

Effects of goat pastoralism on ecosystem carbon storage in semiarid thicket, Eastern Cape, South Africa

A. J. MILLS,^{1,2*} R. M. COWLING,³ M. V. FEY,¹ G. I. H. KERLEY,³ J. S. DONALDSON,² R. G. LECHMERE-OERTEL,³ A. M. SIGWELA,³ A. L. SKOWNO² AND P. RUNDEL⁴

¹Department of Soil Science, University of Stellenbosch, Private Bag X01, Matieland, 7602, ²South African National Biodiversity Institute, Private Bag X7, Claremont, 7735, South Africa (Email: mills@sanbi.org), ³Terrestrial Ecology Research Unit, Departments of Botany and Zoology, University of Port Elizabeth, Port Elizabeth, South Africa, and ⁴Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

Abstract Intensive pastoralism with goats transforms semiarid thicket in the Eastern Cape, South Africa from a dense vegetation of tall shrubs to an open landscape dominated by ephemeral grasses and forbs. Approx. 800 000 ha of thicket (which prior to the introduction of goats had a closed canopy and a *Portulacaria afra* Jacq. component) have been transformed in this manner. Ecosystem C storage in intact thicket and loss of C due to transformation were quantified. Carbon storage in intact thicket was surprisingly high for a semiarid region, with an average of 76 t C ha⁻¹ in living biomass and surface litter and 133 t C ha⁻¹ in soils to a depth of 30 cm. Exceptional C accumulation in thicket may be a result of *P. afra* dominance. This succulent shrub switches between C₃ and CAM photosynthesis, produces large quantities of leaf litter (approx. 450 g m⁻² year⁻¹) and shades the soil densely. Transformed thicket had approx. 35% less soil C to a depth of 10 cm and approx. 75% less biomass C than intact thicket. Restoration of transformed thicket landscapes could consequently recoup more than 80 t C ha⁻¹.

Key words: biomass, carbon stocks, goats, pastoralism, soil carbon, thicket.

INTRODUCTION

Semiarid solid thicket (characterized by a dense canopy of tall shrubs and a *Portulacaria afra* Jacq. component) occupies approx. 1.7 million hectares in the Eastern Cape, South Africa (Lloyd *et al.* 2002). Despite a long association with a diverse assemblage of large and medium-sized indigenous herbivores (Midgley 1991; Kerley *et al.* 1995), thicket is surprisingly sensitive to injudicious pastoralism (Stuart-Hill & Danckwerts 1988; Stuart-Hill 1992). Heavy browsing by goats can transform thicket from a dense closed-canopy shrubland into an open savanna-like system with a cover of ephemeral grasses and forbs within a few decades, and possibly even within a decade (Hoffman & Cowling 1990; Kerley *et al.* 1995; Lechmere-Oertel *et al.* 2005a). Approximately 800 000 ha of semiarid thicket has been transformed in this manner, and the process of transformation is evident in another 600 000 ha (Lloyd *et al.* 2002). We hypothesized that transformation reduces total ecosystem C storage, as loss of above-ground biomass is highly visible (Fig. 1), and soil C is likely to be reduced where canopy cover is removed (Allsopp 1999; Mills

& Fey 2003, 2004a). We asked the question: how much C is lost when thicket is transformed?

Warm, semiarid landscapes are not where one would intuitively expect to find large stocks of ecosystem C. Ecologists are accustomed to a pattern of increasing biomass along a rainfall gradient from deserts to forests (Woodward 1987). The common perception is that low water availability in warm, semiarid landscapes limits accumulation of biomass because water demand tends to increase with an increase in biomass. While this is true, multiple exceptions to such a pattern occur in semiarid and arid lands where water is not the primary limiting factor. Decoupling from water as a limiting factor occurs, for example, in desert areas dominated by phreatophytic species of *Prosopis* which tap groundwater pools. Moreover, with this example, nitrogen fixation by root nodules reduces limitations due to nitrogen as well. Physiological decoupling from water limitation can also occur where crassulacean acid metabolism (CAM) metabolic systems can allow highly efficient use of water and thus relatively high productivity and biomass in areas with very low rainfall. Accumulation of soil C also tends to be limited in these landscapes (Post *et al.* 1982) because soils are exposed to sunlight (as a result of limited plant cover), which enhances rates of mineralization of soil organic matter (via temperature effects) (Jenkinson 1981) and photo-

*Corresponding author.

Accepted for publication May 2005.

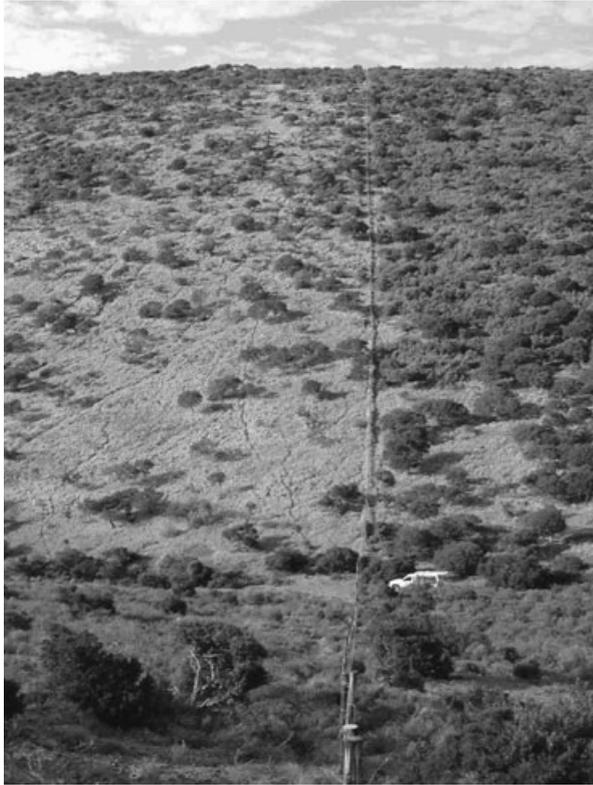


Fig. 1. A fence-line contrast between intact thicket and thicket transformed by goats.

oxidation of surface litter (Moorhead & Callaghan 1994). Semiarid thicket, appears to be an exception to this rule. In its intact state it has a dense canopy cover (approx. 70%) of tall shrubs up to 3 m in height, a thick litter layer (5–10 cm) under the dominant shrub (*P. afra*) and a dark, C-rich topsoil.

In order to ascertain the extent of C accumulation in thicket as well as the effect of transformation on C dynamics, we compared ecosystem C storage, soil temperatures and litter production across fence-line contrasts of intact and transformed thicket approx. 100 km north-west of Port Elizabeth in South Africa's Eastern Cape Province.

METHODS

Eight sites of distinct fence-line contrast (i.e. intact thicket and thicket transformed by goats) were selected within an area stretching approx. 40 km east to west in the vicinity of Kirkwood in the Eastern Cape Province, South Africa (33°30'S; 25°20'E), at an elevation of 300–500 m above sea level. Sites were at least 3 km apart with discrete and separate fence-line contrasts. These eight replicated sites were used as a natural snapshot experiment (Diamond 1986). The biophysical environment (geology, soils, slope angle

and aspect) was assumed to be constant across the fence-lines. Transformation of the vegetation on one side of each fence-line was ascribed to long-term (20–80 years) browsing history by domestic animals primarily boer goats (*Capra hircus*) and angora goats (*Capra aegragus*).

The region has a mean annual temperature of 17.6°C (mean monthly range of 12.3–22.4°C). Daily maximum temperatures in summer regularly exceed 40°C. Rainfall (250–350 mm mean annual precipitation (MAP)) may occur throughout the year, but there are distinct autumn and spring maxima over the long-term. Soil parent materials are sedimentary rocks from the ancient Cape Super Group (shales) and the younger (Cretaceous) Uitenhage Group (mudstones) (Council for Geoscience 1997). Soils are typically loamy sands that include Calcaric Cambisols, Calcic Luvisols, Rhodic Luvisols and Calcaric Regosols (FAO 1998). The vegetation in the study area is an arid form of succulent thicket termed 'Sundays River Thicket' (Vlok *et al.* 2003) and is characterized by a sparse, emergent, evergreen to weakly deciduous tree component (*Pappea capensis* Eckl. & Zeyh., *Euclea undulata* Thunb., *Schotia afra* (L.) Thunb.), surrounded by a matrix dominated by *P. afra*, the so-called spekboom or olifantskos (Afrikaans: 'fat tree' or 'elephant food') that is readily consumed by both wild and domestic herbivores. The *P. afra* matrix is interwoven with a variety of multistemmed, evergreen, spinescent shrubs (*Azima tetraacantha* Lam., *Gymnosporia polyacantha* (Sond.) Szyszyl., *Putterlickia pyracantha* (L.) Szyszyl., *Rhigozum obovatum* Burch., *Rhus longispina* Eckl. & Zeyh.). Untransformed thicket is not fire prone and fire is not used as a management tool (Tainton 1999). The main land use in the region is commercial goat pastoralism. Overstocking with goats results in the loss of the matrix of spekboom and perennial shrubs which is replaced by ephemeral or weak perennial grasses and forbs, often dominated by the alien chenopod saltbush, *Atriplex lindleyi* ssp. *inflata* (F. Muell.) Paul G. Wilson. The result is an open, savanna-like system in which a severely depleted tree component is all that remains of the original thicket (Lechmere-Oertel 2004; Lechmere-Oertel *et al.* 2005a,b). The contrast between intact and transformed thicket is depicted in Fig. 1.

Soil samples were taken from an excavated profile at 10 cm intervals to a depth of 30 cm in intact and transformed thicket at each fence-line contrast (16 profiles in all). Composite samples of surface soil (comprising 15–20 subsamples) were also taken at each site to a depth of 10 cm over an area of 1 ha using an auger. Soils were air-dried, sieved to <2 mm and total C was determined in finely milled soil by complete combustion using a EA Elemental Analyser (Euro Vector, Milan, Italy). The contribution of inorganic C to total C was not determined as free carbon-

ates were deemed absent (or present in negligible amounts) based on noneffervescence in 10% hydrochloric acid. Particle size analysis was performed on composite samples after dispersion in Na hexametaphosphate using the hydrometer method (Soil Classification Working Group 1991). Soil C to a depth of 30 cm was estimated from C concentration and bulk density, the latter derived from soil texture using algorithms described by Saxton *et al.* (1986).

Biomass of the four dominant plant growth forms (canopy trees, succulent shrubs, woody shrubs and ephemeral grasses/forbs) was compared between intact and transformed thicket at each fence-line contrast. Height, canopy diameter and basal diameter of six canopy trees (*P. capensis*) were measured, and the trees were harvested and weighed. Tree dry mass was plotted against canopy diameter and the slope of the fitted function was used to estimate dry mass of all trees in five 25 m line-transects in transformed and intact thicket at each fence-line contrast. Number of trees per unit area was then used to estimate tree biomass ha^{-1} . Above-ground plant material was harvested at each fence-line contrast in six 1×1 m quadrats per growth form. Below-ground biomass was estimated by harvesting all root material in $25 \times 25 \times 40$ cm pits dug beneath each quadrat. Roots were sampled by sieving (<3 mm) and washing the extracted soil. Estimates of above- and below-ground biomass for each growth form were calculated per unit area. These estimates were extrapolated to compare biomass in intact and transformed habitats at all sites using cover data obtained from the 25 m line-transects. Carbon was estimated from dry matter (DM) using a conversion factor of 0.48 (Birdsey 1996; Vogel & Gower 1998).

Litter production was measured for the dominant perennial species: *E. undulata*, *P. capensis*, *P. afra* and *R. longispina*. At each site, 0.5 mm mesh litter traps (0.5×0.5 m square bags suspended between four metal rods) were placed directly beneath the canopies of three individuals of each species on either side of the fence-line contrast (i.e. 24 traps per site). 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. Data were pooled per trap for the total sampling period (506 days) and adjusted to 1 year. A landscape estimate of litter fall ($\text{kg ha}^{-1} \text{ year}^{-1}$) was calculated from the percentage cover of different plant guilds (Lechmere-Oertel *et al.* 2005b). Annual litter production of the non-perennial grass and forb component was estimated to be 50% of standing biomass (West 1981).

Differences in soil temperature across fence-line contrasts were also investigated. Soil temperature measurements were made using HOBO H8 microclimate loggers (Onset Computer Corporation, Bourne,

Massachusetts, USA) with external temperature probes located in intact and transformed habitats on either side of the fence-line at each of the eight sites. The probes were inserted into the soil to a depth of 5 cm. Measurements were recorded hourly for 365 days. Differences in C storage, leaf litter production and soil temperature between intact and transformed sites were analysed with paired *t*-tests using the software package Unistat 5.5.

The $\delta^{13}\text{C}$ ratios of several common thicket species were investigated to provide insights into water use efficiency and photosynthetic pathways. Samples of photosynthetic tissues were collected from each of three individuals of *P. afra*, *P. capensis*, *E. undulata*, *P. pyracantha*, *Crassula ovata* (Mill.) Druce, and *Carissa bispinosa* (L.) Desf. Ex Brenan growing in *P. afra*-dominated thicket communities at eight sites. The sites spanned a wide range of conditions where this formation is found in the Eastern and Western Cape. Samples were air-dried and their natural $\delta^{13}\text{C}$ ratios were measured at the Duke University Phytotron (Durham, NC, USA) on a SIRA Series II isotope ratio mass spectrometer (VG Isotech, Middlewich, UK) operated in automatic trapping mode after combustion of samples in an elemental analyser (NA1500, Carlo Erba Instrumentazione, Milan, Italy). The reference CO_2 , calibrated against standard Pee Dee belemnite (PDB), was obtained from Oztech (Dallas, TX, USA).

RESULTS

Intact thicket had an average 160 ± 10 SE t ha^{-1} of DM in living biomass and surface litter (84 ± 6 SE, 24 ± 2 SE and 53 ± 3 SE t ha^{-1} in above-ground biomass, surface litter and root biomass respectively) (Fig. 2). Soil C averaged 5.2% in the 0–10 cm layer (Fig. 3) and soil C to a depth of 30 cm was estimated at 133 ± 27 SE t ha^{-1} ($n = 8$). Total C storage (soils plus biomass) in intact thicket was estimated at 209 ± 28 SE t ha^{-1} ($n = 8$) (comprising 40, 11 and 25 t C ha^{-1} in above-ground biomass, surface litter and root biomass respectively) (Table 1). Transformed thicket had significantly (approx. 35%) less soil C ($P < 0.05$) in the 0–10 cm layer and significantly (approx. 75%) less biomass C ($P < 0.001$) (losses of 24 and 58 t C ha^{-1} respectively). Mean leaf litter production ranged from $259 \text{ g m}^{-2} \text{ year}^{-1}$ under *R. longispina* to $463 \text{ g m}^{-2} \text{ year}^{-1}$ under *P. afra* (Fig. 4). The landscape estimate of leaf litter production (calculated according to plant guilds, which frequently overlapped) was 4.66 ± 0.21 SE $\text{t ha}^{-1} \text{ year}^{-1}$ in intact thicket and 2.97 ± 0.09 SE $\text{t ha}^{-1} \text{ year}^{-1}$ in transformed thicket ($P < 0.0001$, $n = 8$). The mean daily maximum soil temperature over the period March 2001 to March 2002 was 12°C lower in intact thicket under *P. afra*

than in open grassy areas (23.2 vs. 35.1°C, $P < 0.001$, $n = 8$).

The $\delta^{13}\text{C}$ values of *P. afra* ranged from -17.4 to -20.5‰ , indicating a flexible mode of photosynthesis between CAM and C_3 metabolism. The common succulent *C. ovata*, had $\delta^{13}\text{C}$ values of -15.4 to -17.6‰ , indicating a reliance on CAM. *P. capensis*, *E. undulata*, *P. pyracantha* and *C. bispinosa* all had $\delta^{13}\text{C}$ values of -28 to -25‰ , showing obligate use of C_3 metabolism.

DISCUSSION

Transformation of semiarid thicket by goat pastoralism resulted in an average loss of 82 t C ha^{-1} (24 t C

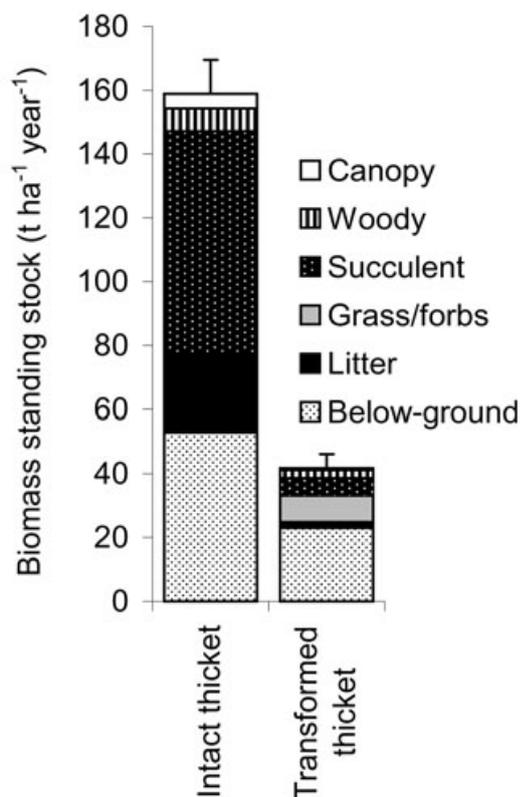


Fig. 2. Standing stock of mean biomass (dry matter) in intact thicket and adjacent transformed thicket. Standard errors given by vertical bars.

Table 1. Mean C stocks (t ha^{-1}) and standard errors (SE) in above-ground biomass, surface litter, root biomass and soil (0–30 cm) in intact and transformed thicket

	Above	Litter	Root	Soil	Total
Intact thicket	40	11	25	133	209
SE	3	1.0	1.3	27	28
Transformed	7	1	11	95	114
SE	1	0.4	0.7	15	14
P^*	<0.001	<0.001	<0.001	0.07	0.002

*One-tailed paired t -test, $n = 8$.

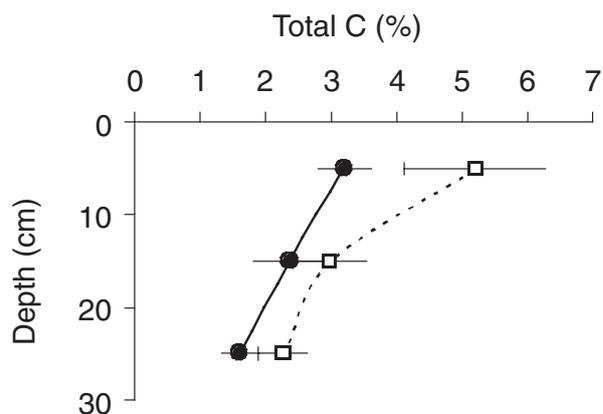


Fig. 3. Change in mean soil C with depth in intact thicket and adjacent transformed thicket. Standard errors given by horizontal bars. (●) Transformed thicket, (□) intact thicket.

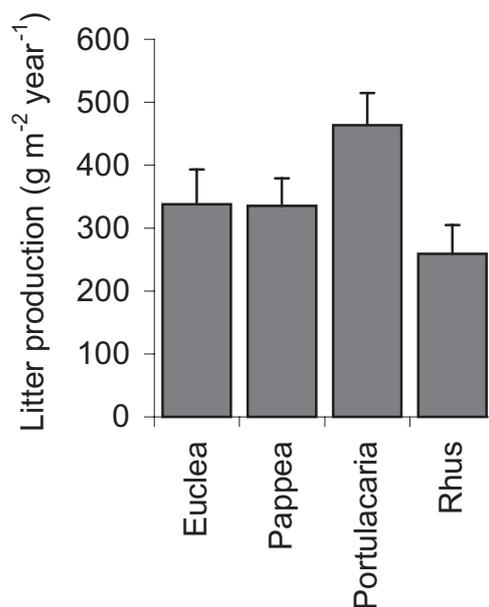


Fig. 4. Mean litter production under different shrub/tree species in intact thicket. Euclea, *Euclea undulata*; Pappea, *Pappea capensis*; Portulacaria, *Portulacaria afra*; Rhus, *Rhus longispina*. Standard errors given by vertical bars.

in soils and 58 t C in biomass). The concentration of C in soils of intact thicket was exceptional for a semi-arid region (Fig. 3), averaging 5.2% in the top 10 cm. A similar soil C concentration, with a range of 5.0–9.6%, has been recorded from thicket in a more mesic climate (approx. 450 mm MAP) (Kerley *et al.* 1999). Climate influences soil C primarily through effects of temperature, moisture and solar radiation on the array and growth rate of plant species and on the rate of soil organic C mineralization (Baldock & Nelson 2000). Soil C tends to be positively correlated with precipitation and at a given level of precipitation negatively correlated with temperature (Post *et al.* 1982). Warm deserts and semideserts consequently have low soil C contents, typically in the range of 0.2–1.7% C in surface soils (0–10 cm) (Whittaker *et al.* 1968; Charley & West 1975; Rundel & Gibson 1996; Allsopp 1999).

The estimated stock of soil C to a depth of 30 cm in intact thicket (133 t ha⁻¹) is exceptionally high for a semi-arid region and is comparable with organic-rich soils in tallgrass prairie, Wisconsin (80–120 t C ha⁻¹, 0–50 cm) (Brye & Kucharik 2003) and European forests (40–193 t C ha⁻¹, 0–50 cm) (Schulze 2000). An explanation for the soil C accumulation in thicket may be found in the dense and succulent nature of the shrub matrix, which not only deposits approx. 4 tonnes of biomass in litter per hectare per year (Fig. 4) but also excludes fire, shades the soil surface and intercepts rainfall (Mills & Fey 2004b). Cooling of the soil surface and a reduction in frequent wetting through rainfall interception are likely to reduce mineralization of organic matter (Birch 1958; Jenkinson 1981; Thurow *et al.* 1987). Succulence of *P. afra* combined with year-round rainfall may constitute a mechanism for overcoming water-constrained photosynthesis to produce more biomass C than would normally be expected on climatic grounds.

Probable mechanisms for loss of soil C in transformed sites are (i) reduced organic matter inputs via roots and leaf litter; (ii) greater microbial activity due to greater soil temperatures (Jenkinson 1981) and more frequent wetting of the soil surface (Birch 1958); and (iii) greater photodegradation of litter (due to greater exposure to ultra-violet light) (Moorhead & Callaghan 1994).

The amount of living biomass and surface litter in intact thicket (160 t DM ha⁻¹) was more typical of forests and woodlands than of semi-arid shrublands. Total biomass (DM) values reported from a range of forests include: 154–405 t ha⁻¹ in European conifer and broadleaf forests (Schulze 2000); 133–265 t ha⁻¹ in Hawaiian montane forest (Schuur & Matson 2001); and 200–920 t ha⁻¹ in high elevation conifer forests in Arizona (Whittaker & Niering 1975). Arid and semi-arid shrublands tend to have considerably less total biomass. Desert scrub and woodlands in regions receiving <650 mm mean annual precipitation (MAP)

in Arizona, for example, have a total biomass range of 6–30 t DM ha⁻¹ (Whittaker & Niering 1975). Total biomass in Middle Eastern desert shrublands are reported to range from 2 to 8 t DM ha⁻¹ (Orshan 1986) and in the Sahel of Chad from 0.3 to 7 t DM ha⁻¹ (Monod 1986). Succulent Karoo shrubland, approx. 350 km to the north-west of our thicket study site, receiving approx. 170 mm MAP, has an above-ground biomass of approx. 3.3 t DM ha⁻¹ (Milton 1990).

The above-ground fraction of biomass in our study (84 t DM ha⁻¹) and another study at Addo Elephant National Park (170–368 t wet biomass ha⁻¹, approx. 450 mm MAP) (Penzhorn *et al.* 1974) is comparable with many mesic, forested systems. Mature oak-pine forests in New York (1240 mm MAP), for example, have an average biomass of 66 t DM ha⁻¹ (Whittaker & Woodwell 1969). In New Hampshire, broadleaf-deciduous forests (1250 mm MAP) ranged in biomass from 102 to 162 t DM ha⁻¹ (Whittaker *et al.* 1974). Above-ground biomass in forests can, however, be considerably greater than these amounts, e.g. climax forests (>2000 mm MAP) in the Great Smokey Mountains, Tennessee (500–610 t DM ha⁻¹) (Whittaker 1966) and *Nothofagus pumila* forest (770 mm MAP) in Patagonia (340 t DM ha⁻¹) (Schulze *et al.* 1996). By comparison, in Patagonian steppe and desert systems (125–290 mm MAP) above-ground biomass ranged from 1.5 to 5.2 t DM ha⁻¹ (Schulze *et al.* 1996) and in creosote bush shrubland of the Mojave Desert was only 1.0–1.3 t ha⁻¹, with another 0.8 t ha⁻¹ of standing dead biomass (Rundel & Gibson 1996).

Forested systems are not, however, restricted to mesic climates. Xeric forests of *Pinus halepensis* and *Quercus ilex*, for example, occur in warm climates receiving 300–600 mm MAP and reach above-ground biomasses of 60–120 t DM ha⁻¹ in Tunisia (le Houerou 1981). These xeric forest systems are therefore comparable with thicket (i.e. a high biomass accumulation in warm, semi-arid environments), although we note that the thicket in the Eastern Cape occurs in more arid environments (some areas receive <250 mm MAP) and is dominated by shrubs as opposed to tall trees. Another important difference between these ecosystems with respect to C sequestration is that xeric forests are likely to experience periodic stand-replacing fires (Bond & Van Wilgen 1996), whereas the thicket of this study does not burn (Kerley *et al.* 1995; Tainton 1999; Vlok *et al.* 2003). Exclusion of fire from thicket, due largely to the non-combustible nature of the evergreen vegetation (Kerley *et al.* 1995), is likely to play a major role in the accumulation of ecosystem C. Fire suppression in fire-prone ecosystems can result in substantial gains in C storage (Tilman *et al.* 2000). In Minnesota, for example, pin oak savannas (receiving 660 mm MAP) that were burned 16–28 times over

a 35-years period had a total C storage of approx. 140 t ha⁻¹, compared with the approx. 225 t ha⁻¹ of fire-protected, closed-canopy pin oak forest (Tilman *et al.* 2000).

Other arid regions with high ecosystem C storage include mesquite woodlands dominated by species of *Prosopis*. When these trees are released from normal limiting factors by tapping groundwater resources and fixing atmospheric nitrogen with symbiotic root nodules, large biomass can accrue. An example of this can be seen in the hyper-arid Sonoran Desert of California where woodlands of *Prosopis glandulosa* support 23 t ha⁻¹ of above-ground biomass in a region with only 70 mm annual rainfall (Sharifi *et al.* 1982). Desert and semidesert succulents which utilize CAM to provide high water use efficiency can also attain high levels of stand biomass and productivity if limiting factors for establishment are removed. Such conditions can be seen in cultivated stands of *Agave* and *Opuntia* in Latin America, which have an above-ground stand biomass of 10–48 t ha⁻¹ and annual net primary production of 4–10 t ha⁻¹ or more without supplemental irrigation (Nobel 1988).

Leaf litter production (e.g. 450 g m⁻² year⁻¹ under *P. afra*) is also high for a semiarid region and suggests that return of ecosystem C may occur more quickly than in other transformed semiarid systems. Reported litter production in desert and semidesert systems of Argentina, Russia, Mexico, South Africa and Australia ranges from 32 to 250 g m⁻² year⁻¹ (Rodin & Bazilevich 1968; West 1981; Maya & Arriaga 1996; Carnevale & Lewis 2001). Litter fall in the Mojave Desert ranges from about 13–39 g m⁻² year⁻¹ (Rundel & Gibson 1996). By contrast, litter production in Hawaiian montane forest (2200–5050 mm MAP) ranged from 400 to 1000 g m⁻² year⁻¹ (Schuur & Matson 2001). Resilience of *P. afra* litter to decomposition may also be a factor contributing to soil C accumulation, although this still has to be demonstrated.

The high productivity of *P. afra* and its tolerance to drought has been ascribed to an unusual physiology whereby the plant shifts from C₃ to CAM photosynthetic mode in response to water and NaCl stress (Ting & Hanscom 1977), increasing daylength (Guralnick *et al.* 1984a), and increasing temperature, irrespective of moisture status (Guralnick *et al.* 1984b). The use of CAM conveys water use efficiency, while the flexibility of switching back to C₃ metabolism helps increase productivity when water is available. Many species of *Crassula* in the thicket community, particularly *C. ovata*, obligately utilize CAM in their photosynthesis. These species have high water use efficiency but lack the high levels of productivity and litter production observed in *P. afra*.

In conclusion, C storage of 209 t ha⁻¹ in intact thicket suggests that the dominant plant, *P. afra*, has a capacity for C sequestration that is unusually high for a species

adapted to aridity. This sequestration includes soil and biomass C and is likely to be related to the high productivity of the plant, the structure of the vegetation, exclusion of fire and possibly the interaction of succulence with year-round rainfall. Re-establishment of *P. afra* in thicket landscapes that have been transformed by goats could potentially sequester more than 80 t C ha⁻¹, an amount comparable with that of afforestation programmes in more mesic climates.

ACKNOWLEDGEMENTS

The study was part of the GEF Conservation Farming Project coordinated by the South African National Biodiversity Institute. Support from the Mazda Wildlife, the South African National Research Foundation (Grant number 2047381); and the Eskom Tertiary Education Support Programme is gratefully acknowledged. The authors extend their thanks to Matt Gordon for analytical work.

REFERENCES

- Allsopp N. (1999) Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. *Plant Ecol.* **142**, 179–87.
- Baldock J. A. & Nelson P. A. (2000) Soil organic matter. In: *Handbook of Soil Science* (ed. M. E. Sumner) pp. B25–B71. CRC Press, New York.
- Birch H. F. (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* **10**, 9–31.
- Birdsey R. A. (1996) Carbon storage for major forest types and regions in the conterminous United States. In: *Forests and Global Change, Volume II: Opportunities for Improving Forest Management* (eds R. N. Sampson & D. Hair) pp. 1–26. American Forests, Washington DC.
- Bond W. J. & Van Wilgen B. W. (1996) *Plants and Fire*. Chapman & Hall, New York.
- Brye K. R. & Kucharik C. J. (2003) Carbon and nitrogen sequestration in two prairie topochronosequences on contrasting soils in southern Wisconsin. *Am. Midl. Nat.* **149**, 90–103.
- Carnevale N. J. & Lewis J. P. (2001) Litterfall and organic matter decomposition in a seasonal forest of the eastern Chaco (Argentina). *Int. J. Trop. Biol. Conserv.* **49**, 203–12.
- Charley J. L. & West N. E. (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *J. Ecol.* **63**, 945–63.
- Council for Geoscience (1997) *Geological map of the Republic of South Africa and the Kingdoms of Lesotho and Swaziland*. Council for Geoscience, Pretoria.
- Diamond J. (1986) Overview: laboratory experiments, field experiments and natural experiments. In: *Community Ecology* (eds J. Diamond & T. E. Case) pp. 3–22. Harper & Row, New York.
- FAO (1998) *World Reference Base for Soil Resources*. Food and Agricultural Organisation of the United Nations, Rome.
- Guralnick L. J., Rorabaugh P. A. & Hanscom Z. (1984a) Influence of photoperiod and leaf age on Crassulacean Acid Metabolism in *Portulacaria afra* (L.) Jacq. *Plant Physiol.* **75**, 454–7.

- Guralnick L. J., Rorabaugh P. A. & Hanscom Z. (1984b) Seasonal shifts of photosynthesis in *Portulacaria afra* (L) Jacq. *Plant Physiol.* **76**, 643–6.
- Hoffman M. T. & Cowling R. M. (1990) Desertification in the lower Sundays River Valley, South Africa. *J. Arid Environ.* **19**, 105–117.
- Jenkinson D. S. (1981) The fate of plant and animal residues in soil. In: *The Chemistry of Soil Processes* (eds D. J. Greenland & M. H. B. Hayes) pp. 505–61. John Wiley and Sons, New York.
- Kerley G. I. H., Knight M. H. & De Kock M. (1995) Desertification of subtropical thicket in the eastern Cape, South Africa: are there alternatives? *Environ. Monit. Assess.* **37**, 211–30.
- Kerley G. I. H., Tongway D. & Ludwig J. (1999) Effects of goat and elephant browsing on soil resources in Succulent Thicket, Eastern Cape, South Africa. *Proc. VI Int. Rangel. Congress* **1**, 116–17.
- Lechmere-Oertel R. G. (2004) The effects of goat browsing on ecosystem patterns and processes in succulent thicket, South Africa (PhD Thesis). University of Port Elizabeth, Port Elizabeth.
- Lechmere-Oertel R. G., Kerley G. I. H. & Cowling R. M. (2005a) Patterns and implications of transformation in semi-arid succulent thicket, South Africa. *J. Arid Environ.* **62**, 459–474.
- Lechmere-Oertel R. G., Kerley G. I. H. & Cowling R. M. (2005b) Landscape dysfunction and reduced spatial heterogeneity in soil resources and fertility in semi-arid succulent thicket, South Africa. *Austral Ecol.* **30**, 615–24.
- le Houerou H. N. (1981) Impact of man and his animals on Mediterranean vegetation. In: *Ecosystems of the World 11: Mediterranean-Type Shrublands* (eds F. di Castri, D. W. Goodall & R. L. Specht) pp. 1–28. Elsevier, Amsterdam.
- Lloyd J. W., van den Berg E. C. & Palmer A. R. (2002) Patterns of transformation and degradation in the thicket biome, South Africa. Report No. 39. Terrestrial Ecology Research Unit, University of Port Elizabeth, Port Elizabeth.
- Maya Y. & Arriaga L. (1996) Litterfall and phenological patterns of the dominant overstorey species of a desert scrub community in north-western Mexico. *J. Arid Environ.* **34**, 23–35.
- Midgley J. J. (1991) Valley Bushveld dynamics and tree eubias. In: Proceedings of the first Valley Bushveld/Subtropical Thicket Symposium, (eds P. J. K. Zacharias, G. C. Stuart-Hill & J. J. Midgley) pp. 8–9. Special Publication, Grassland Society of Southern Africa.
- Mills A. J. & Fey M. V. (2003) Declining soil quality in South Africa: effects of land use on soil organic matter and surface crusting. *S. Afr. J. Sci.* **99**, 429–36.
- Mills A. J. & Fey M. V. (2004a) Effects of vegetation cover on the tendency of soil to crust in South Africa. *Soil Use Manage.* **20**, 308–17.
- Mills A. J. & Fey M. V. (2004b) Soil carbon and nitrogen in five contrasting biomes of South Africa exposed to different land uses. *S. Afr. J. Plant Soil* **21**, 94–103.
- Milton S. J. (1990) Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa. *S. Afr. J. Bot.* **56**, 587–9.
- Monod T. (1986) The Sahel zone north of the equator. In: *Ecosystems of the World 12B: Hot Deserts and Arid Shrublands, B* (eds M. Evanari, I. Noy-Meir & D. W. Goodall) pp. 203–43. Elsevier, Amsterdam.
- Moorhead D. L. & Callaghan T. (1994) Effects of increasing ultraviolet B radiation on decomposition and soil organic matter dynamics: a synthesis and modelling study. *Biol. Fert. Soils* **18**, 19–26.
- Nobel P. S. (1988) *Environmental Biology of Agaves and Cacti*. Cambridge University Press, Cambridge.
- Orshan G. (1986) The deserts of the Middle East. In: *Ecosystems of the World 12B: Hot Deserts and Arid Shrublands, B* (eds M. Evanari, I. Noy-Meir & D. W. Goodall) pp. 1–28. Elsevier, Amsterdam.
- Penzhorn B. L., Robbertse P. J. & Olivier M. C. (1974) The influence of the African Elephant on the vegetation of the Addo Elephant National Park. *Koedoe* **17**, 137–58.
- Post W. M., Emanuel W. R., Zinke P. J. & Stangenberger A. G. (1982) Soil carbon pools and world life zones. *Nature* **298**, 156–9.
- Rodin L. E. & Bazilevich N. I. (1968) *Production and Mineral Cycling in Terrestrial Vegetation*. Oliver and Boyd, Edinburgh.
- Rundel P. W. & Gibson A. C. (1996) *Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada*. Cambridge University Press, Cambridge.
- Saxton K. E., Rawls W. J., Romberger J. S. & Papendick R. I. (1986) Estimating generalized soil-water characteristics from texture. *Soil. Sci. Soc. Am. J.* **50**, 1031–6.
- Schulze E. D. (2000) *Carbon and Nitrogen Cycling in European Forest Ecosystems*. Springer, New York.
- Schulze E. D., Mooney H. A., Sala O. E. *et al.* (1996) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* **108**, 503–11.
- Schuur E. A. G. & Matson P. A. (2001) Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia* **128**, 431–42.
- Sharifi M. R., Nilsen E. T. & Rundel P. W. (1982) Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran Desert of California. *Am. J. Bot.* **69**, 760–7.
- Soil Classification Working Group (1991) *Soil Classification: a Taxonomic System for South Africa*. The Department of Agricultural Development, Pretoria.
- Stuart-Hill G. C. (1992) Effects of elephants and goats on the Kaffrarian succulent thicket of the Eastern Cape, South Africa. *J. Appl. Ecol.* **29**, 699–710.
- Stuart-Hill G. C. & Danckwerts J. E. (1988) Influence of domestic and wild animals on the future of succulent Valley Bushveld. *Pelea* **7**, 45–56.
- Tainton N. M. (1999) *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg.
- Thurrow T. L., Blackburn W. H., Warren S. D. & Taylor C. A. (1987) Rainfall interception by midgrass, shortgrass, and live oak mottes. *J. Range Manage.* **40**, 455–60.
- Tilman D., Reich P., Phillips H. *et al.* (2000) Fire suppression and ecosystem carbon storage. *Ecology* **81**, 2680–5.
- Ting I. P. & Hanscom Z. (1977) Induction of acid metabolism in *Portulacaria afra*. *Plant Physiol.* **59**, 511–14.
- Vlok J. H. J., Euston-Brown D. I. W. & Cowling R. M. (2003) Acock's Valley Bushveld 50 years on: new perspectives on the delimitation characterisation and origin of subtropical thicket vegetation. *S. Afr. J. Bot.* **69**, 27–51.
- Vogel J. G. & Gower S. T. (1998) Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. *Ecosystems* **1**, 386–400.
- West N. E. (1981) Formation, distribution and function of plant litter in desert ecosystems. In: *Arid-Land Ecosystems: Structure, Functioning and Management* (eds D. W. Goodall, R.

- A. Perry & K. M. W. Howes) pp. 608–20. Cambridge University Press, Cambridge.
- Whittaker R. H. (1966) Forest dimensions and production in the Great Smoky Mountains. *Ecology* **47**, 103–21.
- Whittaker R. H. & Woodwell G. M. (1969) Structure, production and diversity of the oak-pine forest at Brookhaven, New York. *J. Ecol.* **57**, 155–74.
- Whittaker R. H. & Niering W. A. (1975) Vegetation of the Santa Catalina Mountains, Arizona. v. Biomass, production, and diversity along the elevation gradient. *Ecology* **56**, 771–90.
- Whittaker R. H., Buol S. W., Niering W. A. & Havens Y. H. (1968) Soil and vegetation pattern in the Santa Catalina Mountains, Arizona. *Soil Sci.* **105**, 440–50.
- Whittaker R. H., Bormann F. H., Likens G. E. & Siccama T. G. (1974) The Hubbard Brook Ecosystem Study: forest biomass and production. *Ecol. Monogr.* **44**, 233–52.
- Woodward F. I. (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.