Rate of Carbon Sequestration at Two Thicket Restoration Sites in the Eastern Cape, South Africa

Anthony J. Mills[1,2,3] and Richard M. Cowling[4]

Abstract

Ecosystem carbon storage in intact thicket in the Eastern Cape, South Africa exceeds 20 kg/m^2, which is an unusually large amount for a semiarid ecosystem. Heavy browsing by goats transforms the thicket into an open savanna and can result in carbon losses greater than 8.5 kg/m^2. Restoration of thicket using cuttings of the dominant succulent shrub *Portulacaria afra* could return biodiversity to the transformed landscape, earn carbon credits on international markets, reduce soil erosion, increase wildlife carrying capacity, improve water infiltration and retention, and provide employment to rural communities. Carbon storage in two thicket restoration sites was investigated to determine potential rates of carbon sequestration. At the farm Krompoort, near Kirkwood, 11 kg C/m^2 was sequestered over 27 years (average rate of 0.42 ± 0.08 kg C m^{-2} yr^{-1}). In the Andries Vosloo Kudu Nature Reserve, near Grahamstown, approximately 2.5 kg C/m^2 was sequestered over 20 years (0.12 ± 0.03 kg C m^{-2} yr^{-1}). Slower sequestration in the Kudu Reserve was ascribed to browsing by black rhinoceros and other herbivores, a shallower soil and greater stone volumes. Planting density and *P. afra* genotype appeared to affect sequestration at Krompoort. Closely-packed *P. afra* planting may create a positive feedback through increased infiltration of rainwater. The rate of sequestration at Krompoort is comparable to many temperate and tropical forests. Potential earnings through carbon credits are likely to rival forest-planting schemes, but costs are likely to be less due to the ease of planting cuttings, as opposed to propagating forest saplings.

Key words: **biomass, carbon sequestration, *Portulacaria afra*, restoration, semiarid landscapes, soil carbon, thicket.**

Introduction

Ecosystem carbon storage in the arid form of South African succulent thicket (Vlok et al. 2003), found in areas receiving 250–350 mm mean annual rainfall, exceeds 20 kg/m^2 (Mills, O'Connor, et al. 2003, 2005). This is an exceptional amount of carbon for a warm, semiarid region and is more akin to mesic forest ecosystems (Mills, Cowling, et al. 2005). In its untransformed state, xeric thicket has an almost complete cover of dense, relatively tall (3–4 m) evergreen vegetation and has a much higher biomass than would be expected under semiarid conditions (Lechmere-Oertel 2004; Mills, Cowling, et al. 2005; Lechmere-Oertel et al. 2005*b*). Much of the biomass comprises the succulent shrub *Portulacaria afra*, known locally as spekboom (Acocks 1953; Vlok et al. 2003). The vegetation has been used for farming goats since the early 1900s. Heavy browsing by goats has resulted in the loss of *P. afra*, which is highly palatable to livestock, and the transformation of thicket to an open "savanna." The transformed savanna comprises ephemerals and short-lived grasses (known locally as "opslag"), whose abundance tracks rainfall events, and scattered remnant trees (Hoffman & Cowling 1990; Lechmere-Oertel et al. 2005*b*). Approximately 45% of *P. afra*–dominated thicket in South Africa (5,519 km^2 out of a total of 12,624 km^2) has been altered in this manner (Lloyd et al. 2002).

Carbon lost as a result of degradation in the arid succulent thicket near Kirkwood, Eastern Cape was estimated to be approximately 4.0 kg/m^2 in soils to a depth of 500 mm and 4.5 kg/m^2 in biomass (above- and belowground) (Mills 2003; Mills, O'Connor, et al. 2005). Effective restoration of transformed thicket could be achieved by planting *P. afra* cuttings because this species propagates vegetatively in nature and takes root from cuttings rapidly (Swart & Hobson 1994). Restoration could potentially return greater than 8.5 kg C/m^2 to transformed sites, but the potential rate of return is unknown. Two lines of evidence suggest that return of carbon may occur faster than in other transformed semiarid systems. Lechmere-Oertel et al. (2005*a*) found that the leaf litter productivity of *P. afra* (0.45 kg m^{-2} yr^{-1}, dry matter [DM]) was similar to mesic forest systems, and Aucamp and Howe (1979) found that the net primary production of thicket was approximately 1.1 kg m^{-2} yr^{-1} wet aboveground biomass (0.45 kg DM m^{-2} yr^{-1} assuming a dry:wet ratio of 0.4). Benefits associated with restoration would include restoration of ecosystem services such as carbon sequestration, herbivore browse and flood control, the restoration of biodiversity, control of soil erosion, and the provision of jobs in

---

[1] Department of Soil Science, Stellenbosch University, Private Bag X01, Matieland 7602, South Africa.
[2] South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa.
[3] Address correspondence to A. J. Mills, email mills@sanbi.org
[4] Terrestrial Ecology Research Unit, Department of Botany, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa.

economically depressed rural areas. It is important to note that arid thicket forms part of the Albany Center of Endemism (Van Wyk & Smith 2001) and harbors a large number of rare and threatened plant species (Johnson et al. 1999). Sources of funding for restoration on a large scale may include carbon credits (Rosenzweig et al. 2002), poverty relief funds, and biodiversity funds. In addition, *P. afra* is a valuable fodder plant, and restored landscapes could further supplement income through sustainable browsing of livestock, wildlife, or both, at the appropriate stocking rate (Stuart-Hill & Aucamp 1993).

An assessment of the potential rate of carbon sequestration is a prerequisite for determining the potential returns from carbon credits and, consequently, the financial feasibility of large-scale restoration program. This study reports on the carbon return in soils and biomass at two sites in the Eastern Cape, which were planted with *P. afra* cuttings in 1976 and 1983, respectively.

Materials and Methods

Restoration Sites

The restoration site at Krompoort is situated west of Kirkwood in the Eastern Cape, at an elevation of 300–500 m (33°33′S; 25°11′E). It has a warm temperate climate with evenly distributed annual rainfall of 250–350 mm. In 1976, the landowner set aside several hectares of transformed thicket on a north-facing slope for rehabilitation with *Portulacaria afra* (Fig. 1). The first *P. afra* cuttings (approximately 10- to 30-mm diameter and 0.5- to 1-m length) were planted in that year, and the landowner continued planting different blocks up until 1998. The Andries Vosloo Kudu Nature Reserve site (hereafter referred to as the Kudu Reserve) is situated northeast of Grahamstown, at an elevation of 300–400 m (33°7.5′S; 26°38′E). It has a warm temperate climate with mean annual rainfall of 400–450 mm, with a distinct late summer rainfall peak. The reserve management planted *P. afra* cuttings (of similar size range to those planted in Krompoort) in 1983 in a disused gravel road. Salient characteristics of the two restoration sites are shown in Table 1 and illustrated in Figures 1–3.

It is important to note that the restoration layout at both sites was not done in a systematic way that was mindful of the principles of experimental design. Our sampling approach and subsequent statistical analyses were constrained by the somewhat haphazard layout.

Portulacaria afra Genotype Differences

At Krompoort, the K5, K7, K13, and K27 blocks were planted with a specific *P. afra* genotype, known locally as "berg spekboom" and cut from a mountain near the town of Steytlerville, approximately 90 km northwest of Krompoort. Berg spekboom has an upright appearance, with most branches extending upward (Fig. 2). The K27R block was planted with a different genotype, the local *P. afra*, cut from the surrounding intact thicket. This local *P. afra* is shorter and has a more rounded appearance than berg spekboom (Fig. 2). The *P. afra* planted in the Kudu Reserve site was also relatively short and round in comparison with the berg spekboom. There are currently no data on genotypic variation in *P. afra*, although pastoralists have long recognized variation in relation to stature and palatability (Ras 1995).

Vegetation

The intact vegetation at both sites is known as spekboomveld, a form of arid succulent thicket (Vlok et al. 2003), and is characterized by a matrix of the succulent shrub *P. afra*, which is interspersed with spinescent shrubs such as Needle-bush (*Azima tetracantha*), Hedge spikethorn (*Gymnosporia polyacantha*), False spikethorn (*Putterlickia pyracantha*), Three-leaved rhigozum (*Rhigozum obovatum*),

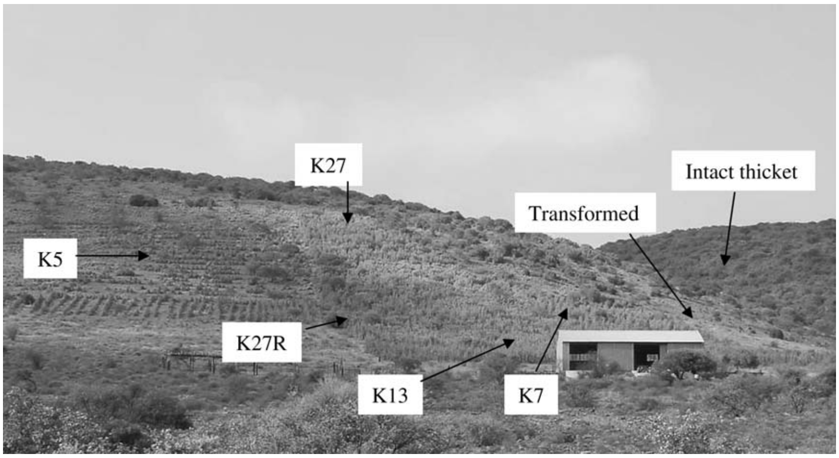

Figure 1. The Krompoort restoration site: a north-facing slope adjacent to the gravel road between Uitenhage and Steytlerville, Eastern Cape, South Africa.

Table 1. Sampling locations at the Krompoort and Kudu Reserve restoration sites, Eastern Cape, South Africa.

Site	*Year of Planting*	*Mean Spacing Rows (m)*	*Mean Spacing Plants (m)*	*Approximate Size of Sampling Location (m^2)*
Krompoort				
Transformed				2,500
K5	1998	4.1	1	2,500
K7	1996	1.9	1.4	2,500
K13	1990	1.5	0.8	2,500
K27R	1976	One row only	3.1	300
K27	1976	2	1.1	2,500
Kudu Reserve				
Restored	1983			10,000
Thicket				20,000

and Spiny currant-rhus (*Rhus longispina*), and low-growing trees (<5 m) such as Jacket-plum (*Pappea capensis*), Common guarri (*Euclea undulata*), and Karoo boer-bean (*Schotia afra*). Transformed sites are characterized by ephemerals or weakly perennial grasses and karroid shrubs, often dominated by the alien chenopod saltbush Little saltbush (*Atriplex lindleyi* ssp. *inflata*). In these sites, the tree component (predominantly *P. capensis*) is the only remnant of the original thicket, with a tree cover often less than 10% (Lechmere-Oertel et al. 2005*b*). By contrast, intact sites have a shrub/tree cover often greater than 60%.

Geology and Soils

Krompoort lies in a broad valley, flanked by the Groot-Winterhoekberge mountain range to the south and the Klein-Winterhoekberge to the north. These ranges are made up of the Table Mountain Group of quartzitic sandstones of the Nardouw Subgroup and the Peninsula Formation. Bokkeveld shales, sandstones, and siltstones of the Ceres and Traka Subgroups are the dominant underlying geology at Krompoort. The parent material of any particular soil profile on Krompoort is likely to be a mixture of transported material and weathered bedrock. The underlying geology of the *P. afra* restoration site on the Kudu Reserve is Beaufort Group shale of the Adelaide Formation on the upper slopes and Ecca Group shale of

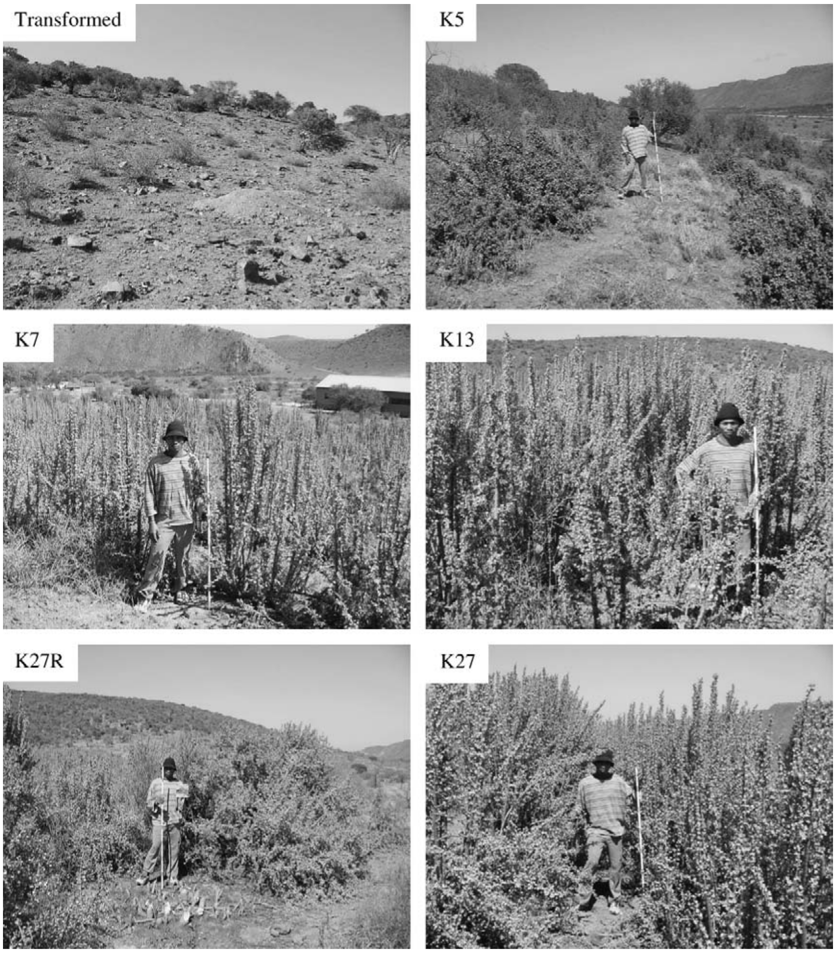

Figure 2. The Krompoort restoration blocks.

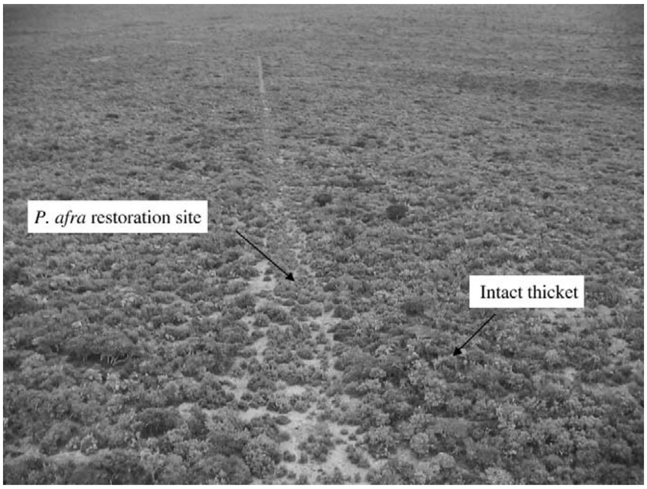

Figure 3. The Kudu Reserve restoration site.

the Fort Brown Formation on the lower slopes. The Ecca Group shale weathers to form a red, highly erodible soil, whereas soils derived from the Beaufort Group shale are more stable. A wide range of soil forms was evident at Krompoort and the Kudu Reserve. Soil forms in the study area include Calcaric Cambisols, Calcic Luvisols, Rhodic Luvisols, and Calcaric Regosols (FAO 1998). Soil properties at a site approximately 2 km west of Krompoort are presented in Table 2 and are reported in greater detail in Mills and Fey (2004). The data include a comparison of composite samples (0–0.1 m) from intact and transformed thicket across a fence-line contrast. Soil properties, other than carbon content and bulk density as described below, were not quantified at the Kudu Reserve.

Carbon Storage Components

Carbon storage within the ecosystem was divided into soil, aboveground biomass, and root carbon. The methods employed for measuring each component are documented below. Results were calculated according to the percentage cover of *P. afra* canopy and open ground for each treatment.

Soil Carbon

At Krompoort, five soil pits were dug to a depth of 1 m in each block (Table 1), that is, five pits at each sampling site, making a total of 30 pits. The location of each pit was selected using a random number table. A few pits were dug slightly shallower than 1 m owing to the presence of rocky colluvium. Each pit was approximately 0.75–1 m in length, with one end of the pit located within a *P. afra* shrub canopy and the other end in open ground between shrubs (except for the Transformed block at Krompoort where no *P. afra* had been planted). Soil samples were taken at the following intervals at the *P. afra* end and open end of the pits: 0–10, 10–30, 30–60, 60–100, 100–150, 150–200, 200–300, 300–500, 500–750, and 750–1,000 mm. For the K27R block, soil samples were only taken from under the *P. afra* canopy because this site had a single row of plants and younger *P. afra* plants bordered the open ground.

Table 2. Soil properties of composite samples (0–10 cm) at an intact transformed thicket fence-line contrast, approximately 2 km to the west of Krompoort.

	Intact		*Transformed*	
	Canopy	*Open*	*Canopy*	*Open*
EC (mS/m)*	21.7	21.8	20.0	35.9
pH in 1M KCl (1:2.5)	6.1	5.9	7.0	6.9
Soluble ions (mmol_c/kg in a 1:5 soil water extract)				
Ca	4.06	7.21	4.96	7.72
Mg	2.55	1.70	1.94	2.83
K	2.39	1.39	3.34	2.82
Na	3.72	0.98	2.16	5.45
Cl	3.22	3.80	1.39	5.00
NO_3	3.43	3.06	0.36	2.73
SO_4	1.30	2.08	0.39	1.71
$(NH_4)OAc$-extractable cations (mmol_c/kg)				
Ca	109	82	115	116
Mg	62	17	36	19
K	2.5	0.9	3.9	3.2
Na	4.8	1.2	2.5	6.4
Bray2 P (mg/kg)	76	59	121	110
Total clay (%)	8	8	7	9
Silt (%)	12	14	16	12
Fine sand (%)	35	34	41	47
Medium sand (%)	21	22	19	19
Coarse sand (%)	24	22	17	14
Total carbon (%)	6.9	3.8	5.7	4.2
Total nitrogen (%)	0.42	0.27	0.4	0.31
CO_2 flux (μmol m^{-2} s^{-1})	2.0	0.5	1.0	0.3

Methods of soils analysis are reported in Fey and Mills (2004).
* Electrical conductivity of a 1:5 soil water extract (mS/m).

At the Kudu Reserve, 10 pits were dug in each site to a depth of 750 mm where possible (i.e., 20 pits). Pits were dug at 20-m intervals along the restored road and 10–30 m into the thicket adjacent to the road. Soils were shallower than at Krompoort, and consequently, pits were not dug to 1 m. Approximately half the pits were shallower than 750 mm, owing to the presence of bedrock. Samples were taken at the same intervals as at Krompoort at both ends of the soil pits (i.e., *P. afra* and in the open in the restoration site, and under thicket canopy and in the open in the adjacent thicket site).

Total soil carbon was analyzed by complete combustion using a Eurovector Euro EA Elemental Analyzer. Samples were air-dried and sieved to 2 mm and then milled with a ball mill to a fine powder before analysis. Calcrete (i.e., calcium carbonate) was evident at the bottom of several pits, and consequently, inorganic carbon contributed to the total soil carbon for some samples. Samples with inorganic carbon were identified as those that effervesced after addition of 3 M HCl. The inorganic carbon content of these samples was determined as described by the U.S. Salinity Laboratory Staff (1954). The procedure entails gravimetric measurement of the loss of CO_2 after reaction of the sample with 3 M HCl. Inorganic carbon was subtracted from total carbon to determine the organic carbon content.

The bulk density of soil under *P. afra* and in the open was estimated by excavating samples 100–150 mm into the soil pit wall for the following depth intervals: 0–100, 100–500, 500–1,000 mm (Krompoort), and 500–750 mm (Kudu Reserve). The dimensions of each excavation for each sample were measured to determine the soil volume. After air-drying, the samples were weighed and sieved to remove roots and stones greater than 2 mm. Stones were weighed, and the volume of stones was determined by the displacement of water. Bulk density was calculated by dividing the mass of soil by the volume of soil (both excluding stones >2 mm). Soil carbon storage was calculated using the soil carbon content, the bulk density of soil, and the volume of stones at each depth interval. The volume of stones was subtracted from each depth layer to provide an estimate of soil volume in each layer.

Root Carbon

Roots were extracted by wet sieving from the same samples used for determining bulk density. The extracted roots were dried in an oven at 60°C until constant mass. The mass of roots per volume (stones included) was determined for each depth layer.

Aboveground Biomass

The *P. afra* plants adjacent to or above each soil pit were harvested and weighed. Biomass was divided into stems greater than 30 mm and less than 30 mm diameter. Leaves were predominantly on the stems less than 30 mm diameter. DM mass was calculated using dry:wet ratios of 0.32 for stems greater than 30 mm and 0.23 for stems less than 30 mm diameter (Skowno 2003). Biomass sampling by Skowno (2003) to determine dry:wet ratios was done at the same time of year as this study (October–November) and consequently under similar climatic conditions. For each harvested plant, the average diameter was determined by measuring two diameters (at right angles) across the center of the plant, and average height was determined by measuring height at 200-mm intervals across one of the diameters. Average distance between plants and between rows in each block at Krompoort was determined from 10 random samples. This information was used to determine the percentage area of *P. afra* canopy in each block. In the Kudu Reserve, six line transects of 20 m were run in the restored site to determine the area of ground covered by *P. afra* canopy.

In the Kudu Reserve, six plots (10- × 2m) were harvested of all aboveground biomass to estimate the theoretical maximum for aboveground biomass. The six plots were situated adjacent to the southwestern boundary fence on a south-facing slope. This site was chosen because vegetation was being cleared to make way for an electrified fence, and thus afforded an opportunity to collect biomass data without otherwise damaging the thicket in a protected area, a stipulation of the management authority. The vegetation on this southern slope was taller and denser than the vegetation where the soil samples were taken. All the aboveground biomass was harvested and weighed on site. DM was calculated using the above mentioned dry:wet ratios for *P. afra* and for all other shrubs using dry:wet ratios of 0.8 for stems greater than 30 mm and 0.5 for stems less than 30 mm (Mills 2004, unpublished data from the Kudu Reserve). The carbon content of biomass was calculated by multiplying DM mass by 0.48 (Lamlom & Savidge 2003).

Litter and "Opslag"

Litter was collected from below each *P. afra* plant before harvesting. The "opslag" (weedy regrowth), comprising desiccated grass and ephemerals, as well as scattered low shrubs of mainly *R. obovatum* (which occupied the space between *P. afra* plants at both Krompoort and the Kudu Reserve) was harvested from 2- × 2-m plots adjacent to the harvested *P. afra* plants. The dry:wet ratio for litter and opslag was obtained from Skowno (2003). Litter and opslag sampling by Skowno (2003) to determine dry:wet ratios was done at the same time of year as this study (October–November). Hot temperatures during the day (frequently >35°C) at this time of year results in rapid drying of litter after rain events, and consequently, litter moisture content for this study and that of Skowno (2003) was assumed to be similar.

Statistical Analysis

Statistical analysis was performed using the software package Unistat 5.5. Differences between means were examined using one-way analysis of variance and least significant difference. Differences were deemed significant where $p < 0.05$. Data were log transformed in order to homogenize variances when appropriate. At Krompoort, means of carbon components in different blocks were compared between open, canopy, and a canopy/open combination. The combination value was calculated from percentage canopy and percentage open data. At the Kudu Reserve, means of carbon components were compared (1) between restored open, restored canopy, intact open, and intact canopy and (2) between restored canopy/open combination and intact canopy/open combination. The carbon components analyzed included aboveground biomass, litter, root, and soil carbon to a depth of 500 mm. Differences between means of root carbon at different depth intervals were also examined. The rates of carbon sequestration at Krompoort were calculated by dividing the difference between the transformed block and the restored blocks by the number of years of restoration. For the Kudu Reserve, the difference between the canopy and the open in the restored area was used to calculate the rate of sequestration. It was assumed that the carbon storage in the open areas was similar to what was present at the time of planting of *P. afra* cuttings. The standard error of the rate of sequestration was solved by algebra, according to the principle that when adding values and their errors, the final error is calculated by taking the square root of the sum of squared errors. This error calculation assumed a linear rate of sequestration.

Results

Soil Carbon

Total, organic, and inorganic carbon showed a trend of decreasing concentrations with depth at all sites, and concentrations were greater below a canopy of vegetation than in the open (Table 3). Inorganic carbon was present in 35% of all samples at Krompoort and only in 3% at the Kudu Reserve. At Krompoort, the inorganic carbon content ranged from 3 g/kg at 0–10 mm to 9 g/kg at 750–1,000 mm, with the percentage of samples with inorganic carbon increasing with depth (13% at 0–10 mm, 53% at 300–500 mm, 94% at 750–1,000 mm). The relative contribution of mean inorganic carbon to mean total carbon content also increased with depth (6% at 0–10 mm, 34% at 300–500 mm, 49% at 750–1,000 mm). At the Kudu Reserve, inorganic carbon was restricted to depths greater than 15 cm and means ranged from 1 to 3 g/kg.

The effect of planting *Portulacaria afra* on soil organic carbon (hereafter referred to as soil carbon) was most evident from 0 to 500 mm. Rocks within the profile prevented sampling of several profiles below 500 mm, and consequently, these data were not included in the statistical analysis of rates of carbon sequestration. At Krompoort, the K27 block had the greatest effect on soil carbon, with approximately 7 kg C/m^2 returning to the system (assuming that the transformed block had reached a soil carbon equilibrium at the time of *P. afra* planting and that it can therefore be used as a surrogate baseline) in the top 500 mm of soil, at an average rate of 0.26 ± 0.05 kg C m^{-2} yr^{-1}. In the Kudu Reserve, soil carbon beneath the restored *P. afra* canopy was not significantly different from open soils (5.7 vs. 5.1 kg C/m^2), but thicket had significantly greater soil carbon than the adjacent restored site (6.9 vs. 5.4 kg C/m^2).

Soil below a canopy of restored *P. afra* or intact thicket tended to have lower mean bulk density than soil in the open (Table 4). At Krompoort, bulk density in layers less than 100 mm were not significantly different across blocks or between *P. afra* canopy and open soil. Mean bulk density values for layers less than 100 mm were consequently used for calculating carbon storage. Stone volumes were also not significantly different across blocks, and mean stone volumes were used to calculate carbon storage (Table 4).

Root Carbon

Root carbon in the 0- to 100-mm layer of soil tended to be greater than in the 100- to 500-mm, 500- to 750-mm, and 500- to 1,000-mm layers and was greater below a vegetation canopy than in the open at all sites (Table 5). At Krompoort, the K27R block had the most root carbon, with approximately 1.4 kg C/m^2 returning to the system (relative to the transformed block) in the top 1 m of soil, at an average rate of 0.05 ± 0.01 kg C m^{-2} yr^{-1}. In the Kudu Reserve, planting with *P. afra* increased root carbon by approximately 1 kg C/m^2 (at an average rate of 0.05 ± 0.01 kg C m^{-2} yr^{-1}) if soil profiles in the open (i.e., outside planted *P. afra*) are assumed to represent an approximate root carbon level at the time of planting.

Biomass Carbon

At Krompoort, planting with *P. afra* in the K27 block increased aboveground carbon (taking the transformed block as a baseline) by 3.5 kg C/m^2 (including *P. afra*, litter, and opslag) at an average rate of 0.13 ± 0.02 kg C m^{-2} yr^{-1} (Table 6). In the Kudu Reserve, planting with *P. afra* increased aboveground carbon (assuming a carbon level of 0.05 kg C/m^2 at the time of planting) by 0.83 kg C/m^2 (including *P. afra*, litter, and opslag) at an average rate of 0.04 ± 0.01 kg C m^{-2} yr^{-1}. The average aboveground carbon in intact thicket on the southwestern boundary of the Kudu Reserve was 3.4 kg C/m^2 (Table 6). The mass of *P. afra* cuttings brought into each block at the time of planting is unknown and was not subtracted from the aboveground biomass. Assuming a cutting mass of 200 g (wet biomass) and a planting density of 2,500 cuttings/ha, the contribution of cuttings at time of planting to carbon storage was only 0.007 kg/m^2.

Total Carbon Storage

At Krompoort, mean total carbon storage (biomass and soil carbon) in the K27 block was 16.1 kg C/m^2 (soil carbon to a depth of 500 mm) calculated according to area under plant canopy (Table 7) and area of open ground. In the Kudu Reserve, mean total carbon storage in the restored site was 6.5 kg C/m^2 (soil carbon to a depth of 500 mm).

Rate of Carbon Sequestration

The average rate of total carbon sequestration at Krompoort (assuming that the transformed block represents carbon storage at the time of planting) ranged from 0.24 kg C m^{-2} yr^{-1} in the K27R block to 0.42 ± 0.08 kg C m^{-2} yr^{-1} in the K27 block and 0.42 ± 0.19 in the K5 block. In the Kudu Reserve, the average rate of total carbon sequestration was 0.12 ± 0.03 kg C m^{-2} yr^{-1} (assuming that open ground in the restored site provides an approximate level of carbon storage at the time of planting). This calculated rate is a conservative estimate because the

Table 3. Distribution of soil carbon at Krompoort and Kudu Reserve thicket restoration sites, Eastern Cape, South Africa.

		Depth Intervals (mm)																													
		0–10	*SE*	*n*	*10–30*	*SE*	*n*	*30–60*	*SE*	*n*	*60–100*	*SE*	*n*	*100–150*	*SE*	*n*	*150–200*	*SE*	*n*	*200–300*	*SE*	*n*	*300–500*	*SE*	*n*	*500–750*	*SE*	*n*	*750–1,000*	*SE*	*n*
		g/kg																													
Krompoort (organic C)																															
Transformed	Open	19	3	5	17	2	5	13	1	5	13	4	4	11	3	4	9	2	4	8	1	4	4	1	4	5		2	3	1	3
K5	Open	24	2	5	24	4	5	19	4	5	16	1	4	15	2	3	12	1	3	9	2	4	7	1	4	5	2	3	5	1	4
K7	Open	18	4	4	19	5	4	17	2	4	17	3	5	14	2	5	11	2	5	10	3	5	8	2	4	4	1	3	5		2
K13	Open	23	4	5	20	6	5	15	4	4	9	1	4	17	3	3	12	7	3	11	5	3	7	4	3	7	2	5	12	4	4
K27	Open	44	4	4	45	4	4	38	3	4	37	5	5	38	3	5	26	1	5	10	3	5	12	2	4	12		2	21		2
K5	Canopy	33	2	5	33	7	5	23	8	5	19	4	5	17	2	5	16	1	4	8	1	4	6	2	4	5	1	4	8	1	3
K7	Canopy	40	11	5	30	7	5	21	2	5	17	2	5	14	2	5	12	2	4	11	2	5	8	3	4	4	1	4	5	2	3
K13	Canopy	27	10	5	34	10	5	16	2	4	14	3	4	12	1	4	12	2	3	13	4	3	8	2	3	5		2	8	3	3
K27R	Canopy	96	6	5	41	8	5	28	3	5	20	2	5	15	2	5	13	5	4	12	4	5	7	2	5	3		2	5	1	5
K27	Canopy	63	9	5	39	9	5	44	13	4	48	8	5	43	7	5	27	2	5	12	1	5	10	1	5	4	2	3	15		2
Kudu Reserve (organic C)																															
Restored	Open	12	1	9	19	5	8	13	4	10	10	1	10	10	0.4	9	8	1	10	6	0.5	9	7	0.5	3						
Restored	Canopy	28	4	9	18	5	9	19	4	9	13	1	10	13	4	9	8	1	8	7	1	7	6	1	6	4		1			
Thicket	Open	19	3	9	21	6	7	20	4	9	15	2	9	13	2	8	11	2	10	7	1	10	7	1	7	10		2			
Thicket	Canopy	61	6	10	33	8	9	24	6	9	20	3	10	12	1	8	12	2	9	8	1	8	7	2	8	7	1	4			
Krompoort (inorganic C)																															
Means for all treatments		3	1	6	4	3	5	4	1	7	4	1	14	6	1	13	5	1	15	5	1	14	4	1	21	6	1	23	9	1	29
Kudu Reserve (inorganic C)																															
Means for all treatments																1		1	1	<0.1	3	3	<0.1	4							

Table 4. Mean bulk density and stone volume at Krompoort and Kudu Reserve thicket restoration sites, Eastern Cape, South Africa.

	Bulk Density (kg/m^3)			*Stone Volume (%)*			
	Mean	*SE*	*n*	*All Profiles*	*Mean*	*SE*	*n*
Krompoort							
Canopy (0–100 mm)	870	40	23	0–100 mm	15.2	1.4	42
Open (0–100 mm)	1,210	70	19	100–500 mm	22.8	1.9	35
All profiles (100–1,000 mm)	1,610	60	44	500–1000 mm	30.3	5.3	9
Kudu reserve							
Restored canopy (0–100 mm)	1,252	75	8	0–100 mm	7.4	0.8	37
Restored open (0–100 mm)	1,347	122	9	100–500 mm	14.9	1.6	25
Thicket canopy (0–100 mm)	1,000	102	10	500+ mm	46.3	8.2	13
Thicket open (0–100 mm)	1,298	90	10				
All profiles (100–500 mm)	1,484	87	25				
All profiles (500+ mm)	1,813	153	7				

open ground in the restored site would have gained carbon as a result of *P. afra* growth (in the form of root and soil carbon), as was evident at Krompoort.

Discussion

Rates of Carbon Sequestration

The calculated average rate of 0.42 ± 0.08 kg C m^{-2} yr^{-1} over 27 years in the K27 block at Krompoort is fast for a semiarid region. Whittaker and Niering (1975) report a rate of net primary production of 0.07–0.1 kg C m^{-2} yr^{-1} for shrublands in Arizona that occur in a similar climate to our study site. The rate recorded at Krompoort implies a net primary productivity exceeding 1 kg DM m^{-2} yr^{-1} for reasons discussed below. Rate of carbon sequestration in soils and biomass will be less than net primary productivity because of carbon lost through microbial respiration (i.e., breakdown of litter and soil organic matter). Mills and Fey (2004) report that soil respiration in intact and transformed thicket at Krompoort ranged from 0.3–2.0 μmol CO_2 m^{-2} s^{-1} or 0.1–0.8 kg C m^{-2} yr^{-1}. Half of this respiration is likely to be root respiration (Ellert & Janzen 1999), and consequently, the range of soil carbon loss is 0.06–0.4 kg C m^{-2} yr^{-1}. If carbon loss through soil respiration is then conservatively estimated at 0.1 kg C m^{-2} yr^{-1},

Table 5. Distribution of root carbon at Krompoort and Kudu Reserve thicket restoration sites, Eastern Cape, South Africa.

		Depth Intervals (mm)								
		0–100	*SE*	*n*	*100–500*	*SE*	*n*	*>500**	*SE*	*n*
Site	*Cover*	*kg C/m^2*								
Krompoort										
Transformed	Open	0.07	0.02	5	0.05	0.02	5	0.03	0.01	5
K5	Open	0.14	0.07	5	0.05	0.01	5	0.305	0.02	4
K7	Open	0.05	0.01	5	0.07	0.02	5	0.02		2
K13	Open	0.08	0.01	5	0.016	0.06	5	0.06	0.03	5
K27	Open	0.30	0.14	5	0.32	0.15	5	0.02		1
K5	Canopy	0.24	0.06	5	0.13	0.08	5	0.06	0.05	5
K7	Canopy	0.19	0.04	5	0.07	0.02	5	0.01	0.00	5
K13	Canopy	0.54	0.26	5	0.12	0.02	5	0.05	0.01	5
K27R	Canopy	0.94	0.37	5	0.60	0.19	5	0.12	0.03	5
K27	Canopy	0.26	0.08	5	0.33	0.09	5	0.36	0.17	3
Kudu Reserve										
Restored	Open	0.13	0.02	10	0.11	0.02	8	0.17		1
Restored	Canopy	0.51	0.11	10	0.74	0.15	8	0.04	0.02	3
Thicket	Open	0.50	0.12	10	0.46	0.23	10	0.08	0.05	3
Thicket	Canopy	0.55	0.13	10	1.37	0.44	10	0.13	0.06	4
Restored	Combined	0.30	0.05	10	0.39	0.05	10	0.09	0.004	10
Thicket	Combined	0.53	0.09	10	1.00	0.31	10	0.10	0.02	10

*500–1,000 mm for Krompoort and 500–750 mm for Kudu Reserve. Where $n < 5$ (Krompoort) or $n < 10$ (Kudu Reserve) this is because rocks interfered with sampling of roots at some profiles. Missing data were substituted with means from the same treatment and depth, in order to calculate total root values within the whole profile. In the case of the Kudu Reserve 500–750 mm, missing data were substituted with the mean across all treatments. Transformed open data were used as substitutes for K27R open data (as K27R open data were not collected).

Table 6. Carbon storage and rate of sequestration in aboveground biomass, roots, opslag, litter, and soils at Krompoort and Kudu Reserve thicket restoration sites, Eastern Cape, South Africa.

	Cover	*Biomass*	*SE*	*Root*	*SE*	*Opslag*	*SE*	*Litter*	*SE*	*Soil C*[a]	*SE*	*Total*	*SE*	*Rate*[b]	*SE*
Site	*kg C/m*^{2}													*kg C m*$^{-2}$ *yr*$^{-1}$	
Krompoort															
Transformed	Open			0.15	0.03^{ab}	0.005	0.002			4.7	0.5^{a}	4.9	0.5^{a}		
K5	Open			0.24	0.07^{ab}					6.5	0.2^{a}	6.8	0.3^{a}	0.38	0.17
K7	Open			0.14	0.02^{a}					6.5	0.9^{a}	6.7	0.9^{a}	0.26	0.10
K13	Open			0.30	0.06^{bc}					6.3	1.1^{a}	6.6	1.1^{a}	0.14	0.04
K27	Open			0.65	0.28^{c}					12.2	0.9^{b}	12.9	0.9^{b}	0.30	0.06
Transformed	Open			0.15	0.03^{a}	0.005	0.002^{a}			4.7	0.5^{a}	4.9	0.5^{a}		
K5	Canopy	0.68	0.1^{a}	0.44	0.13^{bc}	0.05	0.01^{b}	0.01	0.002^{a}	6.2	0.7^{ab}	7.4	0.6^{b}	0.51	0.23
K7	Canopy	0.96	0.03^{a}	0.27	0.06^{ab}	0.06	0.02^{b}	0.05	0.02^{b}	6.7	0.9^{ab}	8	0.9^{bc}	0.45	0.17
K13	Canopy	2.74	0.5^{b}	0.71	0.26^{cd}	0.13	0.06^{b}	0.07	0.01^{bc}	6.5	0.2^{ab}	10.2	0.9^{cd}	0.41	0.11
K27R	Canopy	2.39	0.3^{b}	1.66	0.44^{e}			0.34	0.04^{d}	7.4	1.2^{b}	11.8	0.9^{d}	0.26	0.05
K27	Canopy	3.33	0.4^{b}	0.95	0.15^{de}	0.25	0.15^{b}	0.12	0.03^{c}	11.7	0.8^{c}	16.4	1.1^{e}	0.43	0.08
Transformed	Open			0.15	0.03^{a}	0.005	0.002^{a}			4.7	0.5^{a}	4.9	0.5^{a}		
K5	Combined	0.19	0.02^{a}	0.30	0.05^{bc}	0.05	0.01^{b}	0.003	0.001^{a}	6.4	0.3^{ab}	7.0	0.3^{b}	0.42	0.19
K7	Combined	0.53	0.02^{b}	0.21	0.03^{ab}	0.06	0.02^{b}	0.03	0.01^{b}	6.6	0.9^{ab}	7.5	0.9^{b}	0.37	0.14
K13	Combined	1.42	0.3^{c}	0.52	0.13^{c}	0.13	0.06^{b}	0.04	0.01^{b}	6.4	0.6^{ab}	8.5	0.9^{b}	0.28	0.08
K27R	Combined	2.15	0.3^{d}	1.51	0.40^{d}			0.30	0.04^{d}	7.4	1.2^{b}	11.4	0.9^{c}	0.24	0.05
K27	Combined	3.09	0.4^{e}	0.93	0.14^{d}	0.25	0.15^{b}	0.12	0.03^{c}	11.8	0.8^{c}	16.1	1.0^{d}	0.42	0.08
Kudu Reserve															
Restored	Open			0.34	0.03^{a}					5.1	0.3^{a}	5.5	0.3^{a}		
Restored	Canopy	0.77	0.1	1.33	0.20^{bc}	0.05	0.03	0.05	0.01	5.7	0.3^{ab}	7.9	0.3^{b}	0.12	0.03
Thicket	Open			1.05	0.33^{b}					6.3	0.5^{bc}				
Thicket	Canopy			2.03	0.46^{c}					7.3	0.7^{c}				
Restored	Combined	0.34	0.04	0.78	0.09^{a}	0.05	0.03	0.02	0.01	5.4	0.3^{a}	6.5	0.3		
Thicket	Combined			1.63	0.33^{b}					6.9	0.6^{b}				
SW Fenceline[c]		3.42	0.4												

[a] 0- to 500-mm layer for all sites.

[b] Rate of carbon sequestration calculated with the assumption that the transformed block at Krompoort and the restored open site at the Kudu Reserve represent the carbon present at the time of planting with spekboom.

[c] Thicket biomass at the Kudu Reserve was measured at the southwestern boundary of the reserve, that is, not adjacent to the restoration site. Total values for thicket are consequently not presented; $n = 5$ for each treatment at Krompoort; $n = 10$ for each treatment at the Kudu Reserve; significant differences ($p < 0.05$) between means within each group are indicated by different letters; groups at each site are separated by open lines within the table. Blank cells, no data collected or negligible material available for collection.

primary productivity would be 0.42 + 0.1 kg C m^{-2} yr^{-1} (i.e., 1.1 kg DM m^{-2} yr^{-1}), at least half of which is aboveground production. Such production falls within the range reported for many tropical and temperate forests systems. Aboveground net primary productivity from a range of forests include 0.2–1.9 kg DM m^{-2} yr^{-1} in rainforests of Borneo (Kitayama & Aiba 2002); 0.1–0.9 kg DM m^{-2} yr^{-1} in rainforests of Hawaii; 0.4–1.2 kg DM m^{-2} yr^{-1} in temperate forests of Europe (Schulze 2000); and 0.45–0.62 kg DM m^{-2} yr^{-1} in montane *Pinus* forests of Arizona (Whittaker & Niering 1975). Forest productivity does, however, vary according to climate and soils, with some tropical forests having primary productivities three to four times that of the estimated productivity of the *Portulacaria afra* restoration sites of this study (Raich et al. 1997; Clarke et al. 2001; Roy et al. 2002).

Notwithstanding the greater productivity in some mesic regions, our estimate of 1.1 kg DM m^{-2} yr^{-1} in a semiarid region requires further scrutiny. The leaf litter productivity of *P. afra* (0.45 kg DM m^{-2} yr^{-1}) in intact thicket near Krompoort (Lechmere-Oertel 2005*a*) indicates that a 100% *P. afra* cover could generate 0.45 kg DM/m^2 in leaf litter alone. An additional 0.55 kg DM/m^2 production in branches and roots and a total production of 1 kg DM m^{-2} yr^{-1} under 100% *P. afra* cover is, therefore, conceivable. The K27 block had a *P. afra* canopy of 93%. This canopy cover would have been lower at the time of planting. Nevertheless, the rate of leaf litter production recorded by Lechmere-Oertel (2005*a*) indicates that the

Table 7. Mean canopy cover at Krompoort and Kudu Reserve thicket restoration sites, Eastern Cape, South Africa.

	Canopy	*n*	*SE*
Krompoort			
Transformed	0		
K5	28	5	4.6
K7	55	5	6.6
K13	52	5	7.4
K27R	90	5	6.9
K27	93	5	7.0
Kudu Reserve			
Restored site	44	8	4.6
Thicket*	60		
SW Fenceline	93	6	4.6

*Estimated figure.

rate of carbon sequestration calculated for the K27 block is not unexpected. The effect of genotype on the rate of carbon sequestration requires further investigation. The K27R block (planted with the local *P. afra* genotype) had a lower rate of sequestration than the K27 block, but comprised only one row and was planted at greater intervals (3 vs. 1.1 m).

Aucamp and Howe (1979) measured a net primary production of approximately 0.45 kg m^{-2} yr^{-1} aboveground DM for spekboomveld (assuming a total dry:wet ratio of 0.4). If belowground productivity is assumed to be equal to aboveground productivity (a conservative estimate according to Nadelhoffer and Raich 1992), then the total productivity in the study by Aucamp and Howe (1979) would be approximately 0.9 kg DM m^{-2} yr^{-1}, which suggests that the rate of carbon sequestration calculated for the K27 block at Krompoort is realistic. Furthermore, productivity in the K27 block is likely to be greater than in intact thicket because of the dominance of *P. afra*. Lechmere-Oertel (2005*a*) found that the rate of leaf litter production under *P. afra* canopies was one and a half times greater than other thicket shrubs.

The high productivity of *P. afra* and its tolerance to drought have been ascribed to an unusual physiology whereby the plant shifts from a C3 to a CAM photosynthetic mode in response to water and NaCl stress (Ting & Hanscom 1977), increasing daylength (Guralnick et al. 1984*a*), and increasing temperature, irrespective of moisture status (Guralnick et al. 1984*b*). The N and P richness of soils at Krompoort (Bray2-extractable P range of 59–121 mg/kg, and total N range of 0.27–0.42 %) may also be a factor promoting plant productivity, and is a topic worthy of further research. Although the extractable cation concentrations are relatively low in terms of agricultural crop requirements, ecosystem productivity tends not to be limited by these nutrients, but rather N and P (Chapin et al. 1986). Another soil factor in favor of plant production is the pH range (5.9–7) which is optimal for acquisition of most nutrients by plant roots.

Intact thicket (sampled at eight sites within 20 km of Krompoort) had an average of 15.2 kg DM/m^2 in biomass (Lechmere-Oertel 2004) and 16.8 kg C/m^2 in soils (0–500 mm) (Mills & Fey 2004). The K27 block had a total biomass of only 8.8 kg DM/m^2 and 11.8 kg C/m^2 in soils (0–500 mm) which suggests that its full carbon sequestration potential has not been achieved. The reestablishment of other woody species in the restored plots may be necessary to achieve the full carbon sequestration potential, given that *P. afra* has a greater wet:dry ratio than most other trees and shrubs that occur in thicket.

Arid and semiarid ecosystems tend to have considerably less total biomass and soil carbon than those recorded in thicket. Desert scrub and woodlands in regions receiving less than 650 mm mean annual precipitation (MAP) in Arizona, for example, have a total biomass range of 0.6–3.0 kg DM/m^2 (Whittaker & Niering 1975). Total biomass in Middle Eastern desert shrublands is reported to range from 0.2 to 0.8 kg DM/m^2 (Orshan 1986) and in the Sahel of Chad from 0.03 to 0.7 kg DM/m^2 (Monod 1986). Succulent Karoo shrubland, approximately 350 km to the northwest of our thicket study site, receiving approximately 170 mm MAP, has an aboveground biomass of approximately 0.33 kg DM/m^2 (Milton 1990). It is not clear why the thicket has greater biomass and soil C than other semiarid systems, but we suggest that it is related to the unusual characteristics of *P. afra*. The dense succulent cover afforded by *P. afra* may enable an accumulation of soil organic matter which improves the nutrient and water holding capacity of soils and also results in shedding of rainwater adjacent to the canopy. It is possible that these effects result in the enhanced productivity of other thicket plants.

Upscaling from 2,500 m^2 to tens of km^2 in order to calculate potential carbon credit returns from restoration at a landscape scale is problematic. Part of the transformed landscapes may, for example, be devoid of topsoil or not suitable for *P. afra* growth. It may also be difficult to achieve the planting density found in the K27 block at a landscape scale. Consequently, the rate of carbon sequestration across a restored landscape would probably be several times lower than the average rate of 0.42 kg C m^{-2} yr^{-1} calculated in the K27 block. A landscape scale experiment is presently being implemented to determine the carbon sequestration potential of restoration using *P. afra* cuttings over tens of square kilometers.

Herbivory and Soil Effects on Rate of Carbon Sequestration

In the Kudu Reserve, the average rate of carbon sequestration was markedly lower than at Krompoort (0.12 vs. 0.42 kg C m^{-2} yr^{-1}). The reason for this difference is unlikely to be related to water availability or temperature because both sites were on northern slopes, and the mean annual rainfall is greater at the Kudu Reserve than at Krompoort. The shallower soils and the greater stone volumes at depths greater than 500 mm in the soils at the Kudu Reserve may partly explain the lower rate of sequestration because root development may have been restricted relative to Krompoort. Compaction from vehicles on the road at the Kudu Reserve prior to restoration may also have had a negative effect on *P. afra* growth. The greater herbivore impact in the Kudu Reserve is yet another factor likely to be affecting carbon accumulation. The site at Krompoort is fenced from goats, although the landowner has allowed some goat browsing for a few weeks of the year over the past decade. Kudus (*Tragelaphus strepsiceros*) have on occasion also been observed in the restoration site at Krompoort. By contrast, the Kudu Reserve restoration site is accessible to a large biomass of indigenous herbivores, including Black rhinoceros (*Diceros bicornis*), Kudu, Buffalo (*Syncerus caffer*), and Red hartebeest (*Alcelaphus buselaphus*). The Kudu Reserve site is frequented by seven resident black rhinoceros (B. Fike 2003, Kudu Reserve Manager, personal communication). It is likely that the herbivore pressure on the restoration site is greater than the surrounding thicket because animals use the restoration site for access. Herbivores are likely to influence all components of ecosystem carbon storage. The removal of aboveground biomass in woody plants may reduce root productivity (due to reduced availability of photosynthate), which in turn will reduce the return of root biomass to the soil (Ruess et al. 1998).

Possible Positive Feedback Effects in *Portulacaria afra* Restoration Sites

The carbon storage differences between the K27 and K27R blocks at Krompoort are interesting. The K27 block is made up of "berg spekboom" (a tall, upright plant), with cuttings planted densely (1-m spacing between plants and 2 m between rows) over 2,500 m^2. The K27R block, by contrast, is a single row of local *P. afra* (a shorter, rounded plant). Both blocks were planted at the same time, yet K27 had greater aboveground biomass carbon (3.1 vs. 2.2 kg C/m^2) and greater soil carbon (11.8 vs. 7.4 kg C/m^2, to a depth of 500 mm) but less root carbon (0.9 vs. 1.5 kg C/m^2). Root carbon was distributed more evenly across the soil profile in K27 than in K27R, which suggests that the berg spekboom also has a more elongated root structure than the local *P. afra*. The greater productivity of the K27 block may be a function of the different *P. afra* genotypes, but it may also be related to the density and pattern of planting. Clearly, the haphazard experimental layout prevented us from investigating the independent effects of genotype and planting density. A block of densely planted *P. afra* (K27) is likely to have a greater mean canopy cover than an isolated row (K27R). This may result in the single row being more water limited than the block. The canopy will provide shade and probably reduce evapotranspiration. It will also reduce raindrop impact and therefore soil crusting (Hillel 1998; Mills & Fey 2004), which will result in a greater rate of water infiltration. Water that does run off the soil surface in a block is likely to ultimately flow toward the litter-rich, permeable bases of other plants, where it will infiltrate. An isolated row, by contrast, does not have this water-trapping effect, and water is likely to be lost via runoff. A block of densely planted *P. afra* may, therefore, have a positive feedback effect, whereby the system as a whole is able to capture much of the mean annual rainfall. An isolated row of plants in comparison may lose much of the mean annual rainfall to runoff.

Benefits of *Portulacaria afra* Restoration

Ecological and socioeconomic benefits from restoration of transformed thicket with *P. afra* are likely to include reduced erosion; increased biodiversity; income via carbon credits; an enhanced tourism potential; increased wildlife carrying capacity; provision of browse for livestock; and provision of employment. Erosion on restored sites would probably be less than on transformed sites because of greater plant cover and improved soil quality (Mills & Fey 2004). Biodiversity is likely to increase as *P. afra* will provide perches for birds and thereby facilitate dispersal of seeds of other woody plants from adjacent intact thicket (Sigwela 2004). Restored landscapes will also have greater soil organic matter and reduced soil temperatures, which may promote seedling recruitment (Cowling et al. 1997; Sigwela 2004). The rate of carbon sequestration in restored thicket is likely to be comparable with less water limited ecosystems such as forests but can be achieved in a much more cost-effective manner because start-up costs are low. Plant propagation and nursery construction are not required because *P. afra* cuttings can be cut from intact thicket. Furthermore, ecological knowledge of processes such as succession, which is necessary for restoring poorly studied tropical forest ecosystems, is not required for restoration of thicket. Depending on carbon prices and cost of labor, income via carbon credits from restored sites could potentially exceed income from goat pastoralism. Average net farm income from livestock in farms near Krompoort is reported to be approximately \$0.12 km^{-2} yr^{-1} (Turpie 2003). Restored landscapes are also likely to be more aesthetically appealing to tourists than transformed thicket, and this alteration, together with a greater carrying capacity for indigenous wildlife, would probably enhance the growing tourism economy in the region. Lastly, restoration could provide a supply of much-needed employment within the extremely depressed Eastern Cape rural economy. The South African government has experience with implementing large-scale restoration projects (e.g., the Working for Water program) which are aimed at providing biodiversity and socioeconomic benefits (Van Wilgen et al. 1998). Restoration of thicket using *P. afra* cuttings could be a rewarding adjunct to projects already in operation.

Acknowledgments

Funding for the research was provided by the Wilderness Foundation and Cape Nature. The authors thank Matt Gordon and his team of laboratory assistants for soil carbon analyses, Graham Slater for permission to sample his restoration site on Krompoort, and Brad Fike and Winston Trollope for assistance in the Kudu Reserve.

LITERATURE CITED

Acocks, J. P. H. 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa **40:**1–128.

Aucamp, A. J., and L. G. Howe. 1979. The production potential of the Eastern Cape Valley Bushveld. Proceedings of the Grassland Society of South Africa **14:**115–117.

Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. The American Naturalist **127:**48–58.

Clarke, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications **11:**371–384.

Cowling, R. M., D. Kirkwood, J. J. Midgley, and S. M. Pierce. 1997. Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone fynbos. Journal of Vegetation Science **8:**475–488.

Ellert, B. H., and H. H. Janzen. 1999. Short-term influence of tillage on CO_2 fluxes from a semi-arid soil on the Canadian Prairies. Soil and Tillage Research **50:**21–32.

FAO (Food and Agricultural Organisation). 1998. World reference base for soil resources. Food and Agricultural Organisation of the United Nations, Rome.

Guralnick, L. J., P. A. Rorabaugh, and Z. Hanscom. 1984*a*. Influence of photoperiod and leaf age on Crassulacean Acid Metabolism in *Portulacaria afra* (L.) Jacq. Plant Physiology **75:**454–457.

Guralnick, L. J., P. A. Rorabaugh, and Z. Hanscom. 1984*b*. Seasonal shifts of photosynthesis in *Portulacaria afra* (L) Jacq. Plant Physiology **76:**643–646.

Hillel, D. 1998. Environmental soil physics. Academic Press, London, United Kingdom.

Hoffman, M. T., and R. M. Cowling. 1990. Desertification in the lower Sundays River Valley, South Africa. Journal of Arid Environments **19:**105–117.

Johnson, C. F., R. M. Cowling, and P. B. Phillipson. 1999. The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? Biodiversity and Conservation **8:**1447–1456.

Kitayama, K., and S. Aiba. 2002. Ecosystem structure and productivity of a tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabula, Borneo. Journal of Ecology **90:**37–51.

Lamlom, S. H., and R. A. Savidge. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass and Bioenergy **25:**381–388.

Lechmere-Oertel, R. G. 2004. The effects of goat browsing on ecosystem patterns and processes in succulent thicket, South Africa. Ph.D. thesis. University of Port Elizabeth, Port Elizabeth, South Africa.

Lechmere-Oertel, R. G., G. I. H. Kerley, and R. M. Cowling. 2005*a*. 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., G. I. H. Kerley, and R. M. Cowling. 2005*b*. Patterns and implications of transformation in semi-arid succulent thicket, South Africa. Journal of Arid Environments **62:**459–474.

Lloyd, J. W., E. C. van den Berg, and A. R. Palmer. 2002. Patterns of transformation and degradation in the Thicket Biome, South Africa. TERU Report 39, University of Port Elizabeth, Port Elizabeth, South Africa.

Mills, A. J. 2003. Reciprocal relationships between vegetation structure and soil properties in selected biomes of South Africa. Ph.D. thesis. University of Stellenbosch, Matieland, South Africa.

Mills, A. J., R. M. Cowling, M. V. Fey, G. I. H. Kerley, J. S. Donaldson, R. G. Lechmere-Oertel, A. M. Sigwela, A. L. Skowno, and P. Rundel. 2005. Effects of goat pastoralism on ecosystem carbon storage in semiarid thicket, Eastern Cape, South Africa. Austral Ecology **30:**797–804.

Mills, A. J., and M. V. Fey. 2004. Transformation of thicket to savanna reduces soil quality in the Eastern Cape, South Africa. Plant and Soil **265:**153–163.

Mills, A. J., T. G. O'Connor, J. D. Bosenberg, J. Donaldson, R. G. Lechmere-Oertel, M. V. Fey, and A. Sigwela. 2003. Farming for carbon credits: implications for land use decisions in South African rangelands. African Journal of Range and Forage Science **20**. Proceedings of the VII International Rangelands Congress. Durban, South Africa.

Mills, A. J., T. G. O'Connor, J. Donaldson, M. V. Fey, A. L. Skowno, A. M. Sigwela, R. G. Lechmere-Oertel, and J. D. Bosenberg. 2005. Ecosystem carbon storage under different land uses in three semiarid shrublands and a mesic grassland in South Africa. South African Journal of Plant and Soil **22:**183–190.

Milton, S. J. 1990. Above-ground biomass and plant cover in a succulent shrubland in the southern Karoo, South Africa. South African Journal of Botany **56:**587–589.

Monod, T. 1986. The Sahel zone north of the equator. Pages 203–243 in M. Evanari, I. Noy-Meir, and D. W. Goodall, editors. Ecosystems of the world 12B: hot deserts and arid shrublands, B. Elsevier, Amsterdam, the Netherlands.

Nadelhoffer, K. J., and J. W. Raich. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology **73:**1139–1147.

Orshan, G. 1986. The deserts of the Middle East. Pages 1–28 in M. Evanari, I. Noy-Meir, and D. W. Goodall, editors. Ecosystems of the world 12B: hot deserts and arid shrublands, B. Elsevier, Amsterdam, the Netherlands.

Raich, J. W., A. E. Russell, and P. M. Vitousek. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawaii. Ecology **78:**707–721.

Ras, A. M. 1995. Soetspekboom—soet of suur? Dohne Bulletin **4:**21–22.

Rosenzweig, R., M. Varilek, B. Feldman, R. Kuppallie, and J. Janssen. 2002. The emerging international greenhouse gas market. Pew Center on Global Climate Change, Washington, D.C.

Roy, J., F. W. Moody, and H. A. Mooney. 2002. Terrestrial global productivity. Academic Press, San Diego, California.

Ruess, R. W., R. L. Hendrick, and J. P. Bryant. 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. Ecology **79:**2706–2720.

Schulze, E. D. 2000. Carbon and nitrogen cycling in European forest ecosystems. Springer, New York.

Sigwela, A. M. 2004. The impacts of landuse on vertebrate diversity and vertebrate-mediated processes in the Thicket Biome, Eastern Cape. Ph.D. thesis. University of Port Elizabeth, Port Elizabeth, South Africa.

Skowno, A. L. 2003. Indirect biomass estimation in subtropical thicket vegetation in the Eastern Cape Province of South Africa. Report for the Conservation Farming Project, National Botanical Institute, Cape Town, South Africa.

Stuart-Hill, G. C., and A. J. Aucamp. 1993. Carrying capacity of the succulent valley bushveld of the eastern Cape. African Journal of Range and Forage Science **10:**1–10.

Swart, M., and F. O. Hobson. 1994. Establishment of spekboom. Dohne Bulletin **3:**10–13.

Ting, I. P., and Z. Hanscom. 1977. Induction of acid metabolism in Portulacaria afra. Plant Physiology **59:**511–514.

Turpie, J. K. 2003. The ecological and economic implications of conversion to game farming in the xeric succulent thicket of the Eastern Cape, South Africa. Report for the Conservation Farming Project, National Botanical Institute, Cape Town, South Africa.

U.S. Salinity Laboratory Staff. 1954. Diagnosis and improvement of saline and alkali soils. Agricultural Handbook 60. USDA, Washington, D.C.

Van Wilgen, B. W., D. C. Le Maitre, and R. M. Cowling. 1998. Ecosystem services, efficiency, sustainability and equity: South Africa's working for water programme. Trends in Ecology and Evolution **13:**378.

Van Wyk, A. E., and G. F. Smith. 2001. Regions of floristic endemism in southern Africa. Umdaus Press, Pretoria, South Africa.

Vlok, J. H. J., D. I. W. Euston-Brown, and R. M. Cowling. 2003. Acock's Valley Bushveld 50 years on: new perspectives on the delimitation characterisation and origin of subtropical thicket vegetation. South African Journal of Botany **69:**27–51.

Whittaker, R. H., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. v. Biomass, production, and diversity along the elevation gradient. Ecology **56:**771–790.