

Litter dynamics across browsing-induced fenceline contrasts in succulent thicket, South Africa

R.G. Lechmere-Oertel^a, G.I.H. Kerley^a, A.J. Mills^{b,*}, R.M. Cowling^c

^a Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, Box 77000, Port Elizabeth 6031, South Africa

^b Department of Soil Science, Stellenbosch University, Private Bag XI, Matieland, 7602, South Africa

^c Department of Botany, Nelson Mandela Metropolitan University, Box 77000, Port Elizabeth 6031, South Africa

Received 3 September 2007; received in revised form 27 March 2008; accepted 16 April 2008

Abstract

Semi-arid succulent thicket in South Africa has experienced extensive livestock-induced transformation, reflected in extensive structural changes and loss of biodiversity, biomass and soil carbon. The ecological mechanisms contributing to this transformation are not fully understood but are believed to include the breakdown of ecosystem processes including litter production and decomposition, which are rate-limiting steps in nutrient cycling and incorporation of organic matter into the soil. In this study we investigated the effect of transformation on litter production and decomposition in succulent thicket. We measured litter production and decomposition of four dominant perennial woody plants (*Euclea undulata*, *Pappaea capensis*, *Portulacaria afra* and *Rhus longispina*) across replicated fenceline contrasts. Litter production was measured over 14 months using mesh traps. Decomposition was measured over 15 months using a combination of litterbags and leaf packs. Litter production in succulent thicket was very high for a semi-arid system (approaching that of temperate forests), with the leaf- and stem-succulent *P. afra* contributing the largest component. Transformation caused a significant reduction in litter production at a landscape scale (4126 vs 2881 kg/ha/yr), primarily due to reduced cover of *P. afra*. Surprisingly, transformation had few significant effects on the rate of decomposition of litter, possibly due to a switch from biotic to abiotic decomposition processes. The perennial vegetation in succulent thicket, particularly *P. afra*, appears to play a critical role in the maintenance of the ecosystem by facilitating the incorporation of organic matter into soil. Transformation of succulent thicket leads to a disruption of the carbon cycle, ultimately resulting in degradation of the ecosystem. Successful restoration is likely to depend on increasing the rates of organic matter return to soils. *P. afra* is a potential carbon restoration pump as it is both drought-resistant and easily propagated from cuttings.

© 2008 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: Browsing impacts; *Euclea undulata*; Nutrient cycling; *Pappaea capensis*; *Portulacaria afra*; *Rhus longispina*; Succulent thicket

1. Introduction

In the semi-arid rangelands of the world, transformation as a result of unsustainable stocking rates is primarily recognised through structural changes in the vegetation. This is particularly evident in the arid succulent thickets (Vlok et al., 2003) of South Africa. Up to 70% of this vegetation has been transformed (Lloyd et al., 2002), in the sense that there have been significant losses in biomass. Intact succulent thicket has unusually high

biomass for a semi-arid vegetation (Mills et al., 2005a) and is loosely organised into a two-phase mosaic of perennial vegetation patches (5–50 m across) and bare ground (Fabricius, 1997; Kerley et al., 1999; Lechmere-Oertel et al., 2005). These patches comprise evergreen to weakly deciduous trees (<5 m tall), emergent from a matrix of woody and succulent shrubs, often dominated by the evergreen leaf- and stem-succulent shrub *Portulacaria afra* (L.) Jacq. (Didiereaceae; the common name is ‘spekboom’, which translates from Afrikaans as ‘fat tree’). The *P. afra* matrix is inter-woven with a variety of multi-stemmed deciduous and spinescent shrubs. The nutrient- and clay-rich soil (derived from shales and mudstones) beneath the vegetated patch is covered by a thick (up to c. 10 cm) layer of plant litter.

* Corresponding author. Fax: +27 21 7151560.

E-mail address: mills@sun.ac.za (A.J. Mills).

P. afra is unusual in that it is able to switch between C3 and CAM photosynthetic pathways, depending on soil moisture (Guralnick et al., 1984; Guralnick and Ting, 1987). This enables *P. afra* plants to assimilate carbon even in times of drought. This is an appropriate strategy given the semi-arid climate (mean annual precipitation [MAP] of 25–400 mm distributed throughout the year, with spring and autumn maxima). Rainfall reliability is moderate (CV of 35% for MAP) (South African Weather Bureau, 2002), although droughts of several months do occur frequently, mainly when little rain is recorded in one of the equinoctial seasons. Temperatures range from hot (mean daily temperature of hottest month: 39 °C, highest recorded: 46 °C) to cool (mean daily temperature of coldest month: 15 °C, lowest recorded: –9 °C) with a mean daily fluctuation of 14 °C.

Unsustainable browsing of succulent thicket, mainly by goats, leads to the loss of *P. afra* and other succulents and multi-stemmed shrubs, resulting in a ‘pseudo-savanna’ dominated by a field layer of ephemeral or weakly perennial grasses and dwarf karroid shrubs and scattered, umbrella shaped (owing to browsing) individuals of canopy trees, namely *Pappaea capensis*, *Euclea undulata* and *Schotia afra* (Lechmere-Oertel

et al., 2005). During this process, the canopy of the perennial patches is opened by livestock, exposing the litter layer and soil surface to increased solar radiation and raindrop impact. This goat-induced process of transformation may take several years to occur, depending on stocking regimes. Restoration of transformed succulent thicket does not occur spontaneously (Vlok et al., 2003; Sigwela, 2004), and transformation ultimately leads to degradation of the system measured as structural simplification (Hoffman and Cowling, 1991), loss of biomass (Lechmere-Oertel et al., 2004; Mills et al., 2005a), loss of soil organic matter (SOM) (Mills and Fey, 2004a,b; Lechmere-Oertel et al., 2005) and soil erosion (Lechmere-Oertel, 2003). In a state of extreme transformation, a depleted and dying canopy tree layer is the only remnant of the original perennial vegetation (Fig. 1).

Leaf litter and SOM play a key role in the maintenance of productivity in semi-arid ecosystems. Leaf litter modifies the local physical environment, influences germination and establishment success (Molofsky et al., 2000; Boeken and Orenstein, 2002), controls the distribution and activity of soil organisms (Steinberger et al., 1984; Whitford, 2002), increases soil water

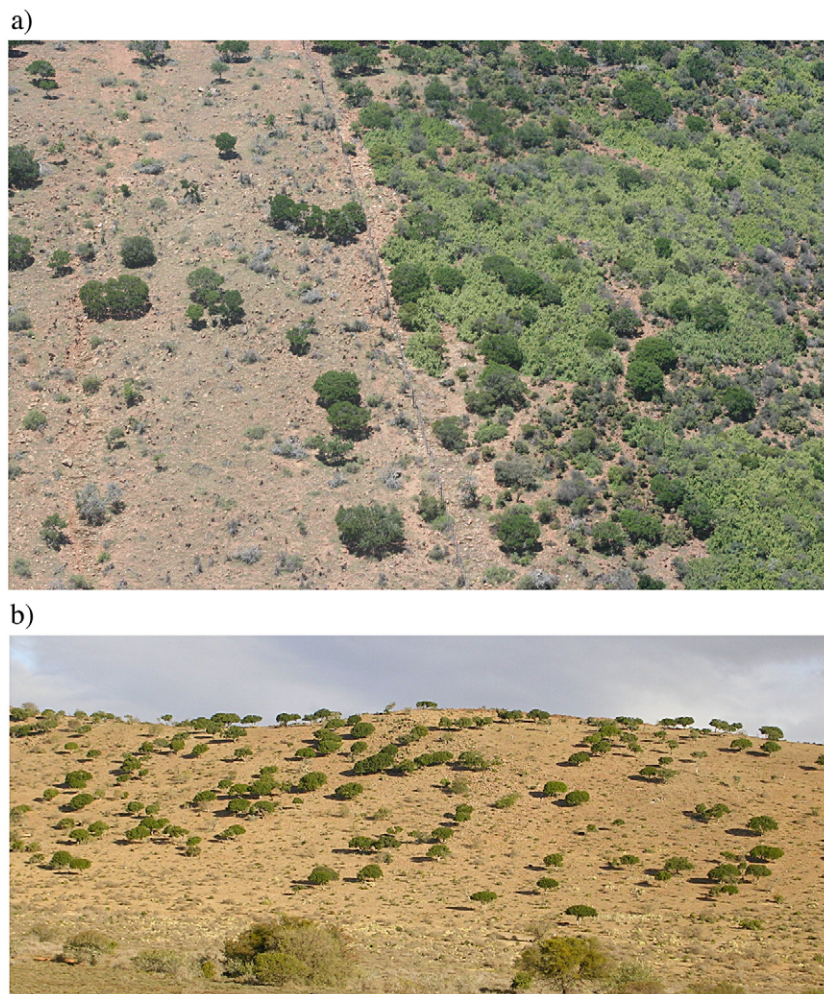


Fig. 1. (a) A fenceline contrast of intact and degraded thicket (photo: M. Powell), and (b) remnant *Pappaea capensis* trees in a degraded thicket (photo: A. Mills). Both photographs were taken west of Steytleville in the foothills of the Groot Winterhoek Mountains.

availability and changes the soil microclimate (West, 1979; Whitford, 2002). Soil organic matter influences key soil properties such as water retention, bulk density, erodability, infiltration (Mills and Fey, 2003, 2004c) and the distribution and abundance of organisms (Whitford, 2002). The rate at which litter is produced, decomposed and incorporated into the soil, together with other factors such as Al content (Percival et al., 2000), have a strong influence on SOM content. Changes in litter dynamics are consequently likely to have a cascading effect across many ecosystem processes.

Although the patterns of transformation in succulent thicket have been well documented (Hoffman and Cowling, 1990; Hoffman and Cowling, 1991; Stuart-Hill, 1992; Kerley et al., 1995; Lloyd et al., 2002; Lechmere-Oertel et al., 2004), no research has been done on understanding the mechanisms underpinning the transformation process. In this study, we compared the rates of litter production and decomposition in relatively intact and transformed thicket across replicated fenceline contrasts, *i.e.* a snapshot natural experiment.

We predicted that perennial plants in intact thicket would be less stressed in terms of water and nutrient supply, and would consequently replace their leaves more often than plants in degraded thicket, leading to greater rates of litter production. Effects of transformation on rates of decomposition were more difficult to predict. On the one hand, removal of the plant canopy is likely to increase the rate of decomposition of surface litter due to: i) greater exposure to UV light (Moorhead and Callaghan, 1994); ii) greater exposure to light rainfall events, and iii) warmer soil surface temperatures. On the other hand, lower rates of decomposition may be expected due to reduced soil water availability as a result of greater rates of evaporation in transformed thicket.

2. Methods

2.1. Study area

The study area was located in the moderately steep (15–25°), north-facing foothills of the Groot Winterhoek Mountains near Port Elizabeth, Eastern Cape Province, South Africa. Five sites, each comprising relatively intact and transformed thicket separated by a fence were identified. The vegetation at the sites is an arid form of Sundays Thicket termed Sundays Spekboomveld (Vlok et al., 2003; Hoare et al., 2006). Transformation status of the sites was subjectively assessed based on

the biomass of the woody thicket component. Above-ground biomass (dry matter) estimates for intact thicket were 67,000–97,000 kg⁻¹ ha⁻¹, and 9500–23,900 kg⁻¹ ha⁻¹ for transformed thicket (Lechmere-Oertel, 2003).

Our study was conducted over a 14-month period. Although this is a relatively short period for observing litter and decomposition processes, our focus was on the comparison between transformed and untransformed states.

2.2. Litter production

Litter production was measured for a dominant perennial species representing each of the four main growth forms (Table 1). Litter traps (0.5 mm mesh, 0.5 m × 0.5 m square bags suspended between four metal rods) were placed directly beneath the canopies of three individuals of each species investigated (Table 1) on either side of the fence line contrast (24 traps per site). The traps were adjacent to the main stem, near the centre of the canopy, and were not exposed to litterfall from other species. Total litter (leaves, twigs, small branches and seeds) was collected from the traps every 60–90 days for 14 months (May 2001–October 2002), dried at 40 °C and weighed. The data for each trap were pooled for the total sampling period (506 days) and transformed using a natural log. The mean monthly rainfall at Adolphskraal and Tygerhoek (weather stations located within the study region) for the period May 2001–September 2002 was 26 and 36 mm, respectively (South African Weather Bureau, 2002). This equates to approximately 310–430 mm MAP, hence a relatively wet period for the study site region.

Annual litter production (kg m⁻² yr⁻¹) was compared across the fenceline contrasts using a separate factorial ANOVA for each species. A landscape estimate of litter production (kg ha⁻¹ yr⁻¹) was calculated by extrapolating the litter production (kg m⁻² yr⁻¹) of each growth form representative, and multiplying it by the proportional cover (Lechmere-Oertel et al., 2005) of that growth form. The annual litter production of the non-perennial grass and forb field layer was estimated as 50% (West 1979) of the standing biomass (Lechmere-Oertel et al., 2005).

2.3. Litter decomposition

The measurement of mass loss of litter placed in 1 mm mesh bags is widely used to estimate litter decomposition rates in

Table 1
Some biological and physiognomic characteristics of the species used in the experiments

Species	Family	Growth form ^a	Foliage	% Cover ^b	Biomass (kg ha ⁻¹)
<i>Euclea undulata</i>	Ebenaceae	Small emergent tree, <3 m	Evergreen, sclerophyllous	8.2 (6.5)	–
<i>Pappea capensis</i>	Sapindaceae	Canopy tree, <5 m	Semi-deciduous, sclerophyllous	16.3 (10.0)	9 190 ^c
<i>Portulacaria afra</i>	Didiereaceae	Multi-stemmed leaf-succulent woody shrub, <3 m	Evergreen, succulent	57.7 (27.1)	97 978 ^d
<i>Rhus longispina</i>	Anacardiaceae	Multi-stemmed spinescent woody shrub, <4 m	Evergreen, mesophyllous	4.1 (4.7)	–

^a The heights in the growth forms are based on individuals measured in the field, not the maximum potential under more mesic conditions.

^b Percentage cover (standard deviation) is the average of five 100 m transects in each of the five intact sites.

^c Biomass was estimated by weighing ten dead trees and extrapolating to area using proportional cover and tree density data.

^d Biomass was estimated by harvesting all above-ground material in ten 1 m² quadrats at each of the five sites, and extrapolating to area using proportional cover.

field studies (Swift et al., 1979; Huang and Schoenau, 1997; Guo and Sims, 1999; Joshi et al., 1999); notwithstanding the fact that detritivores larger than 1 mm do not have access to the litter. A combination of litterbags and unmeshed leaf packs was used to estimate rates of decomposition in this study. A leaf litter mix was made from freshly harvested leaf material of *E. undulata*, *P. afra* and *P. capensis* in a ratio that approximately reflected their proportional abundance at the sites. Approximately 2 g of the dried litter mix was heat-sealed into 10 × 10 cm 1-mm-nylon mesh bags. Leaf packs were made by threading fresh leaves of two dominant perennial species (*P. capensis* and *P. afra*) onto a pre-weighed 10 cm section of thin galvanised wire. Once threaded, the wire ends were twisted to prevent the loss of material, and the packs were dried at 40 °C, and weighed.

Quadrats laid out in a split-plot factorial experimental design were used to evaluate the rates of litter decomposition from the leaf litterbags and packs. Five each of the mixed bags, *P. capensis* packs and *P. afra* packs were pinned onto the soil surface within each 1 m × 1 m quadrat. Three such quadrats were placed in each of the two dominant habitats (under a canopy tree or in the matrix vegetation) on either side of the transformation contrast. If there was litter present in the quadrat, then the bags and packs were nestled into it until covered. The quadrat was protected from curious domestic animals with 20 mm mesh wire.

A mixed bag, *P. capensis* pack and *P. afra* pack were randomly harvested from each quadrat approximately every 3 months for 15 months (May 2001–October 2002), transported to the laboratory in separate paper bags and dried at 40 °C. After reweighing, the samples were ashed at 550 °C for 6 h to estimate contamination by inorganic soil particles (Potthoff and Loftfield, 1998). Percentage mass loss was calculated using Eq. (1). Mass loss due to decomposition was calculated per kg of dry litter as a function of time using Eq. (2). Annual decomposition rate coefficients k were calculated using the single negative exponential decay function (Olson, 1963), reworked into Eq. (3). This constant is useful for comparative purposes (Stamou et al., 1994; Carnevale and Lewis, 2001).

$$\text{Mass Loss(\%)} = (M_t/M_0) \times 100 \quad (1)$$

$$\text{Rate of Loss(g kg}^{-1} \text{ d}^{-1}) = [(M_0 - M_t)/(M_0/1000)]/t \quad (2)$$

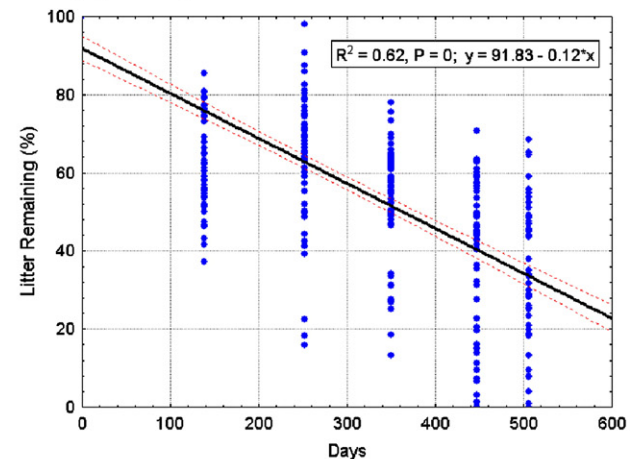
$$\text{Decomposition constant } k = -[\ln(M_t/M_0)]/(t/365) \quad (3)$$

where M_0 is the initial mass of litter, M_t is the ash-free mass of retrieved litter, and t is the number of days the litter was in the field.

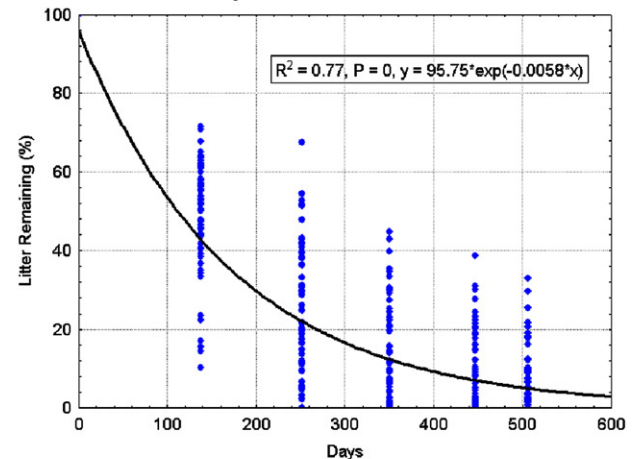
Control bags and packs were harvested immediately after being set out, weighed and ashed to measure mass change due to handling and inorganic material present in the fresh litter. Significant differences within the percent litter remaining (arcsin-transformed), rate of mass loss (ln-transformed) and decomposition constant (ln-transformed) were identified for impact and habitat effects (and interactions) using separate generalised linear models for each litter type. Number of days

(t) was used as a continuous covariable. Tukey *post-hoc* HSD tests were used to separate the means where there were significant differences in the treatment effects.

a) *Pappea capensis*



b) *Portulacaria afra*



c) Mixed bags

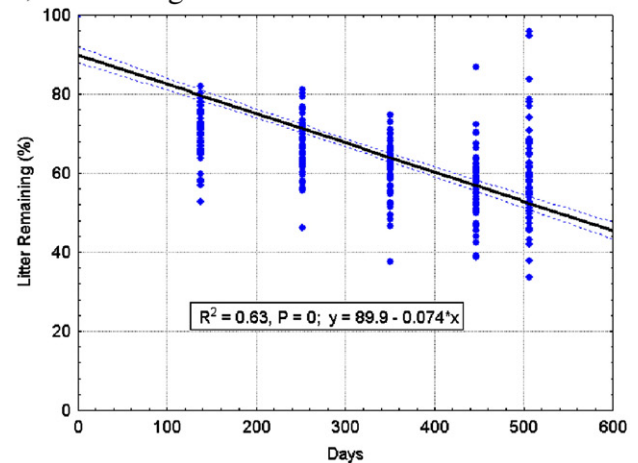


Fig. 2. The percentage of original litter mass remaining as a function (solid line) of days in the field for (a) *Pappea capensis*, (b) *Portulacaria afra*, and (c) mixed litter bags. The function with the greatest r -squared value was chosen from linear, logarithmic, power and exponential fits.

Table 2
Mean (standard deviation) litter production at a small patch ($\text{g m}^{-2} \text{yr}^{-1}$) and landscape scale ($\text{kg ha}^{-1} \text{yr}^{-1}$)

Growth form	Ephemeral field layer	Canopy trees		Woody shrubs	Succulent shrubs	Total
Representative species	50% biomass	<i>Pappia capensis</i>	<i>Euclea undulata</i>	<i>Rhus longispina</i>	<i>Portulacaria afra</i>	
<i>Intact</i>						
Litter yield ($\text{g m}^{-2} \text{yr}^{-1}$)	0.300	335 (116)	338 (146)	120 (259)	464 (135)	
Proportional cover ^a	0.21	0.21		0.20	0.55	
Landscape yield ($\text{kg ha}^{-1} \text{yr}^{-1}$) ^b	630	704		240	2552	4126
<i>Transformed</i>						
Litter yield ($\text{g m}^{-2} \text{yr}^{-1}$)	0.300	151 (99)	132 (83)	132 (132)	453 (154)	
Proportional cover	0.86	0.06		0.09	0.02	
Landscape yield ($\text{kg ha}^{-1} \text{yr}^{-1}$)	2580	91		119	91	2881

Interactions between the species, transformation effects and significant differences from the ANOVAs are shown in Table 3.

^a Totals of the proportions may exceed 1 due to overlapping of plants in a growth form.

^b Landscape scale data were calculated by extrapolating the patch scale data proportionally to percentage cover data (see methods for more details).

2.4. Soil temperature and incipient radiation

Soil temperature at 5 cm below the surface was measured every hour for 373 days from 17/03/2001 to 26/03/2002 using HOBO-H8 loggers with an external HA-6 temperature probe (Onsetcomp Inc., 2001). Twenty loggers were distributed over representative examples of the two habitats on either side of the transformation contrast at each site: intact canopy, intact matrix, transformed canopy and transformed matrix. As there were recording problems with some of the loggers, the data were cleaned to remove extreme outliers that were obviously incorrect, e.g. soil temperatures of -50 °C. The data were summarised (min., max. and SD) by treatment at daily intervals. The summary data were compared between treatments using a factorial ANOVA.

The difference in incident radiation beneath *P. capensis* canopies across the transformation contrast was determined using a Licor LI 185A quantum light meter fitted with a flat sensor. Light readings were taken at c. noon on a clear summer day under ten canopies on either side of the transformation contrast at each site, i.e. a total of 100 readings. A light reading in the open was taken immediately after each canopy reading. The percent change in incident radiation was compared across the transformation contrast using a factorial ANOVA after arcsin transformation of the data. All statistical analyses above were performed in Statistica 6.1 (Statsoft Inc., 2001).

3. Results

3.1. Litter production

Exploratory data analysis of annual litter production showed that the effects of transformation and habitat were growth form specific (Fig. 2). The two canopy tree species, *E. undulata* and *P. capensis*, produced c. 60% and 55%, respectively, less litter in transformed than intact thicket (Table 2), representing a significant transformation effect for these two species (Table 3). There were no significant differences for the succulent shrub *P. afra* and the spinescent multi-stemmed shrub *Rhus longispina*. Litter production of all species was significantly dependent on

site location (Table 3). Irrespective of transformation status, *P. afra* produced more than three times the amount of litter than the other three species (Table 2).

At a landscape scale in intact thicket, succulent shrubs and canopy trees produced 60% and 17%, respectively, of the total litter (Table 2). By contrast, the ephemeral field layer contributed 90% of the litter produced in transformed thicket. The total annual production of litter at a landscape scale was 30% lower in transformed than intact thicket (Table 2). A comparison restricted to the litter production of perennial plants only, showed that transformed thicket produced 90% less litter, most of that difference being associated with a decrease in the proportional area of *P. afra* (Table 2).

3.2. Litter decomposition

Transformation had no significant effect on decomposition for any of the litter types, and site location had the only significant effect on all the decomposition variables (Table 4). There was a trend of an increasing loss rate and decomposition constant from site 1 to site 5, a reflection of decreasing aridity. The only significant treatment effect was the interaction between site and transformation for *P. afra* litter (Table 4). The main qualitative difference between the litter types was that *P. afra* litter had a higher decomposition constant *k* (mean, standard deviation, range: 2.18, 1.08, 0.15–6.04) than *P. capensis* (0.89, 0.56, 0.03–3.51) or the mixed litter (0.58, 0.25, 0.03–

Table 3
Results of a factorial ANOVA of patterns of litter production (log transformed) in relation to site and transformation status

Treatment effect	df	<i>Euclea undulata</i>	<i>Pappia capensis</i>	<i>Portulacaria afra</i>	<i>Rhus longispina</i>
Site	7	9.64**	1.34**	5.20*	1.79 ^{ns}
Transformation	1	91.31**	59.98**	0.56 ^{ns}	0.87 ^{ns}
Site * transformation	7	6.28**	3.29*	2.14 ^{ns}	60 ^{ns}
Error MS	32	0.164	0.166	0.059	0.247

Each species had a separate ANOVA.

Significance levels: * $p < 0.01$, ** $p < 0.001$, ^{ns} = non-significant.

Significant values are highlighted in bold.

Table 4
F-values and degrees of freedom (*df*) for the three decomposition response variables from the split-plot nested ANOVA for the three litter types

Model effect	<i>df</i>	Loss rate (g kg ⁻¹ d ⁻¹)	Decomposition constant (<i>k</i>)	Remaining litter (%)
<i>Mix bags</i>				
Site	4	1.75	2.64*	4.73**
Transformation	1	0.63	1.15	2.97
Site * transformation	4	0.80	0.23	2.32
Habitat	1	0.66	0.90	1.29
(site * transformation)				
Error MS	279	0.20	0.21	17.5
<i>Pappea capensis</i> packs				
Site	4	7.56**	11.14**	9.77**
Transformation	1	0.71	0.88	0.53
Site * transformation	4	0.43	0.58	0.31
Habitat	1	1.37	1.44	0.60
(site * transformation)				
Error MS	268	0.20	0.29	143.2
<i>Portulacaria afra</i> packs				
Site	4	6.11**	20.95**	13.33**
Transformation	1	1.86	3.53	3.72
Site * transformation	4	0.74	2.53*	0.82
Habitat	1	0.50	1.48	0.56
(site * transformation)				
Error MS	238	0.11	0.19	215.6

Significance levels: * $p < 0.05$, ** $p < 0.01$, ^{ns} = non-significant.

Loss rate and *k* were natural log transformed and remaining litter (%) was arcsin-transformed prior to analysis.

1.69) for all habitat and transformation treatments. Inspection of the mass loss curves for the litter types (Fig. 2) showed that *P. afra* litter had the steepest rate of mass loss of all litter types.

3.3. Soil temperature and incipient radiation

There were significant differences ($F = 54.0$, $df = 4$, $p < 0.001$) in soil temperatures between both the habitat and transformation treatments (Table 5). The range and variance of soil temperatures (including upper and lower extremes) were significantly higher in transformed sites for both habitat types. The average daily maximum soil temperature was 52% and 30% higher in transformed sites for matrix and canopy habitats, respectively (Table 5). The average daily minima in matrix and

canopy habitats were 21% and 23% lower, respectively. Both the highest (50.7 °C) and lowest (0.7 °C) temperatures recorded were in the transformed matrix. The daily amplitude of soil temperature was two to three times higher in transformed thicket for the canopy and matrix habitats respectively (Table 5). These patterns held true for both the canopy and matrix habitats, although were more pronounced in the latter.

P. capensis canopies reduced incipient radiation by 85% (SD=5%). Transformation had a significant effect on the percent reduction in light ($F = 7.70$, $df = 1$, $p = 0.007$). Canopies in transformed and intact thicket reduced radiation by 84% (SD=2.7%) and 89% (SD=1.4%), respectively.

4. Discussion

4.1. Impacts of transformation on litter production and decomposition

Litter production in intact succulent thicket is comparable to that of a number of other ecosystems in higher rainfall regimes, such as temperate forests, dry tropical forests, and Mediterranean-type shrublands (Table 6). This may be related to the unusually high biomass of succulent thicket for a semi-arid ecosystem (Mills et al., 2005b), particularly of the dominant *P. afra*, emphasising the keystone role of this species in maintaining carbon cycling. Transformation of succulent thicket reduces litter production to a level more comparable with desert and dry savanna systems (Table 6). Desert perennial shrublands annually shed between 30% and 60% of their total above-ground biomass as litter (West, 1979). In forests, the range is 1% to 5% (West, 1979). Although the data presented here are for one year only, intact succulent thicket shed 4–6% of its standing above-ground biomass, and transformed succulent thicket 12–32%.

The reduced litter production of the canopy tree growth form can be understood in terms of reduced canopy volumes owing to browsing, combined with the drought-resistant nature of the plants. We do not understand yet why the trees are more affected by transformation and the shrubs less so. This will require more information on the ecophysiology of the species in transformed and untransformed sites. The absence of response of *P. afra* to transformation suggests strong drought-resistance. *P. afra* has

Table 5
Soil temperature (°C) data in canopy and matrix microhabitats in intact and transformed thicket

Habitat * transformation	Lowest <i>t</i> recorded	Highest <i>t</i> recorded	Means of daily summary ¹ ($n = 375$ days)				Mean difference (transformed- Intact) ²
			Minimum	Mean	Maximum	Range	
<i>Canopy</i>							<i>Canopy</i>
Intact	7.8	42.9	15.9 (3.5) ^a	19.0 (4.1) ^{a,b}	24.2 (6.3) ^a	8.3 (4.1) ^a	Min: -3.3±2.9
Transformed	0.7	48.0	12.2 (3.8) ^b	19.5 (4.6) ^b	31.1 (7.4) ^b	18.7 (5.9) ^b	Max: 12.0±4.2
<i>Matrix</i>							<i>Matrix</i>
Intact	5.4	36.6	15.6 (3.6) ^a	18.7 (3.4) ^a	23.2 (5.0) ^a	7.6 (4.1) ^a	Min: -3.7±2.0
Transformed	0.7	50.7	12.3 (3.7) ^b	22.0 (5.0) ^c	35.1 (7.2) ^c	22.8 (6.1) ^c	Max: 6.9±5.0

Different letters indicate significant *post-hoc* Tukey HSD tests ($p < 0.001$) within a temperature variable.

¹ Daily summaries were generated for each habitat at each site ($n = 5$ sites). Mean data are the averages (SD) over time (375 days).

² The mean difference is the average of the daily difference (transformed-intact for each site) in minimum and maximum temperatures in each habitat.

Table 6

Litter production in transformed and intact *Portulacaria afra* thicket (shown in bold) in comparison with a range of ecosystems worldwide

Ecosystem	Additional information	Total litterfall (kg ha ⁻¹ yr ⁻¹)	Source
Desert	<i>Larrea</i> shrubland, Nevada	194–530	Strojan et al. (1979)
Desert	<i>Haloxylon</i> shrubland, Russia	440	West (1979)
Fynbos	<i>Protea</i> and <i>Erica</i> shrubland, South Africa	700	Witkowski (1989)
Semi-arid woodland	<i>Eucalyptus crebra</i> , Australia	720	McIvor (2001)
Desert	<i>Eurotia ceratoides</i> , Russia	920	West (1979)
Semi-arid rangeland	<i>Atriplex vesicaria</i> , Australia	1094	West (1979)
Semi-arid woodland	<i>Eucalyptus drepanophylla</i> , Australia	1270	McIvor (2001)
Pine woodland	<i>Pinus pinaster</i> , Spain	1728	Santa Regina (2001)
Oak woodland	<i>Quercus rotundifolia</i> , Spain	2320	Santa Regina (2001)
Desert	<i>Artemisia tridentata</i> , Russia	2500	West (1979)
Transformed thicket	'Pseudo-savanna'	2880	This study
Dry woodland	Russia	2900	West (1979)
Cool temperate forest	Global average value	3100	Bray and Gorham (1964)
Chaparral	Mixed community, California	3550	Mooney et al. (1977)
Intact thicket	<i>Portulacaria afra</i> dominant	4100	This study
Tropical seasonal forest	Average value, Ivory Coast	4440	West (1979)
Warm temperate forest	Global average value	4900	Bray and Gorham (1964)
Temperate oak forest	Average value, Greece	5003	Stamou et al. (1994)
Equatorial forest	Global average value	9700	Bray and Gorham (1964)

several adaptations to cope with prolonged drought stress, such as leaf succulence and the ability to switch between C3 and CAM photosynthetic pathways (Guralnick et al., 1984; Guralnick and Ting, 1987). It is important to note that *P. afra* produced the most litter of all the species tested. This suggests that, at a landscape scale, the significant reduction of litter production is due to the loss of biomass of the component species, particularly of the highly palatable *P. afra*.

Despite the very significant differences in the soil microclimate between the different habitats and across the transformation contrasts, there were surprisingly few significant differences in the decomposition rates and constants (*k*). This is potentially explained by different transformation effects that can decrease as well as increase decomposition. Decreased biotic activity on transformed sites could be expected as a result of reduced litter cover (Steinberger et al., 1984), soil aridity and extreme soil temperatures (Mackay et al., 1986; Cepeda-Pizarro and Whitford, 1990). However, an increase in physical breakdown via raindrop impact (Strojan et al., 1987), and photo-oxidation (Schaefer et al., 1985; Whitford, 2002) may also occur. Indeed, Moorhead and Reynolds (2002) suggest that abiotic forces may be the primary control of decomposition in semi-arid climates, which is consistent with Noy-Meir's (1973) hypothesis of increased abiotic controls in desert systems. Additional effects requiring further research include: i) reduced rainfall interception by the thicket canopy and therefore periodically greater soil water availability in transformed sites; and ii) warmer soil temperatures potentially promoting microbial activity.

4.2. Implications for ecosystem functioning and productivity

The high litter production by *P. afra* may explain the unusually high levels of SOM found in intact succulent thicket (5–10%, Lechmere-Oertel et al., 2004; Mills and Fey, 2004a)

compared to other semi-arid systems; suggesting that it is a keystone species. The combination of the reduction in the quantity of litter produced in transformed succulent thicket and the switch from perennial to ephemeral growth forms (and hence the type of litter) will reduce the incorporation of organic matter into the soil (Whitford et al., 1998; Knoepp et al., 2000; Whitford, 2002). This is evident in the near absence of any accumulated litter in transformed thicket compared to up to 90% litter cover (>5 cm deep) in intact thicket (Lechmere-Oertel et al., 2004). Soil quality (in terms of structure, water holding content and nutrient cycling/supply) is likely to be compromised by the reduction in SOM (Mills and Fey, 2003) which in turn impairs ecosystem functioning. The endpoint of this process is 'desertification', which has already occurred over large areas of succulent thicket (Lloyd et al., 2002).

4.3. Restoring biomass and ecosystem functioning

At a landscape scale, *P. afra* produces most of the litter in succulent thicket (c. 2500 kg ha⁻¹ yr⁻¹). Our data shows that this litter will be incorporated into SOM relatively quickly, with most litter decomposing in less than one year. *P. afra* appears to be the keystone species in this ecosystem, acting as a 'carbon pump', and incorporating carbon into soils at a rate incongruous with the prevailing rainfall regime. Once lost from the system, *P. afra* does not re-establish, even if livestock and game stocking densities are reduced. Fortunately, however, this plant propagates vegetatively and planting of truncheons can consequently be used to restore degraded thicket landscapes (Swart and Hobson, 1994; Mills and Cowling, 2006). Such restoration results in considerable return of carbon in biomass and soils. This sequestered carbon has a market value and can potentially be used to fund large-scale restoration across the thicket biome (Mills et al., 2007).

Acknowledgements

The World Bank Global Environment Facility funded this research through the South African National Biodiversity Institute's 'Conservation Farming' project. Additional funding was provided through the National Research Foundation and the Department of Water Affairs and Forestry Working for Woodlands programme. The Mazda Wildlife Fund sponsored the vehicles. Thanks to the following people for various forms of assistance: Louise Visagie (field and laboratory assistance); Arthur Rudman and Chris Bosch (field accommodation and access to sites); Desmond Slater, Ron Watson, Charlie Bolton and Gered Vermaak (access to sites). Andrew Knight and Ayanda Sigwela provided much insight through discussion.

References

- Boeken, B., Orenstein, D., 2002. The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. *Journal of Vegetation Science* 12, 825–832.
- Bray, J.R., Gorham, E., 1964. Litter production in forests of the world. *Advances in Ecological Research* 2, 101–157.
- Carnevale, N.J., Lewis, J.P., 2001. Litterfall and organic matter decomposition in a seasonal forest of the eastern Chaco (Argentina). *International Journal of Tropical Biology and Conservation* 49, 203–212.
- Cepeda-Pizarro, J.G., Whitford, W.G., 1990. Decomposition patterns of surface leaf-litter of six plant species along a Chihuahuan Desert watershed. *American Midland Naturalist* 123, 319–330.
- Fabricius, C., 1997. The impact of land use on biodiversity in xeric subtropical thicket, South Africa. PhD Thesis. University of Port Elizabeth, South Africa.
- Guo, L.B., Sims, R.E.H., 1999. Litter decomposition and nutrient release via litter decomposition in New Zealand Eucalypt short-rotation forests. *Ecosystems and Environment* 75, 133–140.
- Guralnick, L.J., Rorabaugh, P.A., Hanscom, Z.I., 1984. Influence of photoperiod and leaf age on Crassulacean acid metabolism in *Portulacaria afra* (L.) Jacq. *Plant Physiology* 75, 454–457.
- Guralnick, L.J., Ting, I.P., 1987. Physiological changes in *Portulacaria afra* (L.) Jacq. During a summer drought and rewatering. *Plant Physiology* 85, 481–486.
- Hoare, D.B., Mucina, L., Rutherford, M.C., Vlok, J.H.J., Euston-Brown, D.I.W., Palmer, A.R., Powrie, L.W., Lechmere-Oertel, R.G., Procheş, S.M., Dold, A.P., Ward, R.A., 2006. Albany thicket biome. In: Mucina, L., Rutherford, M.C. (Eds.), *The Vegetation of South Africa, Lesotho and Swaziland*, SANBI, Pretoria, pp. 540–567.
- Hoffman, M.T., Cowling, R.M., 1990. Desertification in the lower Sundays River Valley, South Africa. *Journal of Arid Environments* 19, 105–117.
- Hoffman, M.T., Cowling, R.M., 1991. Phytochorology and endemism along aridity and grazing gradients in the lower Sundays River Valley, South Africa: implications for vegetation history. *Journal of Biogeography* 18, 189–201.
- Huang, W.Z., Schoenau, J.J., 1997. Mass loss measurements and statistical models to predict decomposition of leaf litter in a boreal aspen forest. *Communications in Soil Science and Plant Analysis* 28, 863–874.
- Joshi, C.S., Singh, R.P., Rao, P.B., 1999. Pattern of leaf litter decomposition in forest plantations of Tarai region in Uttar Pradesh, India. *Tropical Ecology* 40, 99–108.
- Kerley, G.I.H., Knight, M.H., De Kock, M., 1995. Desertification of Subtropical Thicket in the Eastern Cape, South Africa: are there alternatives? *Environmental Monitoring and Assessment* 37, 211–230.
- Kerley, G.I.H., Tongway, D., Ludwig, J.A., 1999. Effects of goat and elephant browsing on soil resources in succulent thicket, Eastern Cape, South Africa. *Proceedings of the VIth International Rangeland Congress* 1, 116–117.
- Knoopp, J.D., Coleman, D.C., Crossley, D.A., Clark, J.S., 2000. Biological indices of soil quality: an ecosystem case study of their use. *Forest Ecology & Management* 138, 357–368.
- Lechmere-Oertel, R.G., 2003. The effects of goat browsing on ecosystem patterns and processes in succulent thicket, South Africa. PhD Thesis. University of Port Elizabeth, Port Elizabeth, South Africa.
- Lechmere-Oertel, R.G., Kerley, G.I.H., Cowling, R.M., 2004. Landscape dysfunction and reduced spatial heterogeneity in soil resources and fertility in semi-arid succulent thicket, South Africa. *Austral Ecology* 30, 615–624.
- Lechmere-Oertel, R.G., Kerley, G.I.H., Cowling, R.M., 2005. Patterns and implications of transformation in semi-arid succulent thicket, South Africa. *Journal of Arid Environments* 62, 459–474.
- Lloyd, J.W., Van den Berg, E., Van Wyk, E., Palmer, A.R., 2002. Patterns of degradation and degradation in the Thicket Biome. Unpublished Report, Terrestrial Ecology Research Unit, Department of Zoology, University of Port Elizabeth, South Africa.
- Mackay, W.P., Silva, S., Lightfoot, D.C., Pagani, M.I., Whitford, W.G., 1986. Effect of increased soil moisture and reduced soil temperature on a desert soil arthropod community. *American Midland Naturalist* 116, 45–56.
- McIvor, J.G., 2001. Litterfall from trees in semiarid woodlands of north-east Queensland. *Austral Ecology* 26, 150–155.
- Mills, A.J., Fey, M.V., 2003. Declining soil quality in South Africa: effects of land use on soil organic matter and surface crusting. *South African Journal of Science* 99, 429–436.
- Mills, A.J., Fey, M.V., 2004a. Transformation of thicket to savanna reduces soil quality in the Eastern Cape, South Africa. *Plant and Soil* 265, 153–163.
- Mills, A.J., Fey, M.V., 2004b. Soil carbon and nitrogen in five contrasting biomes of South Africa exposed to different land uses. *South African Journal of Plant and Soil* 21, 94–103.
- Mills, A.J., Fey, M.V., 2004c. Effects of vegetation cover on the tendency of soil to crust in South Africa. *Soil Use and Management* 20, 308–317.
- Mills, A.J., Cowling, R.M., Fey, M.V., Kerley, G.I.H., Donaldson, J.S., Lechmere-Oertel, R.G., Sigwela, A.M., Skowno, A.L., Rundel, P., 2005a. Effects of goat pastoralism on ecosystem carbon storage in semi-arid thicket, Eastern Cape, South Africa. *Austral Ecology* 30, 797–804.
- Mills, A.J., O'Connor, T.G., Donaldson, J.S., Fey, M.V., Skowno, A.L., Sigwela, A.M., Lechmere-Oertel, R.G., Bosenberg, J.D., 2005b. Ecosystem carbon storage under different land uses in three semi-arid shrublands and a mesic grassland in South Africa. *South African Journal of Plant and Soil* 22, 183–190.
- Mills, A.J., Cowling, R.M., 2006. Rate of carbon sequestration at two thicket restoration sites in the Eastern Cape, South Africa. *Restoration Ecology* 14, 38–49.
- Mills, A.J., Turpie, J., Cowling, R.M., Marais, C., Kerley, G.I.H., Lechmere-Oertel, R.G., Sigwela, A.M., Powell, M., 2007. Assessing costs, benefits and feasibility of subtropical thicket restoration in the Eastern Cape, South Africa. In: Aronson, J., Milton, S.J., Blynnaut, J. (Eds.), *Restoring Natural Capital. Science, Business and Practice*. Island Press, Washington DC, pp. 179–187.
- Molofsky, J., Lanza, J., Crone, E.E., 2000. Plant litter feedback and population dynamics in an annual plant, *Cardamine pensylvanica*. *Oecologia* 124, 522–528.
- Mooney, H.A., Kummerow, J., Johnson, A.W., Parsons, D., Keeley, S., Hoffman, A., Hays, R.I., Gilberto, J., Chu, C., 1977. The Producers—Their Resources and Adaptive Responses. *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems*. Dowden, Hutchinson & Ross, Pennsylvania.
- Moorhead, D.L., Callaghan, T., 1994. Effects of increasing ultraviolet B radiation on decomposition and soil organic matter dynamics: a synthesis and modelling study. *Biology and Fertility of Soils* 18, 19–26.
- Moorhead, D.L., Reynolds, J.F., 2002. The contribution of abiotic processes to buried litter decomposition in the northern Chihuahuan Desert. *Oecologia* 79, 133–135.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–51.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Percival, H.J., Parfitt, R.L., Scott, N.A., 2000. Factors controlling soil carbon levels in New Zealand grasslands: is clay content important? *Soil Science Society of America Journal* 64, 1623–1630.
- Potthoff, M., Loftfield, N., 1998. How to quantify contamination of organic litter bag material with soil. *Pedobiologia* 42, 147–153.

- Santa Regina, I., 2001. Litter fall, decomposition and nutrient release in three semi-arid forests of the Duero basin, Spain. *Forestry* 74, 347–358.
- Schaefer, D., Steinberger, Y., Whitford, W.G., 1985. The failure of nitrogen and lignin decomposition in a North American Desert. *Ecology* 62, 654–663.
- Sigwela, A.M., 2004. The impacts of land use on vertebrate diversity and vertebrate-mediated processes in the Thicket Biome, Eastern Cape. PhD. Nelson Mandela Metropolitan University, Port Elizabeth.
- South African Weather Bureau 2002. <http://www.weathersa.co.za/>. Site Accessed on 27 March 2008.
- Stamou, G.P., Pantis, J.D., Sgardelis, S.P., 1994. Comparative study of litter decomposition in two Greek ecosystems: a temperate forest and an asphodel semi-desert. *European Journal of Soil Biology* 30, 43–48.
- Steinberger, Y., Friedman, D.W., Parker, L.W., Whitford, W.G., 1984. Effects of simulated rainfall and litter quantities on desert soil biota: nematodes and microarthropods. *Journal of Arid Environments* 1, 41–48.
- Strojan, C.L., Randall, D.C., Turner, F.B., 1987. Relationship of litter decomposition rates to rainfall in the Mojave desert. *Ecology* 68, 741–744.
- Strojan, C.L., Turner, F.B., Castetter, R., 1979. Litter fall from shrubs in the Northern Mojave Desert. *Ecology* 60, 891–900.
- Stuart-Hill, G.C., 1992. Effects of elephants on the Kaffrarian succulent thicket of the Eastern Cape, South Africa. *Journal of Applied Ecology* 29, 699–710.
- Swart, M., Hobson, F.O., 1994. Establishment of spekboom. *Dohne Bulletin* 3, 10–13.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell.
- Vlok, J.H.J., Euston-Brown, D.I.W., Cowling, R.M., 2003. Acocks' Valley Bushveld 50 years on: new perspective on the delimitation, characterisation and origin of subtropical thicket vegetation. *South African Journal of Botany* 69, 27–51.
- West, N.E., 1979. Formation, distribution and function of plant litter in desert ecosystems., pp. 608–620. In: Goodall, D.W., Perry, R.A. (Eds.), *Arid-land Ecosystems: Structure, Functioning and Management*. vol. 1, Cambridge University Press, London, pp. 647–659.
- Whitford, W.G., 2002. *Ecology of Desert Systems*. Academic Press, San Diego.
- Whitford, W.G., De Soyza, A.G., Van Zee, J.W., Herrick, J.E., Havstad, K.M., 1998. Vegetation, soil and animal indicators of rangeland health. *Environmental Monitoring and Assessment* 51, 179–200.
- Witkowski, E.T.F., 1989. Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos system. *Plant and Soil* 117, 227–235.