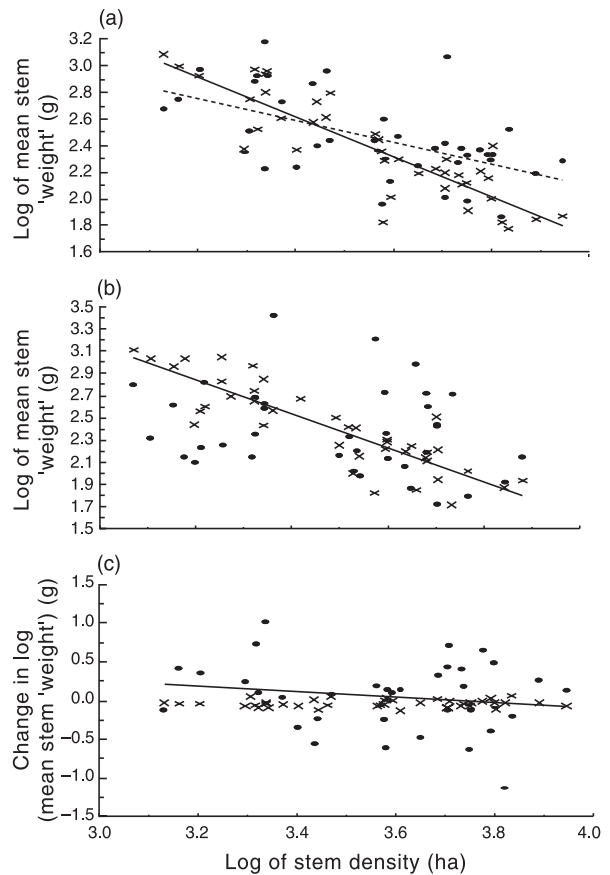


Fig. 4. Relationship between the log of mean stem 'weight' and the log of stem density (ha) for *Colophospermum mopane* on 'live' ($n = 40$) and 'dead' plots ($n = 40$), (a) prior to dieback, (b) after dieback, and (c) change in the log of mean stem 'weight' relative to the log of stem density. Stem density prior to dieback was calculated by adding the number of live and dead stems, while stem density after dieback included only the number of live stems. Refer to text for an explanation of the derivation of mean stem 'weight'. (a) (X) 'Live' plots; (●), 'dead' plots; (—), 'live' linear fit, $y = 7.7 - 1.5x$; (- -) 'dead' linear fit, $y = 7.2 - 1.4x$; (b) (X) 'live' plots; (●), 'dead' plots; (—), 'live' linear fit, $y = 7.6 - 1.5x$; (c) (X) 'live' plots; (●), 'dead' plots; (—), 'dead' linear fit, $y = 2.97 - 0.87x$.

stems] – [live stems]) was negligible (Fig. 4c) and remained constant ($b_1 = 0.015$), irrespective of stem density ($P = 0.665$). This negligible change probably results from low stem mortality. On ‘dead’ plots, however, there was a significant negative ($b_1 = -0.868$) linear relationship between change in the log of mean stem ‘weight’ and the log of stem density ($r^2 = 11.0$, $P < 0.027$), indicating a greater mean individual size after dieback at lower stem densities.

The combined stem basal area of the other three tree species did not differ between ‘live’ and ‘dead’ plots (Table 2). Thus interspecific competition is an unlikely explanation for mortality. Although *S. angustifolia* had significantly greater stem basal area on ‘dead’ plots (Table 2), it was absent on 38% of plots. However, there was a correlation ($r = 0.3$, $P < 0.01$) between its stem basal area and percent dieback of *C. mopane*, so interspecific competition with this species cannot be eliminated as a contributing factor.

Population structure and dieback

For *C. mopane*, mean stem circumference of live and dead trees was similar on ‘live’ and ‘dead’ plots

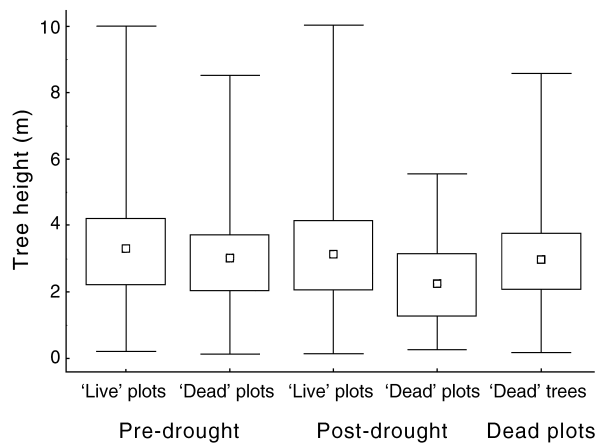


Fig. 5. Box-and-whisker plot of tree height of all *Colophospermum mopane* trees (predrought) on ‘live’ ($n = 2712$) and ‘dead’ ($n = 1519$) plots, of live trees (postdrought) on ‘live’ ($n = 2481$) and ‘dead’ ($n = 236$) plots, and of dead trees on ‘dead’ plots ($n = 1283$).

(Table 2). Trees were significantly taller on ‘live’ than on ‘dead’ plots. However, height may have little ecological significance in explaining dieback (Fig. 5). The tree height distribution of dead trees on ‘dead’ plots was not different ($P > 0.10$) from the distribution of all trees on those plots prior to dieback. Within plots there was no tendency of trees of different heights to suffer different levels of mortality.

Influence of soil type

Vegetation structure and tree size depended on soil type. The distribution of tree height differed among soil types on both ‘live’ and ‘dead’ plots, whereas basal area differed only among ‘live’ plots. No differences were evident for stem density, mean tree height, and mean stem circumference.

Soil types differed in change in Est on ‘live’ ($P = 0.006$) and ‘dead’ ($P < 0.01$) plots, ES ($P = 0.003$) on ‘live’ plots, and SWRC on ‘live’ ($P = 0.034$) and ‘dead’ ($P = 0.048$) plots. These differences may be attributed to differences in texture on ‘live’ ($P = 0.023$) or ‘dead’ ($P = 0.013$) plots. Dundee and Oakleaf soil forms had a greater proportion of sand than Valsrivier and Swartland soils. Sandier soils had a lower ES, a greater SWRC and underwent less change in Est, suggesting that fine-textured soils are more susceptible to degradation and patch dieback. The probability of stem mortality on ‘dead’ plots was affected by soil type ($P < 0.001$), but not by stem basal area or their interaction ($P > 0.05$). Trees growing on Oakleaf soils were less inclined to lose stems than trees growing on the other soil types.

Regression model of dieback

The regression model of dieback was successful, explaining 70% of the variation (Table 3). Variation among plots in dieback was influenced mostly by SWRC and stem density, although ES, Est, vegetation height and pH had effects (Table 3). Less dieback occurred with a greater stem density, greater SWRC, least change in Est, lower pH, and on plots with smaller trees. The poor correlation between stem density and

Table 3. Regression model of percentage mortality (square-root-transformed) of *Colophospermum mopane* ($r^2 = 70.4\%$; $n = 78$)

Added variable	Coefficient	Adjusted R ²	s ²
Surface water retention capacity	-0.9986	48.47	2.243
Stem density	-0.0185	56.70	2.056
Erosion severity	0.7278	61.08	1.949
Change in ecological status	-0.4246	63.10	1.898
Average height	-0.8881	66.85	1.799
pH (subsoil)	-0.9549	70.43	1.699

SWRC ($r = 0.17$) was improved ($r = 0.53$, $P < 0.001$) when 'live' plots containing rills were excluded from the analysis. This suggests an interaction between stem density and SWRC-influenced dieback. Although dieback was associated with decreased erosion, greater erosion severity was associated with the occurrence of sedimented rills, which were found only on 'live' plots (mean rill size: 25 cm deep by 115 cm wide). Sixty per cent of the 33 sites with rills had rills passing through the 'live' plots.

DISCUSSION

Preconditions and causes of patch dieback

Patch dieback is interpreted to have occurred where abiotic factors acted synergistically to reduce available soil water to a level incapable of sustaining the growth of *C. mopane* trees during the severe drought period of 1988–1992. Soil water availability on 'dead' plots was reduced by local and landscape features. For 'dead' compared with 'live' plots, the soil surface did not retain water as efficiently, areas receiving water and sediment changed to sources of these, and erosion was more severe. These variables all reflect a degraded soil surface and a subsequent shift in water availability beyond the threshold of stress of *C. mopane* (cf. Jimenez *et al.* 1985). Rills had consistently developed adjacent to 'dead' plots that would have redistributed run-on to rapid run-off, thereby precluding ponding and infiltration. Roads placed perpendicular to surface flow functioned as rills by intercepting and removing water to drainage lines. Patch dieback was therefore a symptom of a dysfunctional landscape (Tongway & Ludwig 1997) that became manifested during a drought period.

The evidence of self-thinning prior to dieback indicates *C. mopane* experienced intraspecific competition. This was also experimentally shown by tree-thinning trials conducted during the drought in this study area (Smit 1994). Competition, most likely for soil water (Smit 1994) was, however, judged not to be a cause of, but a precondition for patch dieback. Specifically, severe drought-induced dieback suggests intense competition during the drought on 'dead' plots that arose from their dysfunctional character.

The inverse relationship of dieback with stem density is not easily explained. Tree stems may have a similar effect to grass tussocks by intercepting rainfall, impeding surface water flow, and channelling water into the soil (Freudenberger *et al.* 1997). The high litter cover of these *C. mopane* woodlands (up to 42%; O'Connor 1999) is a critical control of infiltration and run-off (Kelly & Walker 1976) that may depend on woodland density. A lower woody density, therefore less litter

cover (O'Connor 1999), would probably intercept less rainfall and expose more bare soil to compaction by rainfall (Finlayson & Statham 1980), thereby reducing infiltration and increasing run-off (Greene *et al.* 1994).

The hypothesis that patch dieback may be a consequence of the senescence of a cohort (Young & Lindsay 1988) was not supported, as the height distribution of dead trees on 'dead' plots covered the height range of live trees prior to dieback. Thus a savanna woodland of heterogeneous rather than homogeneous structure was vulnerable to patch dieback. Synchronous dieback of different-sized trees suggests a species- rather than a size-specific threshold, possibly of soil water, was crossed. This emphasizes the susceptibility of mono-specific compared with species-rich vegetation types to dieback.

The hypothesis that soil salinity may be implicated in dieback (Western & van Praet 1973) was refuted. Although soils were not sodic, the higher sodium concentrations on some 'dead' plots may have predisposed them to dieback through physiological 'drought' compounding natural drought. Dieback, however, occurred on sites across a range of Na concentrations.

Topo-edaphic variation in dieback

Although dieback did not differ among topography, slope or soil type, this study was restricted to dieback areas. However, *C. mopane* was also the dominant species on sandier soils derived from gneisses or aeolian sandstones (O'Connor 1992), on which no patch dieback was found. Sandy soils are not prone to the formation of rills and maintain infiltration, even when cover is poor (Barnes & Franklin 1970). At a broader landscape level therefore soil type, particularly texture and its relationship with SWRC, ES, and Est, was a key control on patch dieback.

Studies on rills have been concerned with water flow and have neglected to take into account their potential influence on vegetation. Rills are usually considered to promote a loss of water by converging flow of water and sediment from upslope along concentrated routes (Finlayson & Statham 1980). However, if rills become sedimented then the sediment can store water that can become available to adjacent trees.

Dieback: Manifestation of a dysfunctional landscape

Patch dieback of the prolific *C. mopane* signifies a dysfunctional system. The degradation of this system coincides with the 50-year period of commercial live-stock ranching. Prior to ranching, the area formed part of a large, unfenced region occupied by wildlife. Aerial

photography from the early time (1955) of agricultural occupation until 1987 provides diverse evidence of degradation. This includes the initiation and rapid expansion of areas of bare soil and gullying (T. G. O'Connor, unpubl. data), invasion of hydromorphic grassland by woody species (O'Connor 2001), a loss of perennial grasses and an increase in bare soil, especially on the fine-textured soils of the study area, which are vulnerable to sealing, run-off and erosion (O'Connor 1983, 1999), and a 20% increase in the cover of *C. mopane* woodland (O'Connor 1983). Most of these changes were precipitated by the severe, extended drought of the 1960s.

The occurrence of patch dieback of *C. mopane* between 1988 and 1992 is therefore interpreted as a consequence of the preconditioning of the system by an increase in *C. mopane* to levels of intense intertree competition (Smit 1994) and an increase in the drought proneness of fine soils through erosion, exacerbated in places by high Na concentrations. Water received during non-drought years was apparently sufficient for survival of these long-lived trees. Previous droughts (1968, 1973) did not result in patch dieback, apparently because the dieback areas were still functioning as sinks of water and sediment. Despite *C. mopane*'s drought tolerance (Prior 1991; Smit 1994), its demand for water could not eventually be met on degrading patches, but could on patches functioning as run-on sinks.

A widespread model of rangeland degradation is an increase in the woody component with associated increases in soil erosion and water lost through run-off (Schlesinger *et al.* 1990). The present study indicates degradation can proceed another step in which previously increasing woody species suffer decline. On dieback patches then, productivity has been seriously impaired, carbon sequestration has become minimal, and soil and nutrient loss continue unabated. These are all indicators of an irreversible change in system functioning.

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APPENDIX I

Table A1. Surface water retention capacity (SWRC), erosion severity (ES), and ecological status (Est) rankings

Class	Litter cover (%) / Status	Description
Surface water retention capacity		
0.5	0–5	No incorporation of litter
1.0	6–10	Smooth surface with very little sediment, capping
1.5	6–10	Intermediate between 1 and 2
2.0	11–25	Flakey surface, cracks present, hoof action, broken cap
2.5	11–25	Intermediate between 2 and 3
3.0	26–50	Uneven surface/relief, closed depressions (0–2.5 cm)
3.5	26–50	Intermediate between 3 and 4
4.0	51–75	Partially or fully sedimented rills (2.5–10 cm)
4.5	51–75	Intermediate between 4 and 5
5.0	76–90	Partially or fully sedimented rills (>10 cm)
5.5	91–100	Litter has moderate contact with soil
6.0	100	Litter has intimate contact with soil
Erosion severity		
4.0	Insignificant	Substantial herbaceous cover, litter accumulation, no surface flow
3.5	Intermediate to 3 and 4	Same as above but with pedestalling and weak sheeting
3.0	Slight	Moderate pedestalling, sheeting and scalding
2.5	Intermediate to 2 and 3	Severe pedestalling, sheeting and scalding, terracettes with shallow walls
2.0	Moderate	Same as above but terracettes with substantial walls, shallow rills
1.5	Intermediate to 1 and 2	Extensive pedestalls, sedimented rills, half exposed gravel on soil surface
1.0	Extensive	Steep-walled rills exposing roots or bedrock, stoney matrix on soil surface
Ecological status		
3	Sink	Rills lead into and end in a site, deposition of sediment, no loss
2	Sink tending to transfer	Slight loss of sediment, but overall a net gain
1	Transfer tending to sink	Slight gain of sediment (run-on), rills passing on outskirts or through a site
0	Transfer	Signs of flow and deposition, net gain of sediment = net loss
-1	Transfer tending to source	Slight loss of sediment (run-off)
-2	Source tending to transfer	Slight gain of sediment, but overall a net loss
-3	Source	Rills originate from a site, flow of sediment, no gain

Surface water retention capacity rankings were increased by 0.5 if the observed litter cover exceeded the value defined for each class, and if the litter was moderately incorporated with the soil.