



Animal, Plant and Environmental Sciences
University of the Witwatersrand

The role of vegetation in regional climate regulation feedback processes

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A thesis submitted to the Faculty of Science in fulfilment of
the requirements for the degree of
Doctor of Philosophy



30 August 2016 in Johannesburg, South Africa

Declaration

I declare that this thesis is my own, unaided work, unless otherwise specified within the text. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any other degree or examination at any other university.

A handwritten signature in blue ink, appearing to read 'K. Smart', with a stylized flourish extending to the right.

Kathleen Grace Smart

30th day of **August 2016** in Johannesburg

Abstract

The presence of *Portulacaria afra* affects the flow of ecosystem services from the thicket landscapes of the Eastern Cape. Degraded and intact thicket ecosystems deliver different bundles of ecosystem services, and within each bundle the services are linked non-linearly, so that land-use and management decisions which seek to increase a particular service affect the delivery of other services. One of the challenges of restoring the historically degraded thicket areas is understanding the trade-offs between various objectives, including re-establishing biodiversity and critical services such as carbon sequestration, climate regulation, water provision and forage supply. This thesis uses a variety of techniques to assess some of these trade-offs at several spatial and temporal scales. The amount, rate and nature of carbon assimilation by *P. afra* at a variety of spatial and temporal scales are also explored.

Methods

At a landscape scale stream flow data from transformed and intact catchments, near Jansenville and Bucklands respectively, are used to compare the freshwater ecosystem services provided by the presence of *P. afra*. Similarly, at a landscape scale, the new high resolution Multi-angle Imaging SpectroRadiometer (MISR-HR) products are used to explore the differences in the surface energy budget of intact thicket and degraded ecosystems. Two simple radiative transfer models are used to assess the radiative forcing (RF) trade-off between carbon uptake-related global cooling and albedo-related global warming.

From samples and measurements taken from a field site 15 km south-west of the town of Kirkwood, radiocarbon and stable carbon isotope analysis, growth ring analysis, dendrometry, infrared thermometry, water use efficiency and eddy covariance data are used to quantify the rate of carbon assimilation by *P. afra*, and unpack the contribution of C_3 - and CAM-derived carbon to total carbon sequestration.

Results

Intact thicket cover results in a higher total yield of water as a fraction of rainfall, fewer extreme high flow events, and a higher volume of low-flow in comparison to landscapes thought to represent transformed former thickets.

Intact thickets have a lower albedo than degraded thickets. Restoring to an intact state will result in a mean albedo decrease of 5% (absolute) which constitutes a direct radiative forcing of +0.019 pW

m^{-2} at a global scale. This warming effect overwhelms the climate benefit derived from carbon sequestration related to *P. afra* growth by a factor of 1.6.

The growth data suggests that *P. afra* produces two growth rings annually on average, with the average growth increment of 0.8mm in diameter. The multi-year and multi-source aboveground relative growth rate mean is $0.006 (\pm 0.005 \text{ SD})$ g DM per g DM per year, which is mean average increment about 1.1% per year. The eddy covariance data highlighted the temporal variability in the system, measuring intact *P. afra* thicket vegetation as a net *source* of carbon to the atmosphere $0.018 \text{ gC m}^{-2} \text{ hr}^{-1}$, over the three short-duration campaigns.

CAM is now understood to come in several variants. The sampled stems, averaged across all rings, had a $\delta^{13}\text{C}$ signature of $-15.8 \pm 1.0 \text{ ‰}$ indicative of “strong CAM” behaviour. *P. afra* plants in the Kirkwood locality over the past decades have derived 61% of their carbon through the CAM pathway and 39% through the C_3 pathway, with substantial inter-stem variation. The soil isotope data suggests 51 - 63% C_3 derived carbon, with values increasing with sampling depth. There are occasional large excursions, always in a single growth ring, towards more negative $\delta^{13}\text{C}$ values (-19.0 ‰); in other words towards the C_3 range. Although thought to be related to water stress, it was hard to determine a single trigger for the switching between C_3 and CAM modes. This is consistent with findings for other strongly CAM plants.

From the dendrometers and infrared thermometry, *P. afra* shows flexible stomatal behaviour on a range of timescales. For the majority of the study period the stomata were open both day and night. There is variation in stomatal closure over the year, which appears strongly seasonal, and suggests a link to the bimodal rainfall pattern experienced in the region. Using decision tree to classify the photosynthetic mode, this data suggest that the individual plants being measured are spending only 4% of the time in classical CAM mode, and the majority of the time in CAM-cycling.

Conclusions

Restoration of transformed thicket will improve freshwater ecosystem services associated with useful water yield, sustained supply, and flood control. It is important to include land-atmosphere feedbacks other than carbon assimilation when assessing the climate service delivered by restoration. The negative and positive radiative forcing will operate over different timelines.

CAM metabolism plays an important but not exclusive role in carbon gain. Contrasting patterns between plant and soil C_3 fraction may relate to allocation issues and the contribution by plants other than *P. afra*. The growth rates of thickets are not substantially greater than similar water-limited ecosystems.

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Dedication

This body of work is dedicated to:

Joan Dolores Mennell

(28 March 1919 – 18 July 2012)

Had circumstances been different she would have been a great natural scientist

and

Julian Keith Smart

(24 May 2014 -)

Sine qua non

Table of Contents

Declaration	i
Abstract.....	ii
Acknowledgements.....	iv
Dedication	vi
Table of Contents.....	vii
List of Figures.....	xv
List of Tables.....	xxi
Introduction	1
Background	2
Ecosystem services and their history	2
<i>Applying the ecosystem services approach in drylands</i>	<i>2</i>
<i>Dryland ecosystem services</i>	<i>3</i>
<i>Water services.....</i>	<i>4</i>
<i>Primary productivity.....</i>	<i>5</i>
<i>Climate services.....</i>	<i>6</i>
Carbon.....	7
Albedo	7
Evapotranspiration.....	8
The thicket history	9
<i>Ecosystem services in South Africa and the thicket</i>	<i>11</i>
Restoration and ecosystem services.....	12
Thesis structure	13
References.....	13

Chapter 1 Preface	14
Chapter 1: Carbon Storage in Terrestrial Ecosystems	15
The Climate Regulation Ecosystem Service.....	15
<i>Mechanisms Delivering the Climate Service</i>	<i>16</i>
<i>Pools and Fluxes</i>	<i>16</i>
<i>The Market for Climate Services</i>	<i>17</i>
What Controls the Magnitude of the Service?	18
<i>Productive Potential.....</i>	<i>18</i>
<i>Mean Temperature</i>	<i>18</i>
<i>Waterlogging of the Soil</i>	<i>18</i>
<i>What Determines How Much Carbon a Soil Can Store?</i>	<i>19</i>
<i>What Determines the Maximum Biomass on a Site?</i>	<i>19</i>
<i>Effects of the Disturbance Regime</i>	<i>19</i>
Thresholds and Tipping Points.....	20
<i>Feedbacks in the Terrestrial Carbon Cycle</i>	<i>20</i>
<i>Tipping Points.....</i>	<i>20</i>
<i>The Hypothesis of Terrestrial C Sink Saturation</i>	<i>21</i>
<i>A Plausible Amazon Drought Tipping Point</i>	<i>21</i>
<i>Permafrost Melting</i>	<i>21</i>
Vulnerability of the Terrestrial Climate Regulation Service to Climate	22
<i>Fire</i>	<i>23</i>
<i>Heatwaves.....</i>	<i>23</i>
<i>Increases in Rainfall, Decreases in Rainfall, and Prolonged Droughts</i>	<i>26</i>
<i>Windstorms</i>	<i>26</i>
<i>Insect Attacks</i>	<i>26</i>
Ways of Reducing Vulnerability	26
<i>Preemptive Microdisturbances</i>	<i>26</i>
<i>Maintaining Ecosystem Function and Biodiversity</i>	<i>28</i>

<i>Reducing Vulnerability to Social Change</i>	28
<i>Dealing with Vulnerability in the Climate Service Market</i>	28
Trade-Offs between Climate Regulations and Other Ecosystem Services	28
Conclusions	28
References	28
Chapter 2 Preface	31
Chapter 2: Assessing water ecosystem services in alternate states of a dryland ecosystem in the Eastern Cape of South Africa	32
Introduction	32
<i>Water regulation in drylands</i>	33
<i>Assessing water ecosystem services</i>	35
Methods	36
<i>Study area</i>	36
<i>Catchments and Gauges</i>	37
<i>Analytical methods</i>	37
Flow duration curves.....	37
Extreme Value Theory.....	38
Run off fraction and fraction yield	38
Results	39
<i>Flow duration curves</i>	39
<i>Extreme Value Theory</i>	40
<i>Catchment conversion efficiency and yield</i>	41
Discussion	42
<i>Drivers of transformation</i>	43
<i>A view on restoration</i>	44
<i>The ecosystem service assessment approach</i>	44
Conclusions	45

References.....	45
 Chapter 3 Preface	46
Chapter 3: Restoration with <i>Portulacaria afra</i>: Using MISR-HR to analyse process trade-offs to total climate regulation service in a semi-arid landscape	47
Introduction	47
Methods.....	50
<i>Albedo measurements</i>	<i>50</i>
Sampling scheme	51
Cleaning the data	52
Selected data products	53
Comparison	53
<i>Trade-off analysis.....</i>	<i>53</i>
Radiative forcing changes due to CO ₂ uptake or release	54
Radiative forcing due to change in albedo	55
Comparison of albedo and carbon related radiative forcing.....	57
<i>Data handling.....</i>	<i>57</i>
Results.....	58
<i>Surface albedo characteristics</i>	<i>58</i>
<i>Radiative forcing comparison</i>	<i>59</i>
Discussion.....	61
<i>Surface albedo characteristics</i>	<i>61</i>
<i>A comparison of thicket albedo values to other vegetation types.....</i>	<i>62</i>
<i>Radiative forcing trade-offs</i>	<i>63</i>
<i>Surface heat and latent energy fluxes</i>	<i>63</i>
Conclusions	64
References.....	65

Chapter 4 Preface	66
Chapter 4: Carbon assimilation rates in <i>Portulacaria afra</i> dominated landscapes of the Eastern Cape	67
Introduction	67
Site and Methods.....	69
<i>Determining the fraction of P. afra in the landscape.....</i>	<i>71</i>
Vegetation transects.....	71
P. afra leaf sampling and analysis for $\delta^{13}\text{C}$	72
Contribution of P. afra to soil organic carbon—sampling and analysis for $\delta^{13}\text{C}$	72
<i>Determining the age of P. afra stems</i>	<i>72</i>
Growth ring analysis	72
Radiocarbon dating.....	73
Dendrometry.....	74
<i>Eddy covariance</i>	<i>74</i>
<i>Water use efficiency calculations.....</i>	<i>75</i>
<i>Data management</i>	<i>77</i>
Results.....	77
Vegetation transects.....	77
Growth rings and radiocarbon dating.....	77
Stem increment from growth rings and dendrometry	79
Net Ecosystem Exchange by eddy covariance.....	84
Water Use Efficiency	86
Discussion.....	89
Landscape-scale assimilation rates based on stem RGR.....	89
Water Use Efficiency	90
Eddy covariance results.....	90
Caveats arising from methodology and datasets	91
Isotopic measurements.....	91

Synchronicity of multiple datasets.....	91
Conclusions	91
References.....	92
 Chapter 5 Preface	 93
Chapter 5: The mix of photosynthetic pathways in <i>Portulacaria afra</i> growing in its natural habitat	94
Introduction	94
Methods.....	96
<i>Climate data and soil moisture modelling</i>	<i>96</i>
The rainfall record since 1960.....	96
Water balance model.....	97
<i>Collection and treatment of sample material</i>	<i>98</i>
Stem cross-sections	98
<i>Stable carbon isotope analysis.....</i>	<i>99</i>
<i>Field instruments for detecting CAM behaviour</i>	<i>100</i>
Weather station	100
Infra-Red Thermometry	100
Dendrometry.....	101
Determining photosynthetic modes.....	101
<i>Data management</i>	<i>102</i>
Results.....	102
<i>Variation in $\delta^{13}C$ between growth rings.....</i>	<i>102</i>
<i>Classification framework.....</i>	<i>106</i>
<i>C₃ and CAM from leaf temperature</i>	<i>108</i>
<i>The variation between C₃ and CAM periods according to dendrometry.....</i>	<i>110</i>
<i>Combined classification of CAM state using IRT and dendrometer</i>	<i>112</i>
Discussion.....	115

<i>Fraction of P. afra growth contributed by C₃ and CAM</i>	115
<i>Fraction of time spent in CAM mode</i>	115
<i>Triggers for switching mode</i>	116
<i>Insights for restoration</i>	117
<i>Photosynthetic modes: separate paths or one axis?</i>	117
<i>Caveats arising from methodology and datasets</i>	117
Isotopic fractionation.....	117
Dendrometry and influence of rooting.....	118
Reconciling the datasets	118
Conclusions	118
References	118
 Concluding Chapter	 119
A summary of the key findings	119
<i>Global scale</i>	119
<i>Landscape scale</i>	119
<i>Plant level</i>	120
Critical thoughts: room for improvement and an opinion on the datasets required	120
Future research – fresh insights	120
Parting thoughts	122
References	122
 Appendix 1	 123
Plate Model Manual	123
Description	123
Adjustable parameters in the plate model	125
Interception subroutine	126
Algorithms	126

References.....	127
Appendix 2	128
Combined Reference List.....	129

List of Figures

Chapter 1

- Figure 1. The key carbon stocks (boxes, Pg C) and fluxes (arrows, Pg C year⁻¹) in terrestrial ecosystems with their approximate magnitude at a global scale and the typical turnover times. The soil carbon excludes wetland soil and permafrost stocks. 17
- Figure 2. Silt plus clay content ('fines', as %) and silt and clay associated carbon concentration (g C kg soil⁻¹) for mineral particles 0–20 µm. (a) The effect of clay mineralogy (1:1 clays, e.g., kaolinite and serpentine, blue triangles; 2:1 clays, e.g., smectite and illite, black circles). (b) In relation to the type of ecosystem. Redrawn from data appendices in Six, J., R. T. Conant, E. A. Paul, and K. Paustian, 2002: Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil*, **241**, 155–176..... 19
- Figure 3. A schematic representation of an ecosystem accumulating carbon following a change in land management. The top panel shows a simple case, where the carbon density rises according to a more or less logistic curve to a new equilibrium level. This can be approximated with linear segments defining a rate and duration of carbon storage. The lower panel shows a case, such as a rotationally harvested plantation, where there are repeated logistic segments interrupted by harvest or disturbance events. The long-term mean carbon density is nevertheless higher than in the preland use change case. 20
- Figure 4. Some of the key interaction that has been postulated to lead to a 'tipping point' in the Amazon basin. The CAPITALS indicate driving factors, the boxes are system properties, the arrows indicate effects (with the sign noted), and the bow-ties indicate the controls over these effects..... 22
- Figure 5. Permafrost melting includes direct and indirect feedbacks involving physical changes to the soil column, changes in surface brightness and fire. Summarized from Schuur, E. A. G., and Coauthors, 2008: Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *BioScience*, **8**, 701–714..... 23

Chapter 2

- Figure 1. A) An individual storm hydrograph showing idealized behavior and ecologically relevant metrics. Following a storm, the volume of water flowing in the river starts to rise due to the rapid process of laterally transferred run-off and the slower process of infiltrated subsurface flow, building to a peak in streamflow. The flow attenuates gradually to some low flow (which may be zero). The integral of the stream discharge curve is the total water yield, but only part of this may be possible to use. Flow rates above a certain threshold may be too

dangerous to access, or too turbid to use. The usable flow is therefore the integral that is below both the discharge curve and this threshold. B) A cumulative plot of rainfall and discharge. In untransformed landscapes, the plot should be more-or-less linear (solid line). A deviation from this line is evidence of hydrological change and indicates a change in the efficiency with which the landscape converts rainfall into streamflow. Note: the slope is unlikely to be one.....	34
Figure 2. Distribution of thicket vegetation along the southern coast of South Africa in transformed and intact states (Pierce 2003). Insets from the Eastern Cape Province show A) the location of the river gauges selected on the Sundays (N2H007) and Riet River (N2H008) within transformed thicket vegetation, and B) the location of the river gauge selected on the Great Fish (Q9H012) within an intact thicket dominated by the succulent <i>Portulacaria afra</i> Jacq. .	35
Figure 3. Flow duration curves on a logarithmic axis (1982-2010). Daily discharge is normalized by the product of catchment size and rainfall. The gray line shows the curve when days of zero flow are included; this curve is missing from the first plot because there were no zero flow days in the intact catchment. The vertical dashed lines mark the flow exceeded 30%, 50% and 70% of the time (Q30, Q50 and Q70 respectively).	39
Figure 4. Statistical analyses of hydrograph records for 01 Jan 1982- 31 December 2010. The return level as a function of return period for the discharge rates. The curves represent the graphic visualization of the shape parameter (ξ) of the fitted Generalized Extreme Value (GEV) distribution. The three curves per plot are the mean and the upper and lower confidence limits. For the intact catchment A) $\xi < 0$ (estimated value -0.7) and the plot is convex with asymptotic limit. This means the probability of a large flow event approaches zero. For both transformed thickets B) and C) $\xi > 0$ (0.6 and 1.0 respectively) and the plot is concave and has no finite bound. Thus extreme flow events are more likely.	40
Figure 5. Plots of cumulative discharge against cumulative rainfall. Note: rainfall has been divided by 1000 for plotting. The grey dashed line joins the first and last point, which is the average catchment fraction yield (see Figure 6).	41
Figure 6. The year-by-year fraction yield for intact and degraded catchments. Deviations from a linear relationship suggest change in the hydrological parameters over time, as transformation progresses. Note: the y-axis is dimensionless, and has been divided by 1000 for plotting clarity.	42

Chapter 3

- Figure 1. A portion of the spatial sampling scheme showing the paired points relative to A) the intact solid thicket containing *P. afra* and transformed thicket boundaries as recorded by the Subtropical Thicket Ecosystem Programme (Pierce 2006), and B) Google Earth (Google Earth 7.1 2015). The dots mark the center of the MISR-HR 275m pixel. 52
- Figure 2. The inverse exponential plot of the cost function values associated with MISR-HR products. X-axis values, which extend to 21, have been truncated at 5 for better visibility. The insert shows the portion of the tail where the beginning of the small mode ($x = 1.5-2.3$) indicates the threshold value which is used to filter out data points from further analysis. In this case, only data points with a cost function value of 1.45 or less were used. 53
- Figure 3. The annual cycle of reflectance for top of canopy (TOC) and soil, separated into the visible (VIS) and near-infrared (NIR) components of the electromagnetic spectrum. Plots for degraded thicket are shown in the top panel, and intact thicket is shown in the bottom panel. The dark lines are the 12 year mean, and the bands show the interannual variation (± 1 SD). 58
- Figure 4. The mean monthly delta albedo for all paired intact and degraded thicket sites over the MISR-HR timeseries March 2000-January 2012. Delta albedo is defined as the albedo of the degraded site minus the albedo of the paired intact site (Equation 6). Note that with a single exception, one month in 2002, the degraded sites have a higher albedo (i.e., brighter and reflecting more solar radiation) than the intact sites. Each point is coloured by the summed monthly rainfall. The linear regression (blue line) shows the trend in delta albedo over the timeseries. 60
- Figure 5. A summary of the land-atmosphere feedback processes affected by thicket restoration using *P. afra*. SE and LE denote sensible energy and latent energy, respectively. Drawn after Findell et al. (2007) and Kirschbaum et al. (2011) 64

Chapter 4

- Figure 1. Map showing the core experimental site and the surrounding long term weather stations. The annotations show the respective distances, as the crow flies (Google Earth 7.1 2015). . 69
- Figure 2. A) The age model constructed using radiocarbon dating on three samples from Stem 1 (S1), outer, mid-point, and centre, corresponding to absolute dates of 2009, 1989 and 1964 respectively. The grey lines show ring production of one, two and three rings per year. Sections B) and C) show photographs of the mid-point ring aquilot which was sent to Beta Analytic. 78

Figure 3. Stem diameter fluctuations measured by the dendrometer bands, in relation to the daily profile available water content calculated from daily climate data, over the period 26 March 2009 to 17 April 2011. The colours of the dots relate to the inferred photosynthetic modes (method described in the text and Table 5). A) Rainfall events, B) diameter as measured by dendrometer 2, C) diameter as measured by dendrometer 1. Diel-cycle stem dynamics are defined by daily sunset and sunset times and calculated as the sum of hourly diameter changes rounded to two decimal places.	81
Figure 4. The relationship between growth ring width and profile water content (PWC): A) The sequence of wet and dry periods over the period 2005-2009, where the red horizontal line indicates the 40 mm PWC growth threshold, and the vertical red lines indicates periods when the PWC is below this threshold; B) the shows number of growth days, defined as when PWC is greater than 40 mm, for the January-June ('mode 1') and July-December ('mode 2') periods, as well as the 1960-2010 mean values; and C) shows the normalised widths of R1-10 for S1-10 versus mode, where R1 occurs in mode 1, R2 in mode 2, R3 in mode 1, and so forth.....	83
Figure 5. The Webb-corrected half hourly carbon flux measurements for the three eddy covariance campaigns: 17 September to 10 October 2008 (22 days), 11 to 22 March 2009 (11 days), and 27 January to 3 February 2010 (7 days). A) Shows the range of values by time of day, and B) shows the variation in range by month. Note: the horizontal positions of the points in part B) are slightly jittered to avoid over plotting.	84
Figure 6. A) the daily Net Ecosystem Exchange (NEE) by month, and B) the daily measurements for the eddy covariance campaign period 27 January to 3 February 2010 for which there are NEE and soil respiration measurements from which Net Primary Productivity (NPP) can be approximated.....	85
Figure 7. Net Ecosystem Exchange (NEE) and derived Net Primary Productivity (NPP) over the course of the short-term eddy covariance campaigns. The derived NPP is proportional to NEE (cf. Equation 4) established for the campaign period 27 January to 3 February 2010. The shaded area shows the NPP (1 SD).....	86
Figure 8. The mean isotopic and water use efficiency values for <i>P. afra</i> tissue and thicket soils. The points are coloured by the source of the carbon: soil in green, <i>P. afra</i> leaf tissue in red, and the <i>P. afra</i> tree rings combined across stems in blue; the labels correspond to Table 5. A) shows intrinsic WUE values (cf. Equation 5), and B) instantaneous WUE values (cf. Equation 6).	87

Chapter 5

- Figure 1. Long term rainfall record for showing A) the daily time series for 2010, B) daily time series from 1960 to 2010, and C) monthly average rainfall. This record was compiled from seven weather stations, the details of which are given in Table 1. 97
- Figure 2. The polished witness disks. Top row: S1-S3, middle row: S4-S6, bottom row: S8-S10. The witness for S7 cracked radially from the pith outward and handling was kept to a minimum; it is not included in this image. 'S' is used to denote stem. 99
- Figure 3. Schematic of the two classification approaches used in this study, both of which draw on the phases of CAM defined by Lüttge (1987). 102
- Figure 4. A histogram overlaid with a kernel density plot of the ratio of stable carbon isotope discrimination ($\delta^{13}\text{C}$) for A) rings (R1-10) from stems (S1-10), and B) rings 1-110 for S1. Note the asymmetric bimodal distribution. Mode means are indicated by dashed lines (---) 103
- Figure 5. The $\delta^{13}\text{C}$ time series measured in successive growth rings (R1-10) on ten *P. afra* stems (S1-10), with the mean $\delta^{13}\text{C}$ value indicated by a solid red line. Our growth model, derived from dendrometry and radiocarbon aging (Chapter 4), suggests that on average two growth rings are produced annually, which is concordant with the typically bimodal rainfall distribution. The ten rings sampled therefore cover a five year period from the date of harvest in late 2009; i.e., from 2005 to 2009. 104
- Figure 6. The $\delta^{13}\text{C}$ measured in successive growth rings (R1-10) on ten *P. afra* stems (S1-10) in relation to the number of days in a 6-month period with a profile available water content greater or equal to 40 mm, and the linear regression (blue line) showing the 95% confidence interval (grey shading). Stem circumference is annotated in the upper left hand corner in bold italic font. The rings are thought to be sub-annual, corresponding to the two annual rainfall modes. Thus, the days of profile available water content were calculated for the January-June and July-December periods. 105
- Figure 7. Ring $\delta^{13}\text{C}$ versus ring width for stems S1-S10, and the linear regression (blue line) showing the 95% confidence interval (grey shading). 106
- Figure 8. Kernel density plot showing the distribution of the occurrence of the 4 CAM phases (Lüttge 1987) in relation to A) time of day, and B) length of day. 107
- Figure 9. The difference between expected leaf temperature, i.e. with zero transpiration from the Gates model (Campbell and Norman, 1998), and the observed leaf temperature as recorded by the IRT for A) the entire timeseries. The temporal spread of stomatal aperture is shown in B) where light blue indicates open stomata and grey indicates closed stomata. 108

- Figure 10. The difference between expected leaf temperature, with zero transpiration from the Gates model (Campbell and Norman, 1998), and the observed leaf temperature as recorded by the IRT for A) 25-28 March, B) 19-22 September, and C) 8-11 August 2010. The vertical gray bars indicate night time. Where leaf temperature (T_{actual}) is less than modelled temperature (T_{expected}) the stomata are open and evapotranspirational cooling is occurring. 109
- Figure 11. The change in circumference from both dendrometers (D1 and D2) for A) the entire timeseries, B) the night- versus day-time changes, and C) the inferred carbon assimilation modes. Change in circumference (mm) was taken as the sum of the hourly change in circumference over night- and day-time periods, reported to three decimal points. Night and day were determined daily based on sunset and sunrise times. 111
- Figure 12. Final mix of modes from a combined IRT- and dendrometer-derived classification approaches, with A) showing the classification on a daily timestep, B) the occurrence of modes on a monthly basis, and C) the difference in classification outcomes when only dendrometer data is used, and when both IRT and dendrometer data are used. 113
- Figure 13. A biplot of the first two components of the PCA on environmental variables, average IRT values for night and day, and hourly stem circumference changes summed over night and day. The multi-coloured ellipses show a normal contour line with a probability of 68% (1 SD), and the correlation circle indicates a probability of 95% (2 SD). 114

List of Tables

Chapter 1

Table 1. A classification and evaluation of vulnerabilities, based on the expert opinion of the authors, informed by a review of the literature. For a definition of terms, see the text.	24
--	----

Chapter 2

Table 1. The attributes and data availability of the catchments used for this case study	37
--	----

Chapter 3

Table 1. Long term weather stations used to compile solar radiation and mean monthly sunshine hours used in the radiative forcing calculations. Source: Agricultural Research Council (ARC).	56
Table 2. Summary albedo values for intact and degraded thicket vegetation for the visible (VIS) and near-infrared (NIR) components of the electromagnetic spectrum (interannual monthly mean $\pm$ 1 SD). P-value results from paired t-tests are reported (N=12, df=11).....	59
Table 3. Radiative forcing due to carbon sequestration and albedo change associated with restoration from a degraded to intact state. Negative sign indicate a cooling effect, and a positive sign a warming effect.	61
Table 4. Summary of published albedo values which form a baseline for comparison to MISR-HR visible (VIS) and near infrared (NIR) values for thicket vegetation.....	62

Chapter 4

Table 1. Mean climate data for the period 1960 to 2010 compiled from seven long term weather stations (altitudes are above sea level): AddoAgric (10561) 33.5667°S, 25.7000°E, 85m (years 1960-2002), AddoSitusNS (20186) 33.5667°S, 25.7000°E, 85 m (1976-1993), AddoOlifantpark (20218), 33.4500°S, 25.7500°E, 152 m (1994-2003), Addo AWS (30561) 33.5685°S, 25.6922°E, 31m (2002-2007), Kirkwood AWS (30787), 33.4038°S, 25.3361°E, 119 m (2007-2010); Kirkwood Prison (20262) 33.4000°S, 25.3500°E, 96 m (1990-2002); Dunbrody AWS (30615) 33.4721°S, 25.5449°E, 61 m (2003-2010). Source: Agricultural Research Council (ARC).....	70
Table 2. Soil properties from a soil pit at 33.5281°S, 25.3781°E. The saturated hydraulic conductivity was estimated to be 82 mm d ⁻¹ , using Schaap et al (2001). The texture class is clay loam. ...	71
Table 3. Radiocarbon estimates of the age of Stem 1 (S1)	78

Table 4. Annual stem diameter increment for S1-10 based on the measured widths of the first ten growth rings, R1-10; as well as the derived diameter at the end of each year, back calculated on the harvest diameter. Measurements are in mm.	79
Table 5. Conditional arguments for defining the photosynthetic pathway used by <i>P. afra</i> based on changes in stem size. Changes in stem size are denoted by: + for swelling, - for shrinkage, and 0 (zero) for stable periods. The diel cycle was split seasonally between night and day using sunrise and sunset times.	80
Table 6. The aboveground relative growth rates (g DM per g DM per year) of <i>P. afra</i> in recent years. Growth ring widths were scaled from dry to wet values using the individual wet:dry ratio for each stem (Table 4, S1-10 mean ratio = 1.21 ± 0.08 1 SD).	82
Table 7. Comparison of WUE determined by eddy covariance and estimated from stem and leaf stable isotope discrimination. All values are given as mean $\pm$ 1 SD, reported to at least one significant figure. Note that WUE from eddy covariance is at the landscape level (i.e., the carbon term includes respiration as well as photosynthesis, and the water term includes evaporation as well as transpiration), whereas the isotopic estimates are at the leaf of whole plant level. Thus the expectation is that landscape WUE estimates are lower than isotopic WUE estimates, as shown here.	88

Chapter 5

Table 1. Long term weather stations used to compile a single weather history for Kirkwood, Eastern Cape. Source: Agricultural Research Council (ARC).	96
Table 2. An hour-by-hour analysis of <i>P. afra</i> stomatal behaviour against the traditional 4 phase CAM framework (Lüttge 1987). Stomatal aperture was inferred from the difference between actual leaf temperature as measured by the IRT, and expected leaf temperature as modelled by the Gates equation (Campbell and Norman, 1998). Two CAM frameworks were used, in which phase 2 and 4 were both assigned either one or two hours duration.	106
Table 3. Stem starting and endpoint circumferences, and details of shrinking and swelling behavior. Means are given with 1 SD in brackets.	110
Table 4. Conditional arguments for defining the photosynthetic pathway used by <i>P. afra</i> based on changes in stem size and stomatal aperture. Changes in stem size are denoted by: + for swelling, - for shrinkage, and 0 (zero) for periods which were not clearly shrinking or swelling, but showing no variation, or simply changes in the range of instrument noise. The diel cycle was split seasonally between night and day using sunrise and sunset times. The <i>a priori</i> classification is marked in black, the <i>post priori</i> additions are marked in red.	112

Conclusion

Table 1. Top future research directions emerging from this thesis.....	121
--	-----

Appendix 1

Table 1. Each plate is represented by the following variables in SiteName.lay.	123
Table 2. Soil profile description variables in siteName.sol.	124
Table 3. PlateGen parameters.	124
Table 4. Daily weather inputs to the plate model.	125

Appendix 2

Table 1. Values used for WUE calculations. Source: http://cdiac.ornl.gov/ftp/trends/co2/iso-sio/SIO_Mauna_Loa_13CO2.txt	128
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Introduction

There are two concepts which have been the most influential in shaping this body of work. The first is *ecosystem services*, and the second is that of *land-atmosphere interactions*. The latter represents “fundamental science” and deals with the flows of energy and matter within a system, while the former explicating links between social and ecological systems. Both concepts deal with feedbacks and interactions. As we are now firmly in the ‘Anthropocene’ (Crutzen 2006), in which we will face unprecedented challenges from climate change and land-use change, I feel these concepts are best unified in notion of *climate regulating ecosystem services*.

Understanding the dynamics of the climate regulation service requires knowledge of the short-term response of vegetation and soils to atmospheric effects, and the longer-term change of species composition, biome dynamics, and nutrient cycling associated with landscape and soil structure changes (Pielke et al. 1998); as well as trends in land use and land management together with local, regional and global climate change trends and projections.

Attempts to explain the processes currently responsible for these dynamics has revealed a complex picture; one which invokes multiple processes acting over various spatial and temporal scales. The biggest research challenge has been a paucity of data, but this is changing as timeseries data accrues from more remotely sensed products and complementary biometeorological instruments (from growth chambers to free atmosphere carbon dioxide (CO₂) enrichment (for example, the FACE experiments, Norby & Zak 2011) and flux tower studies (for example, FLUXNET, <http://fluxnet.ornl.gov/>). Successful scaling frameworks exist for the states and processes in photosynthesis and respiration, from biophysical and biochemical insights through to the leaf and organisms level, and scaled beyond to the canopy and ecosystem level using remote sensing (Osmond et al. 2004)

Here I use the thicket biome in the Eastern Cape as a case study, and apply a portion of our growing data to exploring the consequences of land cover change at various spatial and temporal scales. What follows in this chapter is a brief two-part overview of the topics covered by the thesis as a whole, first of ecosystem services, with particular focus on semi-arid or dryland services, and secondly of the thicket biome. The body of the thesis is written as a series of papers, the first of which is already published and is in the form of a review of climate regulation literature. Later chapters are in preparation for submission. Each of them contains a brief literature review of the issues pertinent to the particular chapter.

Background

Ecosystem services and their history

Ecosystem services emerged in the 1980s as a framework for organising a growing biophysical understanding of ecosystem processes and synthesizing it in terms of human well-being (Mooney & Ehrlich 1997). The Millennium Ecosystem Assessment (MA) was the first formal international effort to this end, and is the benchmark for ecosystem service research (Brauman et al. 2007).

The MA proposed a classification framework that has four top-level classes: *provisioning services*, which are tangible goods and typically have well-defined markets; *cultural services*, based on aesthetic or amenity value, which also often have markets; *regulating services*, which stabilize the supply of either of the above or in other cases reduce the risk of natural disasters; and *supporting services*, which are ecological processes without which none of the above would occur but which are not themselves directly used by people (Millennium Ecosystem Assessment 2003).

The framework (Daily 1997; Millennium Ecosystem Assessment 2003) is one that finds favour with economists, social scientists, conservationists, ecologists, and the (global) stakeholder and policy community, due to explicit notions of linked human and ecosystem wellbeing, the coupling between ecosystem features and processes (for example see: Balvanera et al. 2006; Pereira et al. 2010), and its amenability to costing exercises (for example see: Kareiva et al. 2011). Simultaneously, it has highlighted many research needs (Carpenter et al. 2006; Carpenter et al. 2009).

Applying the ecosystem services approach in drylands

Drylands can be mapped and categorised using the ratio of precipitation to potential evapotranspiration (the aridity index; Middleton & Thomas 1997). They are conventionally divided into four categories: sub-humid, semi-arid, arid and hyperarid. There is a corresponding decrease in primary productivity, human population density, livestock production and attractiveness for agropastoral development across the categories (Safriel 2006). It is often observed that the stresses are greatest in the semi-arid drylands, since the ecological productivity declines faster than the human demand for services, and it is inferred that the impact of global change will be greatest in this zone (Safriel 2006). This is also the most extensive class.

The MA framework has proved useful for research, management and policy challenges in dryland systems (Safriel et al. 2005; Verstraete et al. 2009; Sommer et al. 2011). It provides a robust way to measure of the net change of services and thus assess the consequences of ecosystem change for human wellbeing, and is a useful way to conceptualise desertification (Verstraete et al. 2009).

Drylands exhibit multiple possible ecological and social states, separated by thresholds (Walker & Meyers 2004; Reynolds et al. 2007; Reynolds et al. 2011). A useful adjunct to taking an ecosystem service approach to the dryland management is a shift to a more holistic view of the various different ecosystem states, each offering alternative bundles of ecosystem services and associated livelihoods (Reynolds et al. 2007; Verstraete et al. 2009). Drylands provide some services which are either unique or particularly well-represented there, such as plant biochemicals promoted by the need for physiological adaptation to the dryland environment (Safriel et al. 2005) and large amounts of solar radiation for transformation to alternative energy. Such 'dryland resources' are of relevance beyond dryland systems themselves (Safriel et al. 2005).

According to the MA (Millennium Ecosystem Assessment 2005a) between 10 - 20% of drylands are already affected by desertification, broadly defined as a reduction or loss of biological productivity (Safriel 2006). Climate change is anticipated to increase the global extent of areas affected by desertification (Reynolds et al. 2007; Millennium Ecosystem Assessment 2005a) through an increased frequency, duration and severity of droughts, enhanced evapotranspiration, and even the lowering of mean annual rainfall in some areas (Intergovernmental Panel on Climate Change (IPCC) 2007). This will affect the quantity and quality of ecosystem services as ecosystem functioning declines (Millennium Ecosystem Assessment 2005b; Naeem et al. 2009). The key services of water regulation, water provision, primary production and climate regulation are particularly affected.

Dryland ecosystem services

Safriel et al. (Safriel et al. 2005) highlighted water regulation as the overarching dryland ecosystem service, as its effect cascades through the interrelated supporting, provisioning and regulating services, for example soil conservation, nutrient cycling, primary production, water provision; and the control of floods and associated damage. Similar results were found in Reyers et al. (2009) where losses in water regulating services in a dryland system cascaded through a suite of ecosystem services underpinning the agricultural economy of this semiarid system.

The supporting service of primary production is important both to crop farmers and pastoralists. Primary production also underpins the production of biochemicals and fuelwood which, in dryland systems, generate independent, alternative livelihoods based on medicinal plants and biomass-generated energy (Safriel et al. 2005).

A third ecosystem service, that of climate regulation, is emerging as a desired dryland ecosystem service, less because it is especially prominent in drylands than because of their vast extent and the

apparent paucity of competing land uses. This regulatory ecosystem service has received particular attention in recent years due to its potential contribution to global climate change mitigation efforts.

I examine these three services below, explicitly mentioning the biophysical and biogeochemical land-atmosphere processes that comprise them.

Water services

Water regulation is a regional-scale service which affects the timing and magnitude of runoff, flooding, and recharge (Millennium Ecosystem Assessment 2005c). The regulation of hydrological flow in essence refers to the quantity and duration of water held in the soil profile; recharging the groundwater and connected surface water systems in a catchment; and what leaves the system as streamflow (Sandström 1998).

These and other major fluxes of the water cycle can be expressed as components of a water budget, which in simplest form describes the soil-plant-atmosphere processes as follows: $P = R + \Delta S + ET$, where P is precipitation, ET is evapotranspiration, R is runoff, and ΔS is change in soil moisture storage. Each of these terms can be elaborated – for instance: $ET = I + E + T$, where I is the water intercepted by plant stems and canopy which is assumed to evaporate, E is the evaporation from soil, T is the water transpired by plants.

In drylands, water is the major limiting resource for biological activity and related services (Safriel et al. 2005; Millennium Ecosystem Assessment 2005a). Vegetation structural diversity (Safriel et al. 2005) and the extent of ground cover by vegetation (Verstraete et al. 2011) are noted as being important indicators of dryland condition, because they are instrumental in the water regulation service through the control of evapotranspiration and the partitioning of rainfall.

The most basic distinction in structural diversity (beyond vegetated and non-vegetated) is between woody and herbaceous vegetation. The dominant trends in vegetation transformation in rangelands involve shifts in their proportions: the expansion of woody species at the expense of herbaceous production (Scholes & Walker 1993; Scholes & Hall 1996; Huxman et al. 2005; Wilcox et al. 2005) or the expansion of herbaceous species with simultaneous reduction in woody biomass (Hoffman & Cowling 1990), for instance through a combination of grazing, fire, and clearing for cultivation. The differential affects of woody and herbaceous plants across vegetation abundance and climate gradients is usefully described by Huxman et al. (2005) who have summarised the relative change in the contribution of transpiration and soil evaporation to total evapotranspiration (also see

Evapotranspiration, below). In semi-arid drylands the vegetation structure and cover changes dramatically as a function of varying rainfall (Huxman et al. 2005; Masubelele et al. 2015).

Primary productivity

Primary production is the key vegetation process of plants which underpins many provisioning ecosystem services which are the economic mainstay in drylands, including animal production (Hanan et al. 1998; Safriel et al. 2005; Verstraete et al. 2011).

The atmospheric CO₂ absorbed during photosynthesis is known as gross primary production (GPP). About half of GPP is released shortly after it is captured, through plant respiration (R_a ; Roxburgh et al. 2005). Net primary production (NPP) is the portion of GPP that is assimilated into plant matter, i.e.: $NPP = GPP - R_a$ (note that this is the intuitive way of expressing this relation, in later chapters I will follow a strict sign convention which has fluxes to the atmosphere as positive, while those out of the atmosphere are negative, in which case $NPP = GPP + R_a$). Plant tissue is generally between 42 to 45 % carbon (Scholes & Walker 1993), which can be released into the atmosphere through either heterotrophic respiration (R_h), fire, or other minor processes such as photo-oxidation. R_h is the CO₂ released when organisms digest or decompose plant tissue. The net ecosystem productivity (NEP) for a system is the balance between these two fluxes (Engelbrecht et al. 2004): $NEP = NPP - R_h$.

The balance between NPP and respiration regulates the carbon storage in vegetation and soils, and both terms are sensitive to changes in climate (Cox et al. 2000). The pattern of allocation of carbon between respiration and biomass production, between above- and below-ground biomass, and between short-lived or long-lived tissues is species-specific and shows broad functional-type associated patterns between biomes. Changes in the plant biomass or species composition in response to changing climate or land use will impact the flow of carbon between pools and has the potential to feedback on climate (Litton & Giardina 2008).

Changes in soil moisture and temperature, as well as the quantity and quality of organic matter inputs will alter soil organic carbon decomposition dynamics (Ise & Moorcroft 2006). Understanding the temperature sensitivity of the microbial communities responsible for soil respiration is key to understanding the release of carbon by ecosystems in response to climate change (Balser & Wixon 2009).

Monitoring changes in NPP is not only critically important for local dryland resource management (including carbon sequestration), but also for linking any observed changes to social, economic and policy factors (Nkonya et al. 2011), and potentially allowing sufficient time for any corrective actions to be taken (Verstraete et al. 2011). In mesic systems primary production is relatively constant over

time and a reasonable indicator of system properties such as the status of soil (Reynolds et al. 2011). However, the high inter-annual variation in dryland production (Safriel et al. 2005) means that the detection of directional change in productivity requires long time series of data; typically a decade or more.

NPP can be estimated from remotely sensed imagery by observing patterns of light absorption (Sellers et al. 1995), in particular the Fraction of Absorbed Photosynthetically Active Radiation (FAPAR). The global and regional satellite-based NPP products typically use a reduced set of functional types to describe the vegetation systems of the world (for example: evergreen needle leaf forest, deciduous broadleaf forest, woodland, grassland, cropland, and open shrubland; Running et al. 2000) to which a production efficiency (variously called PAR utilization efficiency, radiation use efficiency, or light use efficiency) is assigned (see Goetz & Prince 1999 for an overview). While a few studies have applied a production efficiency model to dryland areas (Seaquist et al. 2003; Fensholt et al. 2006; Hely et al. 2007) new functional types need to be refined to capture the unique vegetation in drylands, such as grasses and crops with C_4 photosynthetic pathways, and Crassulacean Acid Metabolism (CAM) photosynthetic pathways, in order to quantify plant growth and carbon uptake systematically.

CAM plants (including many succulents from Mesembryanthemaceae, Crassulaceae, Euphorbiaceae, and some crop plants including *Ananas* spp., *Agave* spp. and *Opuntia* spp.) are able to maintain productivity under conditions of severe water stress by temporally decoupling the carbon assimilation processes from the transpiration process (Lüttge 2004). The measured water use efficiency is about twice that of C_3 plants, but only a little better than that achieved by C_4 plants (Winter et al. 2005). The presence of CAM plants in drylands will have an important impact on the ecosystem productivity and carbon storage.

Climate services

Natural and managed ecosystems contribute to the amelioration of the climate of a given area, and the conversion between natural and managed systems has important impacts on the processes through which the land surface modifies the climate (Charney 1975; Pielke et al. 2007). There are multiple biogeochemical (greenhouse-gas regulation) and biophysical (regulation of water and energy) land atmosphere processes involved, some of which work in opposing directions (Betts 2000). A substantial review of these processes can be found in Bonan (Bonan, 2008); the focus here is on carbon (also see *Primary Productivity*, above), albedo and evapotranspiration.

Carbon

A significant part of this regulatory climate service is related to the ability of ecosystems to take up CO₂ from the atmosphere (detailed above). Much research is focused on the net carbon balance of ecosystems, and on improving our knowledge of terrestrial sources and sinks of CO₂ and their spatial and temporal variability. Carbon dioxide is considered the largest *anthropogenic* radiative forcing agent (IPCC, 2007), although numerically, water vapour (H₂O) has a larger overall effect – but the human influence on H₂O is considered a second order consequence of other interferences with the climate system.

Terrestrial ecosystems also strongly affect climate through the changes to the surface reflectivity to solar radiation (albedo) and to the partitioning of energy between latent and sensible heat. A reduction in vegetation through clearing or overgrazing reduces evapotranspiration and associated cooling latent heat flux. That is, energy normally used to evaporate water instead heats the land surface (see Snyder et al. 2004). Simultaneously, a reduction in vegetation typically increases the albedo of the land surface (since most soils are brighter than the typical albedo of live vegetation), decreasing the amount of energy absorbed by the land surface for later transmission back into the lower atmosphere. Albedo changes can under some circumstances overwhelm the radiant forcing changes associated with greenhouse gases (Betts 2000, Cox et al. 2004).

Albedo

Albedo is a measure of the reflectivity of a surface. As a corollary, it therefore also determines the fraction of energy absorbed by the surface and transformed into sensible heat or latent energy. In effect, incoming solar energy is relatively constant over a landscape, but the differences in albedo result in different energy budgets for adjacent patches. The land albedo is a complex function of the angle effects of the sun and viewer, the three-dimensional structure of the vegetation, the surface and spectral characteristics of the vegetation, as well as the colour and moisture content of the underlying soil (Henderson-Sellers & Wilson, 1983; Pielke & Avissar, 1990). It is also dependent on atmospheric conditions, and therefore is not solely property of the surface.

Albedo is the ratio of reflected radiation to incident radiation. This fraction can be expressed as a percentage from 0 to 100%, or as a dimensionless value between 0 and 1. The mean albedo of the earth system is 0.36 ± 0.06 (Dobos, 2006). The albedo is higher for smooth, light-coloured surfaces, and lower for darker and rougher surfaces. Green vegetation cover typically has a low albedo, in the order of 0.07 to 0.2 (Dobos, 2006; Lambers et al., 2008). Only deep open water has a lower albedo, at close to zero, followed by recently-burned vegetation. The dry, sandy soils of South Africa often have a relatively high albedo, reaching between 0.3 and 0.4 (Garratt, 1994, Dobos, 2006).

Biome-scale albedo is to a first approximation the linear sum of the albedo of its component parts, scaled by their cover fraction. Therefore, when a green grass cover dries out and dies, the albedo generally increases, and when vegetation cover is reduced by heavy grazing or tree cutting, albedo usually rises as well. On the other hand, planting an evergreen cover into a seasonal or degraded environment typically decreases the albedo, and thus the amount of energy absorbed by the land surface, for later transmission back into the lower atmosphere. The magnitude of the potential albedo changes is sufficiently high that they can under some circumstances overwhelm the radiant forcing changes associated with uptake of greenhouse gases.

Charney et al. (1975) and Watson and Lovelock's Daisyworld model (Watson and Lovelock, 1983) first drew attention to the feedbacks between solar radiation and surface reflectivity as affected by biological features, but until recently the effects of albedo have not been included in numerical climate models (for an example see Pielke et al. 1993). Policies that seek to promote ecosystem feedbacks to mitigate climate change have focused almost entirely on carbon sequestration. Recent modelling efforts show that climate feedbacks caused by changes in the energy budget may have large and often counterproductive results (Betts, 2000; Caldiera et al. 2008; Lambers et al. 2008)

Evapotranspiration

The radiant energy absorbed by the land surface has three main fates: it can be emitted as longwave radiation; converted to latent heat by evaporating water; or warm up the surface and be conducted away as sensible heat (into the soil or into the atmosphere). In the short term, heat is transmitted into or out of the soil, but at timescales of a year or longer the in-and-out fluxes cancel, and the net effect of this term is negligible. A very small part of the incoming radiant energy (<1%) becomes chemically fixed through photosynthesis.

Thus the energy absorbed by an ecosystem must be balanced by the energy returned to the atmosphere as sensible or latent heat flux. The ratio of sensible to latent heat flux (Bowen ratio) is directly determined by the physiology and structure of the vegetation (the leaf albedo, stomatal and canopy resistance and leaf area index all play a role) and the characteristics of the soil (density, porosity and thermal diffusivity and capacity, all of which are affected by the moisture content) (Pielke and Avissar, 1990; Lambers et al. 2008). The Bowen ratio varies 100-fold among ecosystems, from less than 0.1 in tropical oceans to 10 in deserts. This division of absorbed energy into sensible and latent heat fluxes is an important physical determinant of the climate on local to regional scales (Pielke & Avissar, 1990).

The Bowen ratio is critical because it determines the strength of the linkages between energy exchange and the hydrological cycle. If the surface is moist, or soil water is available within the rooting depth, most of the energy absorbed by the ecosystem is dissipated by evaporating water (Pielke et al. 1993). The land surface remains cool (often cooler than the air passing over it), and the relative humidity high. Ecosystems with abundant moisture therefore have high rates of evapotranspiration and a low Bowen ratio. Strong winds and rough canopies reduces temperature build-up at the surface which drives sensible heat flux, also leading to low Bowen ratios and high evapotranspiration (Lambers et al. 2008)

At the other extreme, if the soil is dry or has little green vegetation, the incoming energy is mostly converted to sensible heat, warming the land surface and overlying air (Pielke et al. 1993). If the land surface, through degradation processes, sheds much of its water as runoff instead of allowing it to infiltrate, then the potential to dissipate energy as latent heat is proportionally reduced.

Therefore, it is important to consider several feedback mechanisms when quantifying climate regulating services and the interactions and trade-offs between processes (Chapin III et al. 2008). There are multiple metrics for weighting the climatic perturbation of emissions of different greenhouse gases (Shine et al. 2005; Johansson 2011), and for the different land atmosphere feedback processes (Anderson-Teixeira et al. 2012; West et al. 2011) to make them functionally equivalent and comparable. The most widely used is the concept of Greenhouse Warming Potentials, whereby all gasses are expressed as carbon dioxide equivalents (CO_2e) (for example, see Betts 2000). Alternately, all climate forcings (including changes in latent energy and albedo) could be expressed in energy terms, as W m^{-2} .

The thicket history

The highest level of ecosystem classification is called a 'biome'. In South Africa, biomes are classified according to the profile of plant functional types they contain (Rutherford, 1997). Terrestrial biomes in South Africa show a strong association with climate (Ellery, Mentis and Scholes, 1990; Rutherford, 1997), and at a sub-biome level there are often characteristic associations with soil, land-form and disturbance regime. The ecophysiological characteristics of the plant functional types, in interaction with soil effects and climate constraints, give each biome a unique set of climate interactions with respect to the nature and strength of the interactions with the atmosphere. At one end are tall evergreen forests with high carbon storage and CO_2 fluxes, high evapotranspiration, low surface reflectance and high surface roughness; and at the other end the desert shrublands with virtually the opposite characteristics. There are some very specific climate-impacting processes, such as fire or

methane emission, which are largely found in certain ecosystems. Fires, for instance, are a key process in savanna systems where they control gaseous emissions and the tree-grass species composition, but they are virtually absent from the sub-tropical thicket, nama and succulent karoo.

The sub-tropical thicket (hereafter called thicket) in South Africa was only recognised as a distinct biome in early-mid 90s (Low and Rebelo 1996), before which it was seen as a mixture or convergence of other different biomes (Cowling et al. 2005). A mid-Palaeogene origin has been suggested, and it was thought to once have been widespread across the globe before climatic conditions reduced its distribution (Cowling et al. 2005). In South Africa, the core of the biome is now over south east portion of the country, where it occurs in a mosaic with other vegetation types (fynbos and succulent karoo in the east, savanna and grassland to the west). It is widespread across the landscape, following the escarpment mountains and foothills.

The thicket can be placed on aridity continuum (Vlok et al. 2003), divided in the solid and mosaic types, separated by topographic position, distinguished by the presence or absence of succulent species, and scrutinized by species evolutionary lineage. This complexity has proved a puzzle and a challenge for ecologists, botanists and biogeographers (Cowling et al. 2005). Subsequent to obtaining 'biome status' it has been studied in great spatial and compositional detail (Lloyd et al. 2002; Vlok et al. 2003; Cowling et al. 2005; Pierce 2006) and interest in the biome and its delineation continues (Duker et al. 2015; Moncrieff et al. 2015; Potts et al. 2015). Thicket composition and structure is maintained largely by herbivores which feed on the densely growing and often palatable species (Aucamp et al. 1978). Plant morphology shows this long browsing history, and many of the species are spinescent, or low growing (Cowling et al. 2005). Anthropogenic factors aside, herbivory is the major cause of disturbance, as fire is not a part of the disturbance regime outside of the fynbos/savanna/grassland mosaic patches (Kerley et al. 1995). Thicket vegetation has been described "stable but brittle" (Cowling et al. 2005) and is vulnerable to excessive browsing by livestock, goats in particular (Hoffman & Cowling 1990; Stuart-Hill 1992). This is particularly true for thicket containing the arborescent leaf and stem succulent *Portulacaria afra*, Jacq., whose removal from the landscape marks the transition of intact thicket into a degraded stable state, which resembles a savanna in moist areas, or in the more arid areas, is bare ground with flushes of annuals (Hoffman & Cowling 1990; Stuart-Hill 1992; Lechmere-Oertel 2003).

The removal of *P. afra* sees the loss of other sub-canopy succulents (e.g. *Crassula ovata*, *Crassula perforata*, *Crassula muscosa*, *Euphorbia hamata*) and some plant community woody shrub and tree species (e.g. *Pappea capensis*, *Putterlickia pyracantha*, *Rhus longispina* and *Gymnosporia polyacantha*) from the landscape over a relatively short period of time (ca. 20-80 years) (Kerley, et

al. 2005; Cowling, et al. 2005). Due to its growth physiology and palatability *P. afra* is the first species removed from the landscape (Stuart-Hill 1992). Significant changes in vegetation composition, cover and structure result: the dense evergreen closed-canopy shrubland is replaced with an open seasonal savanna-like system comprised of isolated remnant trees (predominantly *P. capensis*) and an ephemeral herbaceous layer (Stuart-Hill 1992; Milton & Dean 1995; Kerley et al. 1995; Cowling, et al. 2005). A corollary to this is that *P. afra* is an “ecosystem engineer” (van der Vyver et al. 2013), and is used in restoration activities (see *Restoration and ecosystem services*, below).

Literature on the thicket and its land use options has moved with the times. Keywords/key ideas include: rangeland productivity, carrying capacity, desertification, degradation, transformation, land use change, climate change, resilience, vulnerability, natural capital, carbon sequestration, restoration, carbon credits, and ecosystem services. The prominent theme throughout is productivity of the landscape and the productivity of certain species, most notably *P. afra*.

Ecosystem services in South Africa and the thicket

In South Africa, the ecosystem service approach to research has been particularly well-adopted in the biodiversity and water policy-making sectors (Le Maitre et al. 2007) because it allows for the advancement of conservation in a social context. South Africa is exceptionally rich in biodiversity with high levels of endemism, containing three of the 34 global biodiversity hotspots (Mittermeier et al. 2005). The country also has a large poor rural population (StatsSA 2009) relying directly on the local natural resources – a legacy from South Africa’s well-known historical policy of social segregation: Apartheid. To redress the resulting equity issues the country has adopted a ‘human development path’ to drive increases in economic growth, create employment, eradicate poverty, and redistribute income (RSA 2006). The ecosystem services paradigm allows diverse disciplines and stakeholders to engage on the topic of sustainable development, which is crucial given the demands placed on natural resources by economic development particularly within the ecological reality of severe natural resource limitations (Le Maitre et al. 2007).

South Africa was a major role player in the Millennium Ecosystem Assessment, whose multi-scale assessment, the Southern African Millennium Ecosystem Assessment (SAfMA) (Biggs et al. 2004; Scholes & Biggs 2004) assessed fresh water, food, woodfuel, cultural and biodiversity-related ecosystem services. The SAfMA showed that while ecosystems are highly valued for their cultural services (largely biodiversity-related), the supply and access of other services is unequal, particularly water (Scholes & Biggs 2004; van Jaarsveld et al. 2005).

To date the spatial distribution and quantity of service provision, as well as the congruence between ecosystem services and with biodiversity, have been investigated across South Africa at a broad resolution (Egoh et al. 2008; Egoh et al. 2009); and at a fine resolution for the semi-arid Little Karoo region (Reyers et al. 2009); and the beneficiaries of ecosystem services has been mapped (van Jaarsveld et al. 2005; also see Le Maitre et al. 2007 for an overview prior to 2007). Based on experience in South Africa, Cowling et al. (2008) propose an operational model for achieving the safeguarding of ecosystem services. They focus on including ecosystem service concerns into land- and water- use planning sectors. This approach is particularly useful for developing countries, like South Africa, where decisions regarding competing forms of land use need to be made rationally and towards sustainable ends.

Restoration and ecosystem services

Restoration has been suggested as the most direct and effective remedy for addressing the decline or depletion of ecosystem services (Aronson et al. 2007). *P. afra* has been advocated as the solution to thicket restoration (Mills & Cowling 2006). Although seedling survival of *P. afra* is low (Sigwela et al. 2009) and recovery of transformed thicket does not occur spontaneously (Vlok et al. 2003) the use of truncheons propagation in an active restoration process is both relatively easy and effective (Mills et al. 2007). This has given rise to projects within mega reserves and on privately owned land in order to develop restoration protocols for the area (Mills et al. 2015).

The degraded and intact thicket ecosystems deliver different bundles of services, mostly notably those services which are associated with agricultural production (for instance above-ground carbon stocks, plant productivity, and forage; see Mills et al. 2007). These ecosystem services are quite literally tied together, linked non-linearly, so that restoration or any other land-use and management decisions which seek to increase a particular service may also affect the delivery of other services (Carpenter et al. 2009; Raudsepp-Hearne et al. 2010).

With this in mind, what are the challenges facing projects which seek to restore historically degraded areas, in terms of the trade-off between establishing species and critical services like carbon sequestration and water provision? The extent to which restoration of natural vegetation promotes these depends on trade-offs between water and carbon provision, as well as the environmental context in which one is working.

Thesis structure

The overall aim of this thesis was to determine how the presence of *P. afra* affects the flow of ecosystem services from the succulent thicket landscapes of the Eastern Cape, with particular focusing on carbon sequestration and climate regulation services.

Chapter 1 presents the current understanding of the carbon cycle, and the role of carbon sequestration in the climate regulation service. It is a global review, and contains a mix of perspectives and examples from different ecosystems.

P. afra is a key “service providing” species (Martin-Lopez et al. 2009) and we will explore its various functional traits and relative abundance in relation to climate regulation and different spatial and temporal scales. **Chapter 2** assesses *P. afra* abundance at a landscape scale; it compares the freshwater ecosystem services it provides by analyzing stream flow data from transformed and degraded catchments.

In **Chapter 3** the succulent and evergreen traits of *P. afra* and the role it plays in modifying the surface energy budget is explored at landscape scale. Chapter 3 quantifies the contribution of albedo change to net radiative forcing following restoration using the new high resolution Multi-angle Imaging SpectroRadiometer (MISR-HR) products, and assesses how this trades-off against carbon sequestration.

Chapter 4 and **Chapter 5** assess the contribution of the *P. afra* trait of facultative CAM behaviour to the carbon sequestration service at temporal scales ranging from hours to decades. **Chapter 4** quantifies the rate of carbon assimilation using radiocarbon and stable isotope analysis, growth ring analysis, dendrometry, water use efficiency and eddy covariance data. **Chapter 5** elaborates on the contribution of C₃- and CAM-derived carbon to *P. afra* carbon sequestration by exploring amount of time the species spends in different photosynthetic modes. This is assessed using stable carbon isotopes, dendrometry and infrared thermometry.

References

Please see the Combined Reference List

Chapter 1 Preface

Carbon Storage in Terrestrial Ecosystems

This chapter presents the current understanding of the carbon cycle, and the role of carbon sequestration in the climate regulation service. It is a global review, and contains a mix of perspectives and examples from different ecosystems.

This chapter was written as a contribution to an Elsevier book series on Climate Vulnerability, and it is included in its published form.

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R.J. Scholes was approached by the editors of the series for the contribution. The conceptual outline was generated between R.J. Scholes and the candidate. The content was written equally by both authors. Figures were created by the candidate.

4.09 Carbon Storage in Terrestrial Ecosystems

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4.09.1	The Climate Regulation Ecosystem Service	93
4.09.1.1	Mechanisms Delivering the Climate Service	94
4.09.1.2	Pools and Fluxes	94
4.09.1.3	The Market for Climate Services	95
4.09.2	What Controls the Magnitude of the Service?	96
4.09.2.1	Productive Potential	96
4.09.2.2	Mean Temperature	96
4.09.2.3	Waterlogging of the Soil	96
4.09.2.4	What Determines How Much Carbon a Soil Can Store?	97
4.09.2.5	What Determines the Maximum Biomass on a Site?	97
4.09.2.6	Effects of the Disturbance Regime	97
4.09.3	Thresholds and Tipping Points	98
4.09.3.1	Feedbacks in the Terrestrial Carbon Cycle	98
4.09.3.2	Tipping Points	98
4.09.3.3	The Hypothesis of Terrestrial C Sink Saturation	99
4.09.3.4	A Plausible Amazon Drought Tipping Point	99
4.09.3.5	Permafrost Melting	99
4.09.4	Vulnerability of the Terrestrial Climate Regulation Service to Climate	100
4.09.4.1	Fire	101
4.09.4.2	Heatwaves	101
4.09.4.3	Increases in Rainfall, Decreases in Rainfall, and Prolonged Droughts	104
4.09.4.4	Windstorms	104
4.09.4.5	Insect Attacks	104
4.09.5	Ways of Reducing Vulnerability	104
4.09.5.1	Preemptive Microdisturbances	104
4.09.5.2	Maintaining Ecosystem Function and Biodiversity	105
4.09.5.3	Reducing Vulnerability to Social Change	105
4.09.5.4	Dealing with Vulnerability in the Climate Service Market	105
4.09.6	Trade-Offs between Climate Regulations and Other Ecosystem Services	105
4.09.7	Conclusions	105
References		106

4.09.1 The Climate Regulation Ecosystem Service

The Millennium Ecosystem Assessment (2003) proposed a classification framework for ecosystem services, which has four top-level classes: provisioning services, which are tangible goods and typically have well-defined markets; cultural services, based on aesthetic or amenity value, which also often have markets; regulating services, which stabilize the supply of either of the above, or in other cases reduce the risk of natural disasters; and supporting services, which are ecological processes without which none of the above would occur, but which are not themselves directly used by people. The latter two service classes seldom have existing markets.

The 'climate service' provided by ecosystems – in other words, their contribution to ensuring that the climate of a given area is within certain desired bounds – is usually classified as regulating service. A substantial part, but by no means all, of this service is related to the ability of ecosystems to take up carbon dioxide from the atmosphere. With the creation of tradable carbon credits – formally through the Kyoto Protocol,

and whatever treaties may succeed it, and informally through a variety of 'voluntary' schemes – ecosystem carbon uptake and storage has effectively become a provisioning rather than a regulating service. Just like other provisioning services, it is a physical quantity with a market and a price. Land stewards can choose to manage their land to include carbon storage as one of the commodities it provides.

At the global scale, it is easy to demonstrate that terrestrial ecosystems provide a large and crucial climate service. Life exists on this planet because of the particular atmosphere that is present here. The composition of the atmosphere is dependent on the organisms and ecosystems that have coevolved with the atmosphere over a period of many billions of years. Without this biota, the temperature, rainfall, and atmospheric circumstances on Earth would be very different, and not able to support human life. Thus the 'total value' of the climate regulating services is infinite. The more useful (and difficult) question is what is the value of a marginal change in the climate service, for a subset of the planet of perhaps just a few hectares? Can this service be relied on in the future?

Specifically, is carbon storage biophysically dependable, against a backdrop of the substantial variability in the preindustrial climate of the Holocene, and the nonsteady state nature of the current perturbation of the global carbon cycle (National Research Council 2005)?

4.09.1.1 Mechanisms Delivering the Climate Service

The land surface modulates the climate in many different ways and at many scales. People have understood the microclimatic ameliorating effects of vegetation for centuries. It is the underlying principle of windbreaks, shade trees, and gardens. These effects are provided by slowing the wind, raising the humidity, intercepting solar radiation, and partitioning absorbed solar radiation into latent energy of evaporation rather than heat. The vegetated surface also helps to buffer humans from the consequences of climate extremes such as droughts, floods, or windstorms. These are all important parts of the 'climate service'. The focus of this chapter, however, is at a larger scale the role of the terrestrial surface in mitigating human-induced global change, specifically by acting as a sink for carbon dioxide, but also through non-CO₂ mechanisms (McAlpine et al. 2010). The climate system is never in a steady state, either interannually (e.g., Elis et al. 1978), or on longer timescales (Rial et al. 2004). The contemporary Earth climate system has, in addition, a significant human influence (National Research Council 2005). It is adjusting to a human-caused perturbation including the total emission of about 11 Pg C year⁻¹ as carbon dioxide, 582 Tg CH₄ year⁻¹ as methane, 17.7 Tg N year⁻¹ as nitrous oxide, and an average 19 185 Tg year⁻¹ of aerosols into the atmosphere (Solomon et al. 2007). These emissions are largely from the burning of fossil fuels, and with a significant additional component resulting from human-induced land cover change. Globally ecosystems absorb around half of the human-caused CO₂ perturbation, more or less evenly between the ocean and land (Prentice et al. 2001; Houghton 2003). The land uptake constitutes what is known as the 'terrestrial carbon sink'. It varies substantially in magnitude from year to year, much more so than the oceanic sink (Canadell et al. 2007; Rowhani et al. 2011). Inversion studies and *in situ* observations confirm that the terrestrial sink is widely distributed over the Earth's surface, though not evenly so (Gurney et al. 2004; Phillips et al. 1998). In addition, the pervasive human-induced changes in the land surface directly modify the climate through altering the surface fluxes of heat and water vapor.

This chapter focuses on the carbon storage aspect of climate on land. There is no general agreement on the relative contribution of the several processes thought to underlie the terrestrial carbon sink (Scholes et al. 1999). It is observed that when plants are exposed to higher levels of CO₂, their rate of carbon assimilation increases – a phenomenon known as CO₂ fertilization (Lobell and Field 2008). Many parts of the world are simultaneously experiencing N fertilization, either deliberately or as an unintended consequence of air pollution, which also increases production (Reay et al. 2008). Thirdly, large parts of Europe and North America are undergoing forest regrowth following clearing in past centuries – thus in the present time they act as carbon sinks (Nabuurs et al. 2003; Goward et al. 2008). A transient sink inevitably arises when a series of

slow-turnover pools must be filled before respiration fluxes catch up with photosynthetic fluxes, trees must grow, die, and then decompose.

In addition to CO₂, several other radioactively active gases and particles produced or absorbed by the land surface also participate in the present imbalance in the global energy budget. The main ones are methane and nitrous dioxide, but carbon monoxide, a range of nonmethane hydrocarbons, and oxides of nitrogen contribute indirectly as precursors to tropospheric ozone, which is a powerful, but short-lived greenhouse gas. Organic aerosols and soot particles affect the radiation balance directly or indirectly by acting as cloud condensation nuclei. Change in the properties of the surface itself, especially its reflectance (known as albedo), alters the energy absorbed by the surface. For instance, when a bright surface such as snow is replaced by a dark surface such as a conifer canopy, the net result is warming (Betts 2000). There are other circumstances, such as the conversion of southwest Australian bushlands to agriculture, which could produce a cooling effect (Nair et al. 2007). 'Carbon', which has come to be used as shorthand for 'carbon dioxide', has tended to overshadow these other gases and processes, but this is a misleading simplification. Although CO₂ has the largest single direct human radiative forcing effect globally, in particular circumstances the other mechanisms are significant, even to the extent of overwhelming the carbon effect locally (e.g., Avila et al. 2012). If a net benefit to the climate system is the objective, rather than simply selling carbon into an undiscerning market, all the main known effects must be checked to ensure that the important ones have been taken into account under any given circumstance. It is perfectly feasible for an ecosystem to show an increase in carbon, but have a net detrimental effect on climate suitability for human purposes.

4.09.1.2 Pools and Fluxes

Carbon held within the ecosystem as a stock (also known as a 'pool', and having the general units of g m⁻²) has little direct effect on the climate as long as the total magnitude of that stock does not change. What causes a change in the global atmospheric concentration, and thus the climate, is a net flux of CO₂ out of the atmosphere and into the terrestrial ecosystem stock, or vice versa. Fluxes have units of g m⁻² year⁻¹; in other words they are rates. The confusion arises because fluxes are often measured as the difference between stocks at two times. It must always be remembered that it is not the magnitude of the stock that matters per se, but the change in the magnitude of the stock. When terrestrial stored carbon is sold, it is not the stock that is sold, but the flux it represents.

Carbon is held in terrestrial ecosystems in several interconnected pools of different sizes and turnover times (Figure 1). Turnover of some pools, such as the simple organic compounds and microbial biomass that make up the 'fast' pool, are fleeting – they may last only minutes to hours. Others, like live or dead leaves, decay over a period of months to years. Yet others, such as the trunks and coarse roots of trees, and the clay-associated organic carbon in the soil, last for decades. Finally, there are several pools that may persist for centuries or millennia such as charcoal, or the structurally complex, high

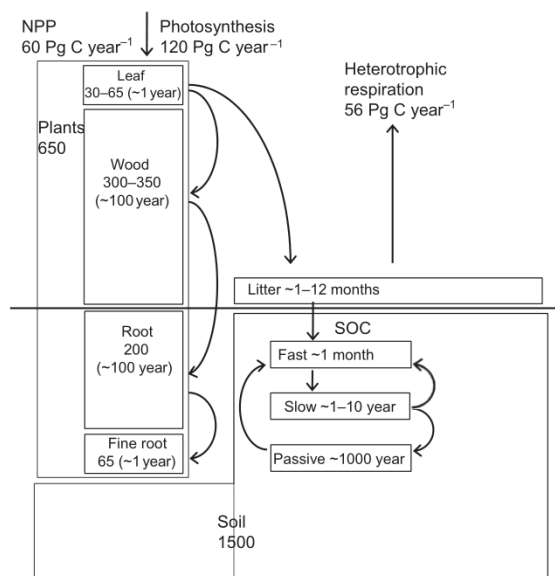


Figure 1 The key carbon stocks (boxes, Pg C) and fluxes (arrows, Pg C year⁻¹) in terrestrial ecosystems with their approximate magnitude at a global scale and the typical turnover times. The soil carbon excludes wetland soil and permafrost stocks.

molecular weight forms of soil organic carbon 'humic compounds'. The faster turnover pools are usually not counted when the carbon credits are calculated. There is an unwritten guideline that a pool must persist for 20 or more years before it is considered 'sequestered' rather than 'stored'. This aims to address the issue of the 'permanence' of land-stored carbon.

The total flux of carbon into and out of terrestrial ecosystems is always bigger than the portion of the flux that becomes stored, in most cases, one to two orders of magnitude bigger. For instance, at the global scale, over 100 Pg C year⁻¹ is assimilated by the terrestrial vegetated surface through photosynthesis (Solomon et al. 2007). This overall amount is the gross primary production of the terrestrial biosphere. About half of this is directly returned through respiration by the plants themselves, leaving a net primary production of about 60 Pg C year⁻¹. In a steady state, which we would expect to be approximated in long-term undisturbed vegetation, virtually all of this would be lost back to the atmosphere through heterotrophic respiration (e.g., by microbes and animals feeding on the plants or their residues). Alternately, the carbon could be returned to the atmosphere relatively abruptly through a fire (for instance see Tilman et al. 2000) or major disturbance. In production landscapes, a significant amount of carbon is extracted through the harvest of crops or timber. A small amount of carbon is transported laterally out of the ecosystem in the form of aerosols, sediments, or dissolved organic carbon. Since the terrestrial biosphere is currently not in a steady state, about 2% of the assimilated flux is retained in terrestrial ecosystems, where it manifests as an increase in biomass, litter, and soil carbon (Malhi 2002; Solomon et al. 2007).

The small size of the stored flux relative to the turnover flux makes the accurate measurement of the former very challenging – the uncertainty in flux measurement is often

larger than the stored flux. Similarly, the change in ecosystem stock is usually small, relative to the total stock, unless it is allowed to accumulate for several years. The relative error of estimation for the different components making up the global carbon stocks and fluxes range from about 1 to 90% (Scholes et al. 2009), with an average of 10–20%.

4.09.1.3 The Market for Climate Services

Despite the down turn and economic volatility in capital markets since the 2008–09 financial crisis, and a decline in carbon prices in 2011, the global carbon market amounted to USD 176×10^9 (Kossov et al. 2012) in trades in 2011, making it one of the largest global commodity markets. Only a small part of this is 'land-based carbon'; the majority consists of reductions in industrial carbon dioxide or other greenhouse gas emissions. The main distinction is between the 'official market', e.g., that associated with international treaties such as the Kyoto Protocol, and the 'voluntary market'. The official market is always certified, in other words, backed up by accounting standards and audits. The voluntary markets are usually also certified, but with varying degrees of rigor. Since the signatories to international treaties are sovereign countries rather than individuals or corporations, countries are ultimately in control of the official market, and define its size through the regulations they set. The price of carbon in the official market is much higher than the price in the voluntary market, but so is the cost of participating in it.

Both the sellers and buyers of certified carbon credits are typically in the private sector. In the case of land-stored carbon, the sellers are land owners or land stewards, who through their management practices have caused the carbon density of the land (e.g., the mass of carbon within eligible classes per unit land area) to increase. In principle, the simultaneous effects of changes in the other greenhouse gases or land surface properties that also result from the management action must be considered as well, but in practice seldom are. The ultimate buyers are entities that have emission reduction commitments, which they either cannot meet or cannot do so at a price less than the market price for certified carbon credits. Between the sellers and buyers are a range of brokers and certifiers, and the agencies appointed by governments to oversee carbon trades. The complex structures and onerous certification rules add greatly to the transaction costs. Since the transaction costs do not scale proportionately with the amount of carbon involved, effectively, only large entities can trade profitably in carbon (Wise et al. 2009).

In the official market, two conditions need to be met. First, the carbon stored must be 'additional', in other words, as a result of some deliberate action, which otherwise would not have occurred. This is important, given that the terrestrial biosphere is taking up 2 Pg C year⁻¹ without any intentional human assistance. In practice, since the mechanisms of the terrestrial carbon sink are not well understood, it is very hard (perhaps impossible) to attribute changes in land carbon between those arising from management and those that would have occurred anyway. Generally, a more or less arbitrary 'baseline' is agreed, and deviations from this baseline become the tradable commodity.

The second consideration is 'leakage' (Murray et al. 2004), which means that carbon storage in one location should not

simply result in a carbon loss elsewhere. For instance, if a forest is permitted to accumulate carbon by restricting harvests, from where is the unchanged demand for wood being met? Again, this consideration is hard to implement with complete confidence. The usual approach is to insist on 'wall-to-wall' accounting within units large enough to encompass likely leakage, such as entire countries. If leakage is detected, it is hard to attribute it to any specific project.

The participation of 'non-Annex 1' countries (e.g., countries without emission reduction commitments, which translates mainly to developing countries) in the Kyoto Protocol carbon market is via the Clean Development Mechanism (CDM). It only recognizes a limited set of land-based storage activities (essentially, afforestation). The number of land-based carbon projects in the CDM has been low. Over and above the additionality and leakage conditions, CDM trades must demonstrate that they are consistent with sustainable development. For instance, a land carbon storage project, which results for instance in a large loss of biodiversity, water yield, or livelihoods, would in principle be disqualified.

Reduced Emissions from Deforestation and Degradation (REDD) introduces a new concept to the carbon trade. Instead of paying for the (imperfect) restoration of carbon on deforested land, it aims to pay a maintenance fee to keep the carbon on the land in the first place, while incidentally protecting biodiversity, water yield, etc. (Strassburg et al. 2009; McAlpine et al. 2010). This is a particular case of a general concept known as Payment for Environmental Services (PES). The principle difficulties with REDD involve monitoring what is cost effective, but nevertheless has sufficient sensitivity to detect partial losses (degradation); avoidance of leakage; ensuring that the land custodians are the major beneficiaries of the payment; and determining a reasonable price, given that the payments occur year after year, potentially forever – more like rental of stored carbon than a purchase of a change in stock.

4.09.2 What Controls the Magnitude of the Service?

In general, the carbon storage-related climate service offered by ecosystems is finite, since it represents an adjustment to a new equilibrium between carbon uptake and carbon loss. Once the equilibrium is reached, the net flux is zero and the stock quantity is unchanging in the long-term, even though large turnover might be taking place. Exceptions to this 'limited time' feature occur in the cases where carbon is continuously exported in a sequestered form (such as timber), or the captured carbon is used as a substitute for fossil fuels (e.g., biofuels), or in the 'rental' agreement in REDD. The service in general can be thought of as having a rate and a duration whose product constitutes the magnitude. Net primary productivity (NPP), ambient temperature, and soil waterlogging are the key determinants of the rate. The upper limits of soil carbon storage and biomass set the total magnitude.

4.09.2.1 Productive Potential

Terrestrial ecosystems cannot accumulate carbon at a rate exceeding net primary production. In practice, they generally store carbon at a much lower rate; nevertheless NPP is a good

first order indicator of locations with high storage potential versus low storage potential. The broad-scale predictors of terrestrial NPP are well known: The absence of water stress, warm but not excessively hot temperatures, sufficient solar radiation, and a sufficient supply of the essential elements needed for plant growth (Running et al. 2004). The constraints applied by the carbon market – high transaction costs and the necessity for relatively frequent periodic inventories, means that ecosystems with low NPP, even if they technically could store a lot of carbon thanks to their large area – are not financially viable as storage locations. The carbon increment per area over a 5-year period is too low to detect except with an inordinate investment of effort.

Different broad ecophysiological groups of plants – plant functional types or PFTs (Grime 1977; Box 1996) – have different characteristic carbon uptake rates and sensitivities to environmental drivers. Some of the key top-level PFTs are plants with 'conventional photosynthesis', the C_3 pathway (most trees, herbs, temperate and wetland grasses, crops such as wheat and rice); C_4 photosynthetic systems (tropical grasses and crops derived from them, such as sugarcane and maize); and Crassulacean Acid Metabolism (CAM) succulents. The distribution of PFTs shows geographical patterns related to the climate, and specifically to water stress, and temperature.

Plants with CAM (including Agave, Cactus, and *Portulacaria afra*) are able to maintain productivity under conditions of severe water stress by temporally decoupling the carbon assimilation processes from the transpiration process. This may allow them to accumulate carbon at unusually high rates even in arid areas, but it does not relieve them totally from water constraints (Osmond 1978). The measured water use efficiency is about twice that of C_3 plants, but only a little better than that achieved by C_4 plants (Winter et al. 2005).

4.09.2.2 Mean Temperature

Other factors being equal, cool locations accumulate more soil organic matter and biomass than hot locations (Jenny 1980). This is apparent on altitudinal gradients – Montane forests have a higher carbon density than lowland forests, for instance, and on latitudinal gradients within, for instance, the Great Plains of North America (Parton et al. 1987). The reason is the strong and exponentially increasing effect that high temperatures have on increasing respiration rates, whereas carbon assimilation rates initially increase with temperature, but peak and decline above around 30 °C.

4.09.2.3 Waterlogging of the Soil

Soils which are waterlogged for more than a few weeks become anaerobic. Decomposition continues, but at a much reduced rate and via a methanogenic pathway rather than one that produces CO_2 . These soils accumulate large amounts of carbon in the form of peat, both in temperate-cool areas and in nutrient-poor regions of the tropics (Hooijer et al. 2010). Paradoxically, flooding a soil for this purpose is counterproductive, because the methane and nitrous oxide generated offset the carbon gain (Sampson and Scholes 2000). Conversely, draining a peat box releases carbon dioxide, but eliminates a source of methane, and the two effects more or less cancel each other out.

4.09.2.4 What Determines How Much Carbon a Soil Can Store?

The global amount of carbon stored in soils vastly exceeds that stored in plant biomass or the atmosphere (1500–2000 Pg C for soils, 466–654 Pg C for biomass, 750 Pg C in the atmosphere; Prentice et al. 2001). Aside from the special case of waterlogged soils, described above, the maximum amount of carbon a given soil can store is mainly controlled by its texture (the fraction of clay and silt it contains) (Jenny 1980; Parton et al. 1993; Schimel et al. 1994) and the mineralogy of the clays (Six et al. 2002; Denef et al. 2004). The key slow turnover carbon pool in the soil is intimately associated with clays, and especially with large surface area clays such as smectites and illites (Six et al. 2002) (Figure 2(a)). Clayey soils facilitate the formation of C pools with slow turnover times due to the physical protection of SOM by clay minerals (Christensen 1992; Silver et al. 2000).

Once this storage surface is occupied, carbon can further accumulate as particulate organic carbon (tiny fragments of

biomass), but is susceptible to relatively rapid loss (Six et al. 2002). Shallow or very stony soils can also not accumulate large amounts of carbon. Soil organic carbon stocks vary across ecosystems (Figure 2(b)) due to complex interactions among biotic and abiotic factors (Six et al. 2002; Schmidt et al. 2011).

4.09.2.5 What Determines the Maximum Biomass on a Site?

The aboveground biomass that can accumulate on a site is determined by the vegetation cover and its height. Cover increases with rainfall, up to a maximum of essentially continuous canopy (Sankaran et al. 2005). Further biomass increases beyond this point rely on increasing height. The fundamental limits to the height that trees can reach are set by biomechanical considerations, such as the ability to anchor the tree against winds and the ability to lift water to the leaves (Koch et al. 2004). The importance of height, and the woody structural tissues needed to attain it, is why forests are the carbon storage ecosystems of choice. Ecosystems can store a substantial amount of carbon belowground, in the form of fine and coarse roots (Jackson et al. 1997), but belowground carbon does not count in many carbon market schemes, for no logical reason except that it is hard to see and tedious to measure.

4.09.2.6 Effects of the Disturbance Regime

Many terrestrial carbon storage projects involve the exclusion or reduction in frequency or intensity of disturbances that would otherwise lead to carbon loss. For instance, fire exclusion in savannas and grasslands, reduced-impact logging in forests, or reduced tillage in crop agriculture. The main disturbances, which disrupt the carbon cycle and can cause the loss of accumulated carbon, are fires, insect herbivore outbreaks, windstorms, harvest of plant material by humans, and disruption of the soil by cultivation or drainage. These disturbances are neither mutually exclusive, nor independent of one another. For instance, the dead material caused by a pest outbreak can increase the risk of fire.

Disturbance is often characterized as if it were a simple binary variable. Does it occur or not? In reality, disturbance regimes consist not only of the probability (or, equivalently, the frequency) of occurrence, but also the intensity of the disturbance and often more subtle characteristics, such as their relation to phenological or growth stages and their coincidence with other disturbances. A change to any of the determinants of a disturbance regime is likely to have consequences for the carbon cycle (e.g., in tropical savannas; Bird et al. 2000; Arabinbar et al. 2003), but not all effects will be dramatic. Small changes in the regime will generally result in small changes to the stored carbon.

It is possible for an ecosystem to accumulate carbon in the presence of disturbances, provided that the carbon lost as a result of the disturbance is less than the carbon accumulated between disturbances. For instance, it is possible for a 'production forest', in which trees are felled rotationally to nevertheless have a higher average carbon density than a non-forested site (although probably less than an unharvested forest, Figure 3). Exactly how much more depends on the specifics of the management regime – how often does harvest

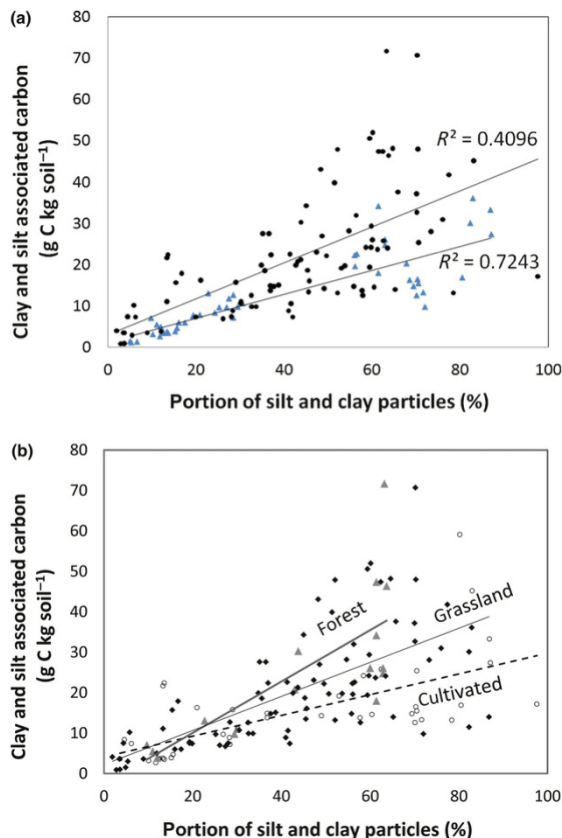


Figure 2 Silt plus clay content ('fines', as %) and silt and clay associated carbon concentration (g C kg soil^{-1}) for mineral particles 0–20 μm . (a) The effect of clay mineralogy (1:1 clays, e.g., kaolinite and serpentine, blue triangles; 2:1 clays, e.g., smectite and illite, black circles). (b) In relation to the type of ecosystem. Redrawn from data appendices in Six, J., R. T. Conant, E. A. Paul, and K. Paustian, 2002: Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil*, **241**, 155–176.

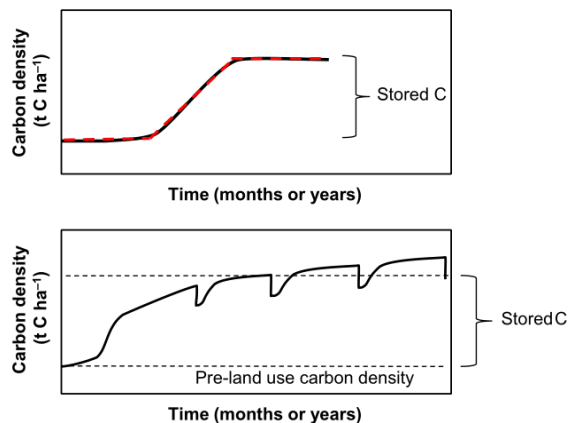


Figure 3 A schematic representation of an ecosystem accumulating carbon following a change in land management. The top panel shows a simple case, where the carbon density rises according to a more or less logistic curve to a new equilibrium level. This can be approximated with linear segments defining a rate and duration of carbon storage. The lower panel shows a case, such as a rotationally harvested plantation, where there are repeated logistic segments interrupted by harvest or disturbance events. The long-term mean carbon density is nevertheless higher than in the preland use change case.

occur, what fraction of carbon is removed, and how much collateral damage is caused.

It is important to tolerate some level of disturbance in terrestrial ecosystems under management for carbon storage for several reasons. Firstly, an evolutionarily appropriate disturbance regime is required to maintain ecosystem characteristics such as biodiversity. Secondly, small disturbances help to preempt large disturbances (this point is discussed in more detail in Section 4.09.5). Thirdly, there is a theoretical argument (largely untested empirically) that protection from disturbances leads to the gradual loss of system capacity to cope with disturbance when it inevitably occurs – in other words, a loss of resilience (Gunderson and Holling 2002).

4.09.3 Thresholds and Tipping Points

4.09.3.1 Feedbacks in the Terrestrial Carbon Cycle

Feedback occurs when a change in one element of a system generates a response, propagated through the rest of the system, that eventually returns to have an effect on the first element that changed. Feedback is ‘negative’ (or stabilizing) when its net effect is to dampen the initial change and ‘positive’ when the net effect is to amplify it. Where more than one feedback pathway exists and the signs are different, the net effect can still be calculated, but this requires knowledge of the relative magnitudes of the individual effect terms and their nonlinear interactions. Positive feedbacks can lead to ‘runaway change’ if they are sufficiently large, but do not necessarily do so. In general, the effect of a positive feedback is simply to increase the size of the initial perturbation somewhat. If the net feedback effect is larger than the initial perturbation, the system is said to have crossed a threshold, a ‘tipping point’ in popular terms, and will move under its own internal dynamics into a new stability domain. As a result of such interactions, new

states can develop (Peters et al. 2004). There is an obvious positive feedback loop of terrestrial carbon with the rest of the climate system. An increase of temperature leads to the release of carbon from soils, which could lead to a further increase in temperature from the added radiative heating. But within plausible ranges of near future warming, the feedback by this mechanism alone is not believed to be strong enough to cause ‘runaway warming’ (Prentice et al. 2001). In conjunction with speculated (but not demonstrated) effects such as a large increase in vegetation fires, or a large accompanying release of methane from frozen soils, a runaway scenario leading to a persistently much warmer future state of the Earth’s climate system may be possible.

4.09.3.2 Tipping Points

Moderately complex systems exposed to external forcing do not change smoothly and gradually, especially where some or all of the effect links between elements are themselves nonlinear, or lagged in time (e.g., Scheffer and Carpenter 2003, Rial et al. 2004). Rather, they appear to resist change or be insensitive to applied driving forces over some domain, and then change more or less abruptly. The climate system, including its biospheric and human system couplings, has all these characteristics. Therefore, the response of the terrestrial carbon cycle to increased effects from atmospheric and other climatic effects is unlikely to be continuous and incremental at the global spatial scale.

The terms ‘tipping point’ and ‘threshold’ have been used in a variety of ways in this context, not always consistently (Rau-pach and Canadell 2008; Lenton et al. 2008). The notions also become confounded with other limit-based ideas, such as (1) the amount of change that is policy relevant, (2) ethically important, (3) important for human welfare, and (4) ecologically important (Lenton et al. 2008; Krieger et al. 2009; Martin et al. 2009). Often ‘threshold’ is used to describe either a more or less arbitrary level, which people agree not to transgress. Alternately, it may describe a point where the rate of change begins to steepen, but does not yet constitute a separation between two system states. The terrestrial carbon system has many such thresholds, which are important, but not necessarily critical.

In this chapter we use ‘tipping point’ exclusively to refer to a threshold where the internal dynamics of the system cause it to continue to change after the forcing effect has ceased, carrying the system quasi-irreversibly into a new state. Beyond the tipping point, the future state and development of the system is qualitatively different (Lenton et al. 2008). We consider it only ‘quasi-irreversible’, because although in the short term the system will not revert of its own accord, it may be possible to manage it back to the former state with some input of effort. In the longer term, another series of changes may be triggered, which eventually lead the system back to its original state.

Inherent in the notion of tipping points is the idea that a small perturbation in their vicinity can have potentially disproportionate, persistent impacts on the system. Such tipping points have been suggested to exist for several subsystems or spatial regions of the global terrestrial carbon system, within the plausible range of contemporary environmental change.

For instance, the melting point of ice near 0 °C constitutes a physically determined threshold with important consequences for the carbon cycle of frozen soils. If large areas of permafrost melt, their contribution to global atmospheric CO₂ and methane, plus the darkening of the surface resulting from pools of water, makes it increasingly unlikely that they will spontaneously refreeze – to do so would require a sustained return to a much cooler climate. Another example, which has been suggested, is the susceptibility of tropical rainforests to fire if they experience prolonged dry spells. Once the forest burns, the canopy is opened up, favoring the growth of grasses, which in turn makes future fires more likely. These examples are elaborated below.

4.09.3.3 The Hypothesis of Terrestrial C Sink Saturation

The likely presence of thresholds can sometimes be predicted from a qualitative knowledge of the form of the interactions in a system. For instance, both heterotrophic and autotrophic respirations increase with rising temperature. The relationship is conventionally represented by an exponential function. Furthermore, the respiration rate is more or less proportional to the soil carbon and biomass pools, respectively. The global mean temperature, over multi-year timescales, is approximately proportional to the global atmospheric CO₂ concentration. On the carbon uptake side, photosynthesis on land is a saturating function of atmospheric CO₂ and a hump-shaped function of temperature with a peak below 30 °C. Scholes (1999) and Kirschbaum (2000) both speculated that the consequence of this set of interactions would be that the land would initially be an increasing carbon sink, as photosynthesis rose in response to rising atmospheric CO₂ concentration. The sink would peak and then decline (eventually becoming a net source) as respiration, in response to rising temperature and accumulating C stocks, caught up with and overtook photosynthesis.

There is a second reason to expect the terrestrial biosphere to behave initially as a sink, but later to become a source, before returning to approximate neutrality. The time lags intrinsic to the terrestrial carbon cycle – the life span of a tree, for instance, or the turnover rate of soil carbon – means that there is inevitably a delay between photosynthesis and respiration, since the carbon must first be captured before it can be respired.

Subsequent detailed quantitative and spatially explicit modeling efforts have tended to substantiate these qualitative predictions (Canadell et al. 2007). Most global climate models with a global C cycle model suggest that the current net global terrestrial carbon sink could peak in the twenty-first century and then decline, in some cases smoothly to a new equilibrium between respiration and uptake, but more often with some overshoot in favor of respiration (Friedlingstein et al. 2006). Carbon in the ‘fast turnover’ soil pool has a higher temperature dependency than more ‘passive’ soil carbon, and it is the increased turnover of this labile soil carbon, which contributes to the sink saturation rather than the release of recalcitrant carbon from the ‘slow’ pools (Fang et al. 2005; Knorr et al. 2005).

4.09.3.4 A Plausible Amazon Drought Tipping Point

One of the possible ‘inevitable surprises’ (Lenton et al. 2008) on the IPCC short list of plausible abrupt climate change

scenarios (Solomon et al. 2007) is modification to the extent, structure, and behavior of the rainforest in the Amazon Basin. A combination of changes in tree fraction, regional rainfall, and summer temperatures, due to a complex interplay between land use change, and anthropogenic and natural climate forcing is simulated, which in some models induces a partial dieback in the Amazonian rainforests (Cox et al. 2000, 2004; Betts et al. 2004; Malhi et al. 2009).

The majority of precipitation in the Amazon basin is recycled, e.g., it originates from water vapor evaporated in the basin itself. Therefore a change in the land surface – deforestation, or shift to more savanna-like species – could in principle lead to a positive feedback in the water cycle of the region (Figure 4). Modeling results hypothesize that dry-season water stress could increase in the twenty-first century, promoting a climate, which supports a seasonally deciduous forest (Malhi et al. 2009) or an open woodland with grasses (Betts et al. 2004; Cox et al. 2004), rather than the present evergreen forest. Such a state change could further reduce regional rainfall due to a reduction in hydraulic redistribution (Lee et al. 2005) and increase the regional temperature. It would also release CO₂ to the atmosphere. Higher atmospheric CO₂ also leads to stomatal closure, further reducing evaporation and ultimately, precipitation Costa and Foley (2000). Higher temperatures and reduced rainfall lead to reductions in NPP (Betts et al. 2004; Cox et al. 2004), and make the biomass carbon in the replacement seasonal forests vulnerable to fires (Malhi et al. 2009). Rainforest trees seldom experience fire and are therefore susceptible to fires in the litter layer and the near-ground vegetation. Generally the ground vegetation is kept sparse by the closed tree canopy and the litter layer is too wet to burn. A dry spell lasting several months can dry out the litter layer. If land clearing activities damage the forest margin, allowing fire in, the canopy trees can be killed, which lets in light, allows grasses to spread, and makes future fires more likely. A further feedback on rainfall could occur through the increased number of aerosols and cloud condensation nuclei produced by burning (Andreae et al. 2004).

4.09.3.5 Permafrost Melting

Estimates of the size of the carbon stocks in permanently frozen (permafrost) soils vary from 200–800 Pg C (excluding wetlands; Gruber et al. 2004), 400 Pg C (northern hemisphere only, Tarnocai et al. 2009), 900 Pg C (Zimov et al. 2006) to 1672 Pg C (in the northern circumpolar permafrost zone, including 277 Pg in peatlands (Schuur et al. 2008).

Schuur et al. (2008) show that permafrost thawing is not just driven by increased air temperature causing CO₂ release due to temperature sensitive decomposition. It includes other energy balance and physical processes (Figure 5). In thawing areas where ground-ice content is high, the risk of regional carbon loss through soil subsidence (thermokarst) and erosion increases (Schuur et al. 2008). While the heterogeneity and adaptiveness of soils makes the parameterization of turnover times a nontrivial task (Knorr et al. 2005; Davidson and Jassens 2006) we know that an increase in the rates of thawing and warmer soil temperatures would result in greater heterotrophic respiration. Assuming a temperature increase of 2 °C, up to 5 Pg C could be released from melting permafrost over a period

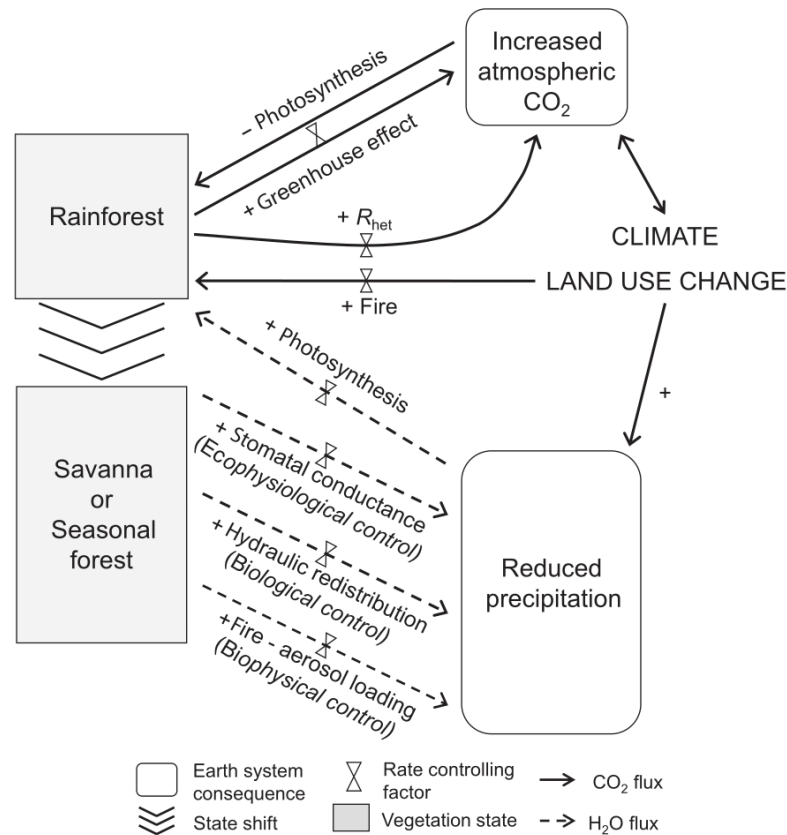


Figure 4 Some of the key interaction that has been postulated to lead to a ‘tipping point’ in the Amazon basin. The CAPITALS indicate driving factors, the boxes are system properties, the arrows indicate effects (with the sign noted), and the bow-ties (X) indicate the controls over these effects.

of 20 years, and up to 100 Pg C over 100 years (Gruber et al. 2004). Therefore, the vulnerability of permafrost carbon stock to temperature increases is potentially the most important feedback of terrestrial carbon within the climate system.

4.09.4 Vulnerability of the Terrestrial Climate Regulation Service to Climate

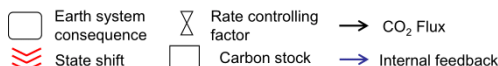
Here we follow the conventional vulnerability assessment approach, which considers vulnerability to be the product of exposure to a threat, sensitivity to that threat, and (lack of) capacity to adapt to the threat. We will consider adaptive capacity within a resilience framework that does not restrict the adaptations to those which keep the system more or less as it was, but allow it to transform to new states.

One ‘threat’ is surface temperature increases in conjunction with either increasing or decreasing water stress, depending on the region. Equally important are the accompanying changes in the probability of extremes of heat and cold, flooding or drought, and the changes in disturbance regimes which they can trigger (Field et al. 2012). Indirect effects include changes in the exposure to pests, diseases, and fire. Surface temperature change is just one of a series of environmental effects, such as rising CO₂, nitrogen and sulfur deposition, land management

practices, and declining biodiversity. Exposure to this syndrome of stresses is spatially variable, but no part of the terrestrial biosphere is immune from them.

In evaluating ‘sensitivity’ we have drawn on two ideas developed above, the form (shape) of the relationship, and the sign and strength of any feedbacks that exist. Sensitivity is low if a change in the ‘threat’ parameter produced a much less than proportionate change in the outcome of an affected system, and high if the effect is more than proportionate. A concave functional response (one that becomes progressively steeper as the size of the driving threat increases) is initially insensitive, but becomes highly sensitive beyond some point. Convex or saturating functions, on the other hand, become progressively less sensitive. A threshold response is one with an abrupt point at which they become sensitive. Sensitivity needs to be explored over timescales of decades to centuries, given that many of the processes are gradual and the pools can be long-lived (Table 1).

Several approaches have been applied to evaluating the sensitivity of carbon fluxes and pools to climate. Gruber et al. (2004) used a risk-assessment approach incorporating expert opinion. The C⁴MIP experiment (Friedlingstein et al. 2006) used complex climate models with a carbon cycle. Raupach and Canadell (2008) used a less numerically intensive ‘perturbation-based approach’ in which they compare the effects of a disturbance in coupled and uncoupled semiquantitative models.



4.09.4.1 Fire

Variation in the areas burned is responsible for a significant part of the variation in the annual CO₂ balance (van der Werf et al. 2006). Over a course of season, year, or longer term depending on the ecosystem, the terrestrial carbon losses from fires are generally compensated for by gains in biomass as vegetation regrows following a burn, but if changes in land use, land management, or climate affect the frequency or intensity of fires, the recovery may be less than complete, or overcompensate. It is during such periods of regime transition that long-term trends in carbon accumulation change from net uptake to net release, or vice versa (Raupach and Canadell 2008).

Fire can occur in almost all terrestrial biomes, but the current extent of fires and the quantity of carbon consumed are concentrated in the tropical savannas and the boreal forests (van der Werf et al. 2010). The area burned in savannas annually is very large, but the fires consume relatively little fuel per unit area, since they burn mostly dry grass, leaving the trees intact.

Boreal forests are one of the largest world biomes. Some estimates have them storing over one-third of terrestrial biospheric carbon, particularly in the form of forested peatlands (Kasischke et al. 1995). Approximately two-thirds of the boreal forests lie in the Russian Federation, with the rest falling mostly in Canada and Alaska (Wooster and Zhang 2004). The landscape is a matrix of different forest types, each storing differing amount of carbon. Together with differences in the severity of the fire, this affects the total direct carbon emissions from fires in

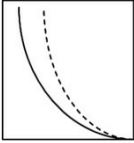
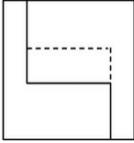
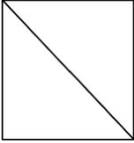
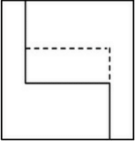
boreal forests by as much as 50%. The emissions in extreme fire years are 37–41% greater, due to soil organic matter combustion (Soja et al. 2007). The probability of more fire in boreal forests in the future is high (Achard et al. 2008), with consequences for the global carbon cycle (Conard and Ivanova 1997; Soja et al. 2007).

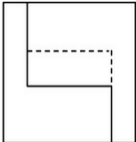
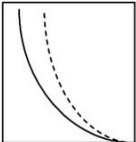
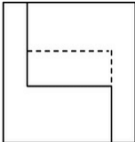
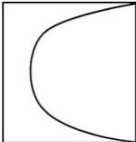
4.09.4.2 Heatwaves

Episodes of above average temperature with or without below average rainfall have the potential to significantly alter carbon fluxes and stocks. For example, Europe experienced a heat wave in the summer of 2003, with July temperatures up to 6 °C above long-term means and annual precipitation deficits up to 300 mm year⁻¹, about 50% below the average (Ciais et al. 2005). A significant reduction in gross primary productivity (GPP) was experienced throughout the continent (Ciais et al. 2005). The productivity of the temperate forest and grasslands ecosystems (Ciais et al. 2005; Granier et al. 2007) and croplands (Granier et al. 2007) Europe-wide was affected. A dramatic reduction in crop yield occurred in France, Italy, and south Germany. Tree radial growth was reduced especially in the year following the drought (Granier et al. 2007).

Both autotrophic and heterotrophic respirations were controlled by water availability to varying degrees across Europe (Grainer et al. 2007). Although 2003 is not the driest year on record, the impacts of the water stress was amplified by the high summer temperatures and soil water deficits carried

Table 1 A classification and evaluation of vulnerabilities, based on the expert opinion of the authors, informed by a review of the literature. For a definition of terms, see the text

<i>Driver of change ('Threat')</i>	<i>Affected system</i>	<i>Sensitivity and form of relationship</i>	<i>Adaptive capacity</i>	<i>Vulnerability outcome</i>
Changes in surface temperature	Carbon in non-wetland, non-frozen soils	High and concave 	Microbial communities change, but respiration still increases with increased temperatures	High
	Carbon in permafrost soils	Very high and controlled by a threshold 	None	Very high
Increasing or decreasing water stress	Wetland soils (peats)	Convex for further wetting of wet systems, threshold for drying below limit for wetland persistence 	Loss (or gain) of C compensated by decrease (increase) in CH ₄ emission	Medium
	Net primary production	Linear, with a threshold for extreme droughts 	Results in long-term species composition shifts but NPP remains affected. Higher diversity helps	Medium
Extreme wind and rain events	Forest biomass	Threshold effect where winds exceed bending or root strength tolerance 	High recovery in systems with a history of exposure, occurs through succession	Low

Fires	Biomass, especially of trees, and litter layers or peat	Threshold effect for unadapted systems, concave for adapted systems		Replacement by fire-adapted vegetation, but net reduction of stored C	High
Pest outbreaks	Biomass and net primary production	Concave, thresholds for some pests; interaction with fire		Long term re-equilibration between predators and prey. Higher diversity may help	Medium
Land use change	Soil and biomass C	High, often a threshold effect use type changes rather than use intensity		High adaptive capacity through policy (e.g., REDD) and innovation	High
N and S deposition	Tree biomass	Hump-shaped curve – initial stimulation, depression at high cumulative levels		Long-lasting ecosystem function, composition and structure changes. Technological adaptive capacity to reduce deposition	Medium

over from the previous spring (Ciais et al. 2005). Because both GPP and the respiration fluxes were reduced, the absolute decrease in NEE was smaller than the reduction in GPP (Ciais et al. 2005; Grainer et al. 2007). The consequence for the net carbon balance was that European temperate forests became a strong net source of carbon dioxide ($0.5 \text{ Pg C year}^{-1}$), which reversed the effects of four preceding years of net ecosystem carbon sequestration (Ciais et al. 2005).

An analysis of the northern hemisphere terrestrial carbon fluxes shows that since 1994, the enhanced carbon uptake due to a progressively earlier spring has been canceled by decreased uptake during summer, due largely to hotter and drier summers in the mid and high latitudes (Angert et al. 2005). Enhanced productivity with warmer temperatures and longer growing seasons might be counterbalanced by more frequent heat and drought events. Thus, although the forests of the world currently constitute a large sink (Yude et al. 2011), the reliability of this sink under hotter, sometimes drier, more variable climates could be spatially and temporally more variable.

4.09.4.3 Increases in Rainfall, Decreases in Rainfall, and Prolonged Droughts

The interannual variability of the growth in atmospheric carbon dioxide is largely due to variability in the terrestrial term. Most of that variability is located in the tropics, a large fraction of which is in Africa. The variation is strongly associated with climate indices such as ENSO. It is inferred that much of the variation is due to the source or sink behavior of the tropical season savannas rather than the continuously moist evergreen rainforests. A multi-year record of carbon fluxes exists for the flux station at Skukuza in South Africa that supports this argument. The site is a carbon sink during wetter-than-average years, and a source during drier than average years. Overall, over the period of record, it has been a source (Archibald et al. 2009a).

A disproportionate part of the interannual variation in Fraction Absorbed Photosynthetic Radiation (FAPAR) in this mixed tree-grass system is due to the grasses. As has been observed in other savannas, the tree leaf area duration varies little from season to season, but the grass leaf area is highly dependent on rainfall (Archibald and Scholes 2007). Contrary to conventional wisdom, the area burned in African savannas and the amount of biomass consumed by fire both decrease in dry years, because the available fuel decreases (Archibald et al. 2009b).

4.09.4.4 Windstorms

Windthrow of trees is one of the most common disturbance dynamics in forests. An example involving a tropical hurricane in Puerto Rico is described by Walker (1991) and its carbon cycle consequences are explored by Sandford et al. (1991). They found a net release of carbon dioxide resulting from the loss of foliage and the increase in the litter and dead wood pools, but a relatively rapid return to net sink status as the rapidly growing trees establish a complete cover. Long-term simulations suggest that the forest can continue to be a net sink of carbon, on average, even with a major hurricane disturbance once a century.

Knohl et al. (2002) measured carbon exchange from an area of Siberian temperate forest 2 years after a major storm disturbance. They found a daytime sink, but a larger respiration source once the nighttime fluxes were added. From the quantity of downed timber and the observed log decay rate, they concluded that the storm event would have consequences for the carbon balance of the site for decades. Kramer et al. (2004) followed the carbon dynamics across wind-disturbed stands of various ages in Alaska and found remobilization and transport of carbon between fractions in the soil and vegetation.

These examples suggest that carbon stores are relatively robust to windthrow disturbances, but if the frequency of severe windstorms were to increase, the mean landscape stored carbon would be somewhat reduced.

4.09.4.5 Insect Attacks

The impact of insects on forest carbon dynamics is not only felt through the reduction in carbon uptake due to canopy loss, but also through increases in future carbon dioxide emissions from the decay of the killed trees (Kurz et al. 2008). In western Canada, the unprecedented severity and extent of the Mountain pine beetle (*Dendroctonus ponderosae*) outbreak experienced over the last decades has been attributed to two major factors: (1) a larger extent of suitable pine hosts due to forest stand maturation and (2) an expanded distribution range of the Mountain pine beetle due to warmer and drier weather (Kurz et al. 2008).

4.09.5 Ways of Reducing Vulnerability

Vulnerability can in principle be reduced by addressing any of its three components: reducing the level of the threat; reducing the sensitivity of the system; or increasing the adaptive capacity. Reducing the threat, for instance, requires policy approaches to minimize the impact of human climate forcing on the climate system (e.g., Metz et al. 2007; Pielke 2010), since the scope for reduced sensitivity and increased resilience has limits: mitigation efforts must be sufficient to keep the terrestrial biosphere within an adaptable domain. The following broad classes of actions have been proposed as ways of reducing sensitivity or increasing resilience.

4.09.5.1 Preemptive Microdisturbances

A hypothesis of resilience theory (Gunderson and Holling 2002), paraphrased in the context of carbon storage, is that systems cycle through phases of accumulating biomass and connectivity, leading to increased vulnerability, collapse, reconfiguration, and rebuilding. The implication is that these are inevitable phases, but the rate of progression through them could be manipulated by management. One approach is to deliberately initiate small destruction–reorganization cycles during the accumulating phase, in order to extend it and preempt a catastrophically large reorganization. In some ways this is similar to the ‘intermediate disturbance hypothesis’ (Connell 1978), which suggests that biodiversity and ecosystem function are maximized neither under a zero disturbance, nor under a maximal disturbance regime, but under some

intermediate regime. A practical example is the use of small, frequent fires in forest or woodland management to prevent the build up of fuel that would eventually lead to a large fire that consumed more biomass in total, or damaged the capacity of the system to recover (Richards et al. 1999; Beverley et al. 2009).

4.09.5.2 Maintaining Ecosystem Function and Biodiversity

Preserving the integrity of ecosystem processes has been suggested as a necessary condition for maintaining both the buffering capacity of ecosystems (e.g., reducing sensitivity) and adaptive capacity (e.g., Smithers and Smit 1997). It is often inferred that maintaining biodiversity (in its broad sense – not only what species are present, but their relative abundances and within species genetic variability, as well as the landscape-scale structural, compositional, and functional diversity of ecosystems) is a proxy ecosystem integrity. The exact links between the various aspects of biodiversity and the dimensions of ecosystem function remain unclear, but there is empirical evidence that they exist (Zavateła et al. 2010). They may account for only a portion of adaptive capacity and buffering, may relate more to the diversity of functional groups rather than species per se, and are likely to be saturating functions, which level off at levels of biodiversity substantially below the maximum (Díaz et al. 2005).

4.09.5.3 Reducing Vulnerability to Social Change

It is increasingly indefensible to regard ecosystem change as divorced from social change. In reality they are intimately linked as social–ecological systems (Folke 2006; Chapin, this volume). Very frequently the change dynamics are initiated within the human part of the system, or the feedback processes operate via the human system. Land use change, leading to land cover change, is a major vulnerability of soil and biomass carbon (Marland et al. 2003). It is principally controlled by demographic, political, and economic factors (Lambin et al. 2001), but there may in the century timescale be climate feedbacks, as areas formerly suitable for certain uses become unsuitable, and new areas become suitable. The key vulnerability reduction actions are related to policy: what land uses may be practiced, who has rights to practice them and with what security of tenure; who pays for externalities such as those due to human climate forcing; and what prices (including subsidies) are paid for the various land-based commodities. The general recommendations for increasing the resilience of social-economic systems involve creating a sense of local ownership, stewardship and reward, effective multiscale participatory governance, and enhancing adaptive capacity through learning and innovation (Berkes et al. 2003).

4.09.5.4 Dealing with Vulnerability in the Climate Service Market

The discussion which follows is not about reducing the fundamental vulnerability of land-based climate regulation services, but on how to establish a viable market-based service for carbon in the presence of that vulnerability. In particular, it addresses the problem of the impermanence of stored carbon on land.

There are two main approaches. The first is based on portfolio theory. By increasing the scale of projects, including different types of projects that are assumed to have uncorrelated risks, and taking to market a service that is smaller than the total amount within the portfolio, it is possible to reduce the variability of carbon services product below the fundamental variability of the service at any given location (Laurikka and Springer 2003).

The second approach is to treat the climate service as a renewable short duration contract, rather than a permanent asset. In other words, the client rents the service on a year-by-year basis for as long as it persists, rather than purchasing it outright. This is consistent with the observation that the terrestrial carbon storage service is a flux (a change in stock) rather than a stock itself. This is the logic behind the field of PES, of which REDD is a specific example relating to the climate service and also to biodiversity and other ecosystem services (Kindermann et al. 2008).

4.09.6 Trade-Offs between Climate Regulations and Other Ecosystem Services

When single-mindedly maximized, provisioning services (such as carbon sequestration) occur at the detriment of competing provisioning services, most regulating services, and sometimes cultural services (Millennium Ecosystem Assessment 2005). For instance, if a monocultural tree plantation were established in a formerly biodiverse and water limited area, the river flow would decrease, and biodiversity would be lost, as would the opportunity to grow other crops or to graze the land. If maximum stored carbon were the goal, the production of timber from the plantation would be reduced.

Such stark, mutually exclusive trade-offs are not inevitable. It is usually possible to get some level of climate service from a landscape without completely compromising other land use objectives. There are even cases of synergy, where management for the climate regulation service is also beneficial for other services. For example, the REDD+ notation suggests that protection of the climate regulation service provided by tropical forests can also confer biodiversity, water, and livelihood benefits.

4.09.7 Conclusions

The climate regulation service provided by terrestrial ecosystems is real and substantial. It occurs through a variety of mechanisms, whose relative importance varies from place to place. The carbon storage mechanism at global scale has increased over the past few decades, largely through autonomous mechanisms (in other words, not as the result of deliberate human actions). The terrestrial carbon sink cannot continue to grow indefinitely. There are several feedback processes, which may cause it, perhaps within decades, to change from a sink at the global scale to a net carbon source, even though at local or regional scale some areas may remain as sinks.

The terrestrial carbon storage service is in general relatively vulnerable, both to climate itself and to associated environmental change factors such as changes in fires, windstorms, and pest outbreaks. It is also vulnerable to economic and political

factors, which may or may not be linked to climate. The magnitude of the carbon storage service can be moderately increased at local scale through management actions, and at regional and global scale through policy decisions, but doing so tends to increase the vulnerability of the service. The vulnerability of the service can probably be significantly reduced, but not eliminated through a combination of management and policy actions.

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Chapter 2 Preface

Assessing water ecosystem services in alternate states of a dryland ecosystem in the Eastern Cape of South Africa

This chapter assesses *P. afra* abundance at a landscape scale and uses an analytical approach to compare the freshwater ecosystem services provided by intact and transformed catchments.

This chapter was written with contributions from the following people, and their affiliations at the time their contribution were made are listed below:

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A breakdown of the author contributions is as follows:

The conceptualization of this work; writing; GIS work and figure creation; data acquisition, management, and analysis was conducted by the candidate.

Alecia Nickless helping with the initial R coding for the extreme value theory portion of the analysis.

The work in this chapter was initially included the light-use efficiency Net Primary Production model developed at the CSIR and model outputs for the plant functional types of the thicket. The model was developed by R.J. Scholes, S. Archibald and the candidate. R.J. Scholes, S. Archibald read the work in this original format and made suggestions regarding structure and model description.

B. Reyers read the work in this original form and made suggestions to the structure and references.

Subsequently, the water-related aspects of the work were extracted and form Chapter 2 of this thesis. Both S. Archibald and R.J. Scholes have proof read and commented on the final version as preparation for submission for publication.

Chapter 2: Assessing water ecosystem services in alternate states of a dryland ecosystem in the Eastern Cape of South Africa

Introduction

In many developing countries, agriculture and pastoralism contribute significantly to both local livelihoods and national economies. The livestock sector, for example, makes up 50 to 80% of developing country Gross Domestic Product (World Bank 2007). In turn, these are some of the most ecosystem service dependent land uses, requiring sustained levels of services like water supply, forage production, pollination, nutrient cycling, erosion protection and primary production. Dryland systems are characterized by low and highly variable amounts of rainfall and high levels of evaporative demand. These attributes combine to limit the type and productive potential of livelihood systems and land use options open to inhabitants (Mortimore et al. 2009). The levels of human wellbeing in drylands lag well behind those of the rest of the world (Safriel et al. 2005). Improving the wellbeing of dryland populations will depend on informed and sustainable management (and enhancements) of the ecosystem services underpinning agricultural and pastoral livelihoods (see Mortimore et al. 2009; Middleton et al. 2011); and in particular, those that relate to water.

There are several global initiatives to improve the monitoring of dryland ecosystem services. This includes a proposed Global Drylands Observing System (Verstraete et al. 2011) and past and current regional projects such as the BIODiversity monitoring Transect Analysis in Africa (BIOTA AFRICA) project. There is a growing set of tools for dryland policy and management actions (Reynolds et al. 2007, 2011; Sommer et al. 2011) yet over a decade has passed since the United Nations Convention to Combat Desertification (UNCCD) came into effect and its Parties have no accurate estimates of the extent of desertification (Reynolds et al. 2011). Data availability remains a serious constraint (Berry et al. 2009), as do the diversity and usefulness of indicators (Layke et al. 2012).

Ecosystem services in drylands are understudied in existing global monitoring frameworks (Safriel et al. 2005). Of all ecosystem services, the regulating and supporting services in particular lack useful indices which are easy to quantify and implement (Layke et al. 2012). These gaps in our ability to measure and monitor dryland ecosystem services make it hard to inform decision makers of the possible consequences of particular land use decisions and interventions.

We focus on freshwater ecosystem services because these are a critical resource in their own right, as well as playing a fundamental controlling role in the delivery of other ecosystem services such as forage and animal production, fuel wood, medicinal plants and climate regulation (Safriel et al. 2005;

Reyers et al. 2009; Mortimore et al. 2009; Middleton et al. 2011). Here we highlight three functionally different aspects of freshwater as an ecosystem service in dry lands, develop landscape-level methods for assessing them, and demonstrate their use in a partially transformed arid landscape, undergoing restoration, in the Eastern Cape of South Africa.

Water regulation in drylands

The regulation of hydrological flow refers to the quantity and duration of water held in the soil profile (Sandström 1998), which is both a cause and consequence of the partitioning of the incoming water supply into that which supports vegetation growth, that which evaporates without passing through a plant, that which recharges groundwater and that which runs off into drainage system, either usefully or destructively. The amount of vegetation cover (together with rainfall, soil and topographical characteristics) impacts the timing and magnitude of runoff, flooding, and recharge by controlling the amount of infiltration and transpiration at a site (D’Odorico and Porporato 2006). Increased leaf area duration (often of fast-growing invasive species) has been shown to result in increased transpiration, and thus reduce recharge and river flows (Bosch and Hewlett 1982; Stednick 1996; Dye and Jarman 2004).

In drylands the extent and condition of the exposed soil surface is a key factor controlling whether rainfall infiltrates the soil or runs off in the form of brief, intense floods in otherwise ephemeral river systems (D’Odorico and Porporato 2006). The vegetation and the river may be seen as ‘competing’ for the limited water supply, but in dry environments increased vegetation cover and water in the river or aquifer may not always be antagonistic objectives. Vegetation cover promotes infiltration (for instance, see Mills and Fey 2004; Ilstedt et al. 2016), leading to recharge of aquifers and more gradual and usable release of water to the rivers as baseflow. These patterns have been conceptualized by Huxman et al. (2005) but have not been well tested, particularly for arid and semi-arid systems.

From an ecosystem service perspective, the most important stream flow features are: (1) the low flow; (2) the destructive flood peaks, and (3) the quantity of useful water (i.e., of quality fit-for-use and able to be captured). We have conceptualised this in Figure 1. Low flow meets human, livestock and biodiversity needs in the dry season and also increases yields for storage dams (Reyers et al. 2009). However, the low flow may be zero for extended periods in the intermittent rivers that are characteristic of arid lands (Smakhtin 2001)

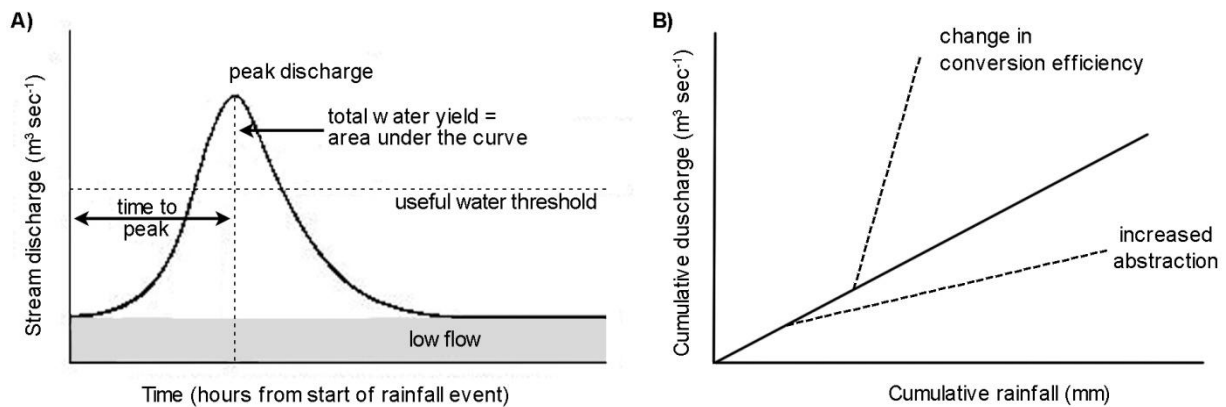


Figure 1. A) An individual storm hydrograph showing idealized behavior and ecologically relevant metrics. Following a storm, the volume of water flowing in the river starts to rise due to the rapid process of laterally transferred run-off and the slower process of infiltrated subsurface flow, building to a peak in streamflow. The flow attenuates gradually to some low flow (which may be zero). The integral of the stream discharge curve is the total water yield, but only part of this may be possible to use. Flow rates above a certain threshold may be too dangerous to access, or too turbid to use. The usable flow is therefore the integral that is below both the discharge curve and this threshold. B) A cumulative plot of rainfall and discharge. In untransformed landscapes, the plot should be more-or-less linear (solid line). A deviation from this line is evidence of hydrological change and indicates a change in the efficiency with which the landscape converts rainfall into streamflow. Note: the slope is unlikely to be one.

This case study was conducted in an area of the Eastern Cape Province, in the southern part of South Africa, formerly covered by subtropical thicket vegetation (Figure 2). Agro-pastoral practices over the past two centuries are believed to have transformed over 80% of the former extent of *Portulacaria afra* dominated thicket vegetation, estimated at 4 million ha, to a moderately or severely altered state (Lloyd et al. 2002) (Figure 2). This transformed vegetation has much lower standing biomass (Mills et al. 2005) and biodiversity and does not support high wildlife or livestock numbers (Stuart-Hill and Aucamp 1993; Bothma et al. 2002; Sims-Castley 2002).

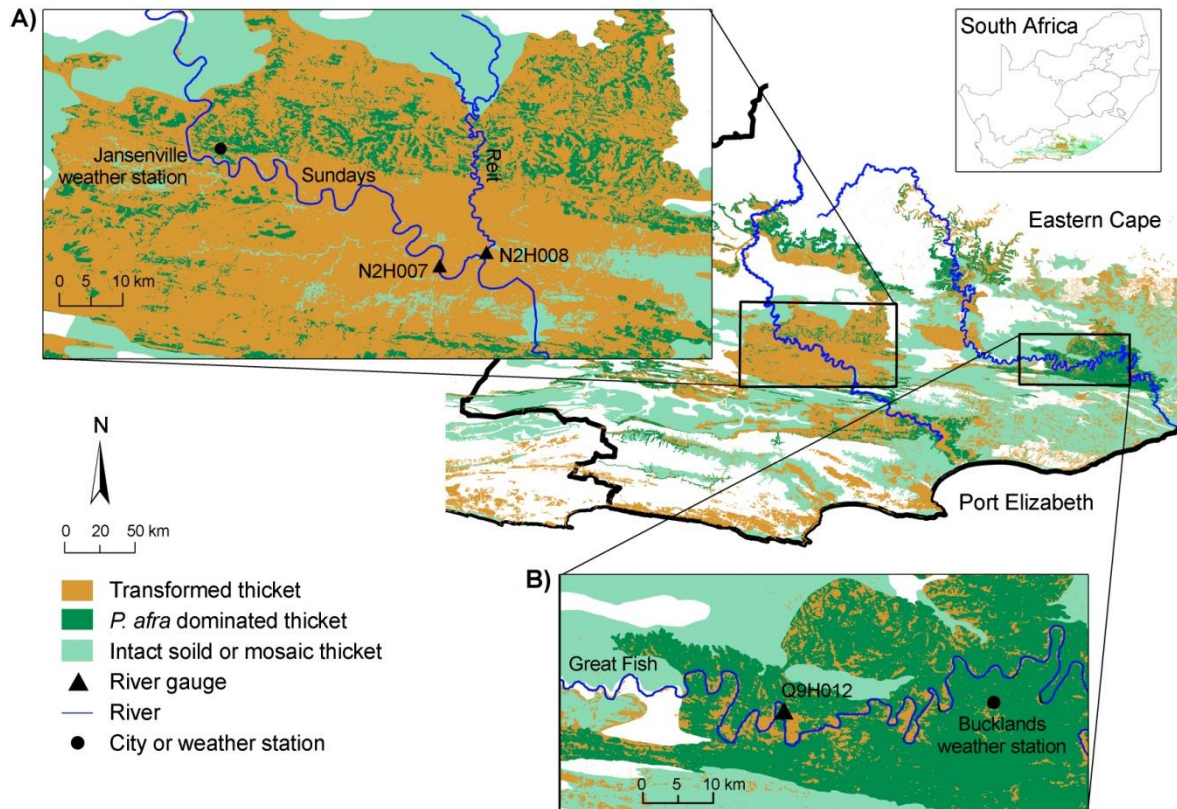


Figure 2. Distribution of thicket vegetation along the southern coast of South Africa in transformed and intact states (Pierce 2003). Insets from the Eastern Cape Province show A) the location of the river gauges selected on the Sundays (N2H007) and Riet River (N2H008) within transformed thicket vegetation, and B) the location of the river gauge selected on the Great Fish (Q9H012) within an intact thicket dominated by the succulent *Portulacaria afra* Jacq.

Assessing water ecosystem services

Paired catchment (watershed) experiments are one of the classical approaches to studying the relationships between vegetation changes and water yield. They compare the flow characteristics of two adjacent or close catchments, one as control, and the other as a land use treatment (Li et al. 2011). While ideal, this approach is often not feasible unless carefully-paired experimental catchments were established decades in the past. More typically, what is available is observed discharge data from river systems, which *a posteriori* are interpreted in relation to the differences in land use within the catchment. Stream discharge records provide an integrated measure of the amount of infiltration, recharge, and available water in the upstream catchment (Smakhtin 2001). In South Africa and most other countries, the ability to assess of water services from this observed data record is restricted due to the limited density of the gauge network, the short duration of datasets,

data gaps, and the lack of gauges operating over the same period of time (Smakhtin 2000). Moreover, changes in vegetation cover often coincide with changes in water extraction or other modifications to flow, which makes it difficult to use these data for assessing the impacts of individual drivers on freshwater ecosystem services.

We analyzed changes over time within single catchments with different land use histories but within the same broad climatic and potential vegetation zone to test the effect of transformation on water regulation.

Methods

Study area

Thicket vegetation spans a rainfall range of 250 to 800 mm yr⁻¹, with most in the lower part of this range. The rainfall is erratic, with a broadly bimodal seasonal distribution, peaking in spring and autumn. In its pre-transformed state the vegetation is characterized by a dense layer of evergreen and weakly deciduous shrubs and low trees (2 to 5 m in height) which are often spinescent; several of the dominant species are succulents. The thicket has several distinguishing characteristics: (1) the grass component is noticeably sparse in closed canopy thicket; (2) the system is not fire prone; and (3) succulent plants are prominent. See Cowling et al. (2005) for a description and history of the vegetation.

The thicket growth form suggests that there has been a long history of mammalian herbivory (Kerley et al. 1995). The biome presently supports an abundant and diverse mammal fauna, including 28 large mammal herbivores including the African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*) and kudu (*Tragelaphus strepsiceros*) (Kerley et al. 1995; Cowling et al. 2005). In common with drylands generally (Millennium Ecosystem Assessment 2005a), the succulent thicket is sensitive to over-utilization by domestic livestock (Hoffman and Cowling 1990; Stuart-Hill 1992), which largely replaced indigenous ungulate populations by the early 20th century (Milton and Dean 1995). The drier forms of thicket (<450 mm yr⁻¹; Vlok et al. 2003) dominated by the arborescent stem and leaf succulent, *Portulacaria afra* Jacq., are particularly vulnerable to transformation (Stuart-Hill 1992) to a sparsely-covered shrubby grassland dominated by weakly perennial and sometimes unpalatable plants, including invasive species such as *Atriplex* spp. and *Psilocaulon pagae* (Lechmere-Oertel et al. 2005).

Catchments and Gauges

Although there are in excess of one hundred gauged catchments in this region, only a small subset were useful for this assessment. We chose two transformed catchments in the area east of Jansenville and one intact catchment in the Fish Valley Thicket (Vlok et al. 2003) (Figure 2). We chose gauging stations least likely to be affected by water transfer schemes that move large quantities of water between catchments (Table 1). The stream orders of the intact and the larger transformed catchments are roughly comparable, but it was not possible to find a small, gauged, intact catchment for comparison with the small transformed catchment.

Table 1. The attributes and data availability of the catchments used for this case study

Catchment		River name	Gauge name	Total upstream area of vegetation transformation		Duration of gauge timeseries	Weather station used	Modifications to flow ^a
Vegetation	Size ^a (km ²)			Quaternary catchment (%)	Tertiary catchment (%)			
Transformed	341	Reit	N2H008	55	N/A	1979 - present	Jansenville	downstream
Transformed	13 428	Sundays	N2H007	85	70	1978 - present	Jansenville	downstream
Intact	23 067	Great Fish	Q9H012	14	10	1932 - present	Bucklands	upstream from 1975 ^b

Notes:

- South African Department of Water Affairs (<http://www.dwaf.gov.za>)
- Water transfer scheme from Orange River into Great Fish, a large proportion of this is transferred upstream to the Little Fish (at Elandsdrift weir via Cookhouse tunnel, 1978) and Sundays River (1987, completion of De Mistkraal Weir and Skoenmakers Canal) mainly because of abstractions for irrigation. The mean annual discharge of the lower river has changed little (O'Keeffe and De Moor 1988).

Analytical methods

Flow duration curves

The flow duration curve (FDC) for a catchment provides a graphical representation of streamflow variability over time: it summarizes the complete range of flows and the proportion of time a given streamflow is equaled or exceeded in the period of measurement (Smakhtin 2001). Daily and annual flow duration curves (FDC) were derived for each catchment time series, from 1 January 1982 to 31 December 2010, a period of 29 years.

Periods of zero flow were included in the FDC. All non-zero flows are normalized by rainfall and catchment area for each catchment; thus the units of the resulting curves are cubic meters per second per mm rainfall per square kilometer and comparable to one another. Flow characteristics, the duration of zero flow periods, the quantity of 'useful' water (taken as the flow equaled or exceeded 10% of the time) and damaging floods, can be evaluated by inspecting the shape of the curve and the fraction that is contained in the upper and lower tails. The analysis was performed using the R statistical software (R Core Team 2015), using the hydroSTM package (Zambrano-Bigiarini, 2012).

Extreme Value Theory

The occurrence of rare but damaging floods is best evaluated using extreme value theory (EVT). In EVT, maximum (or minimum) events in a data set are the focus, rather than the mean, and often need to be extrapolated from short-term records which do not contain examples of such extreme events. The daily streamflow data are fitted to the Generalized Extreme Value (GEV) distribution, described by three parameters: location (μ), scale (σ), and shape (ξ). Of these ξ gives information about which extreme value distribution is most suited to the data (de Haan and Ferreira 2006).

We used the annual maximum method of return time estimation (see Embrechts et al. 1997). The annual maxima were extracted from the daily record of discharge rate data between 01 January 1982 and 31 December 2010. A GEV distribution was fitted to each dataset, the distribution parameters were extracted, and a return level plots were constructed. The analysis on these datasets was performed using the R statistical software package (R Core Team 2015), using the evd (Stephenson 2002) and extremes (Gilleland and Katz 2011) packages.

Run off fraction and fraction yield

Intact and degraded sites were also compared using their runoff yield fraction: the cumulative annual streamflow (Mm^3) for the period 01 January 1982 to 31 December 2010, plotted against the cumulative product of annual rainfall ($\text{mm}/1000$) and size of the catchment area (km^2). Thus the units of the product are also Mm^3 , which we term 'accumulated catchment rainfall'. The slope of this relation is the fraction of water falling on the catchment which is yielded as streamflow. This fraction yield was calculated on a year-by-year basis, as the cumulative annual streamflow divided by accumulated catchment rainfall. We assume that the weather station records (Figure 2) are representative of the rainfall levels experienced in the different catchment. Rainfall was normalised by catchment area size. The analysis on these datasets was performed using the R statistical software package (R Core Team 2015), and plotting was done using the ggplot2 package (Wickham 2009).

Results

Flow duration curves

The steep tails in the flow duration curves from the three catchments is typical of streams in semi-arid area (Figure 3) (Peters 1994). The steep slope of the high-flows (left hand tail) implies little surface storage and flows resulting mainly from rainfall events (rather than from the steady drainage from aquifers). The steep slope at low-flows (right hand tail) indicates minor groundwater contribution to low flow.

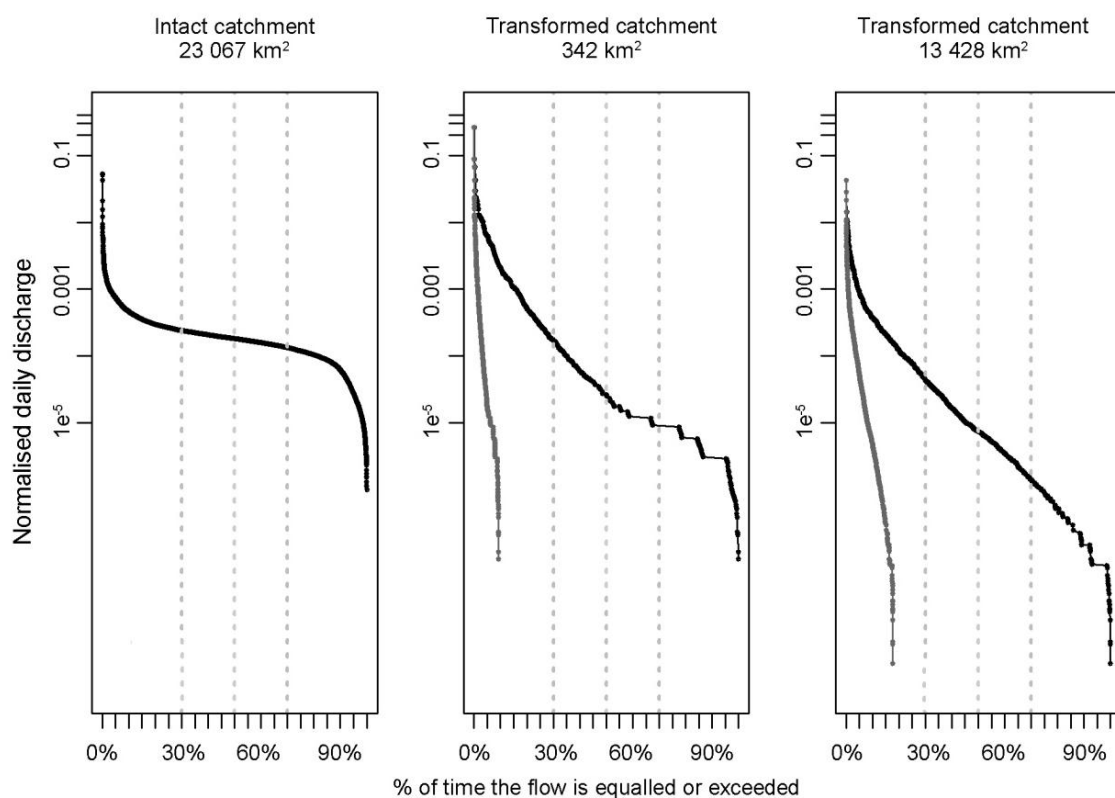


Figure 3. Flow duration curves on a logarithmic axis (1982-2010). Daily discharge is normalized by the product of catchment size and rainfall. The gray line shows the curve when days of zero flow are included; this curve is missing from the first plot because there were no zero flow days in the intact catchment. The vertical dashed lines mark the flow exceeded 30%, 50% and 70% of the time (Q_{30} , Q_{50} and Q_{70} respectively).

The intact catchment has a higher and more stable flow evidenced from the strong S shape to the body of the curve. The useful water yield, approximated as the flow exceeded 50% of the time (Q_{50}), is greatest in the intact catchment. The high- and low-flows (taken in this case as Q_{30} and Q_{70} respectively) are within an order of magnitude of one another in the intact catchment, but greater than an order of magnitude in both transformed catchments (Figure 3).

Zero flows comprise greater than 80% of the record in the transformed catchments (gray curves in Figure 3). The steeper and disjointed low-flow tails of the transformed catchment FDCs suggest reduced infiltration and larger contribution of immediate run-off to flow relative to the intact catchment. The larger transformed catchment has lower and more variable low-flows. Despite a larger catchment, the river flow is more variable, perhaps due to the larger proportion of transformed vegetation upstream of the gauging station (Table 1).

Extreme Value Theory

The analysis of the catchment peak discharge using EVT also shows strong differences between the transformed and intact sites (Figure 4). Large storm peaks are more likely in the transformed catchments. As would be expected, larger discharge events occur more frequently in the large catchment than in the small one (Figure 4B and C).

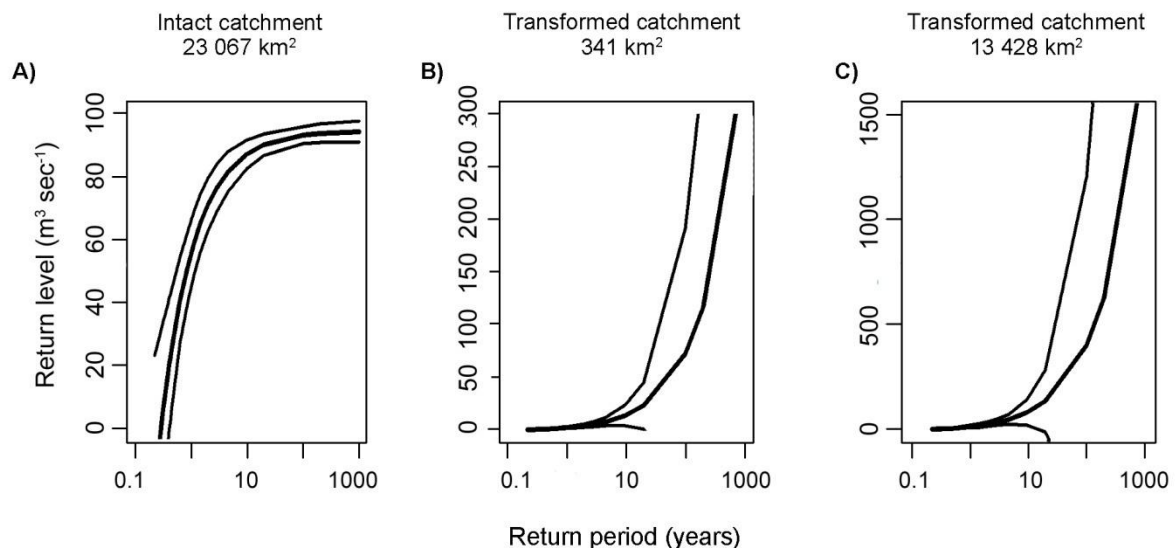


Figure 4. Statistical analyses of hydrograph records for 01 Jan 1982- 31 December 2010. The return level as a function of return period for the discharge rates. The curves represent the graphic visualization of the shape parameter (ξ) of the fitted Generalized Extreme Value (GEV) distribution. The three curves per plot are the mean and the upper and lower confidence limits. For the intact catchment A) $\xi < 0$ (estimated value -0.7) and the plot is convex with asymptotic limit. This means the probability of a large flow event approaches zero. For both transformed thickets B) and C) $\xi > 0$ (0.6 and 1.0 respectively) and the plot is concave and has no finite bound. Thus extreme flow events are more likely.

Catchment conversion efficiency and yield

The slope of the cumulative rainfall versus cumulative rainfall plot progressively increases over time in the transformed catchments (Figures 5B, C) which suggests a decrease in water retention by the catchments as they became more transformed. In contrast, the intact catchment (Figure 5A) remains near-linear throughout the observation period. There are deviations from the general observed pattern of increasing conversion efficiency, suggesting that other processes are simultaneously occurring in the transformed catchments, such as the building of runoff-retaining farm dams, or the diversion of water for irrigation.

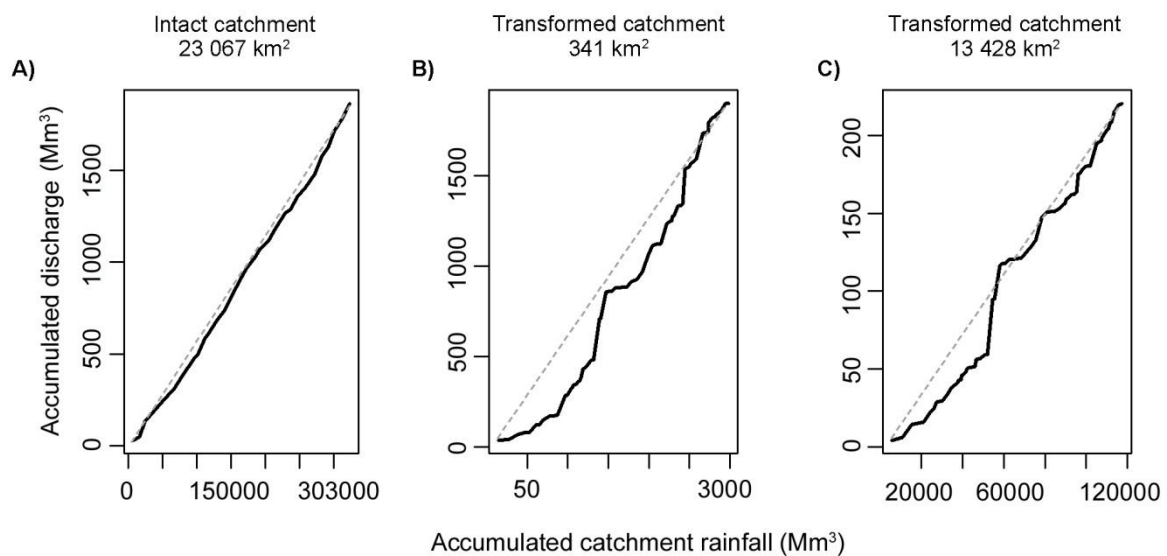


Figure 5. Plots of cumulative discharge against cumulative rainfall. Note: rainfall has been divided by 1000 for plotting. The grey dashed line joins the first and last point, which is the average catchment fraction yield (see Figure 6).

The overall yield is higher and more consistent (mean 0.02, $\pm$ 0.005 (1 SD)) in the intact catchment (Figure 6) supporting previous results showing fewer extreme discharge events (Figures 3 and 4).

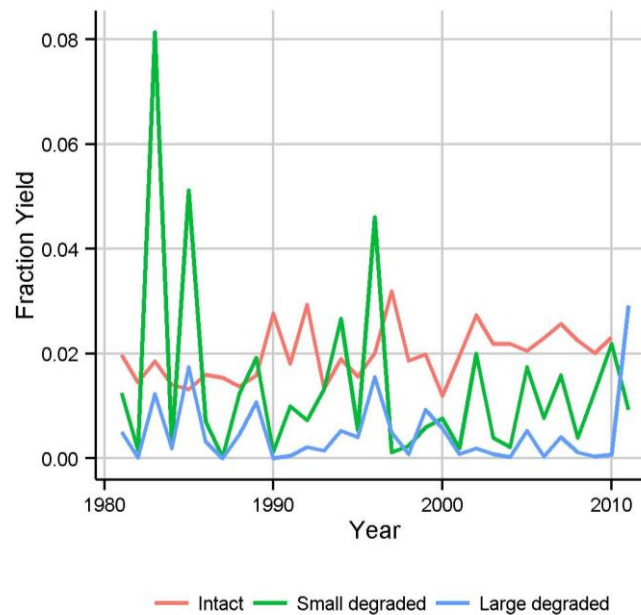


Figure 6. The year-by-year fraction yield for intact and degraded catchments. Deviations from a linear relationship suggest change in the hydrological parameters over time, as transformation progresses. Note: the y-axis is dimensionless, and has been divided by 1000 for plotting clarity.

Yield from transformed thickets is lower and much more variable (small degraded: mean 0.01, $\pm$ 0.017; larger degraded: 0.004 ± 0.006 ; Figure 6). The smaller catchment often converts a larger fraction rainfall to stream flow, owing to a bigger contribution from lower order streams (Figure 2), however, the resulting flow is likely to be less useful to people because it is likely to carry more sediment.

Discussion

In this semi-arid system, a dense evergreen thicket cover results in a higher total yield of water as a fraction of rainfall, fewer extreme high flow events, and a higher volume of low-flow in comparison to landscapes thought to represent degraded former thickets. The higher leaf area duration of the thicket cover may lower water yields to the river system through two processes: high interception – the highest recorded in the literature at 30-51% (Cowling and Mills 2011); and a longer period of transpiration. On the other hand, the evaporation from the soil surface under intact thicket is probably lower than in the degraded catchments (due to shading and litter-mulching in the former (van Luijk et al. 2013). Furthermore, the instantaneous transpiration rate of succulent and sclerophyllous trees is likely to be lower than that of grasses, and the thicket cover appears to increase infiltration (Mills and Fey 2004) and extend low flow (van Luijk et al. 2013). The latter trend is likely due to decreased raindrop energy due to the high interception rates, as well as a greater soil

aggregate stability of the more organic-rich soil beneath the canopy compared to soil properties outside the canopy (Lechmere-Oertel et al. 2008; Mills and Cowling, 2010; Mills and Fey, 2004). The net outcome on the various aspects of the water service reflects the balance of these effects.

The influence of vegetation cover on streamflow in dryland areas with a low mean annual rainfall is highly variable (Wilcox 2002; Görgens and van Wilgen 2004; Huxman et al. 2005). Our results indicate that the reduction in the canopy species and canopy cover is associated with a in the decrease fractional water yields of the catchment. Despite an increasing efficiency in converting rainfall into streamflow, the amount of useful water in the transformed catchments is less because it has a reduced baseflow or low flow, and the presence of storm peaks likely to carry more eroded sediment. Laboratory and *in situ* comparisons of soil properties and hydrological attributes of thicket vegetation (Mills & Fey 2004a; van Luijk et al. 2013) the notion of increased erosion and thus reduction in the usable fraction.

Drivers of transformation

The process of vegetation transformation has an indeterminate start date, but was active during the period of hydrological record. Literature reports concerns about vegetation shifts and declining productivity in the Eastern Cape in the early to mid 1990's (Hoffman & Cowling 1990; Stuart-Hill 1992; Stuart-Hill & Aucamp 1993; Milton & Dean 1995). In South Africa, small stock population (goats and sheep) peaked at 50 million in 1930, due to increased water provision and fencing around farms, but decreased and remained stable at 35 million from 1933 (Milton & Dean 1995). Thereafter, declines in population numbers are inferred to show reduced productivity. However, the small stock grazing capacity remained a huge overestimation of the carrying capacity (Milton & Dean 1995).

Both degraded sites sit closed to Jansenville, where fine hair Angora goats are selectively bred (Snyman 2004). This livestock industry supplies a large proportion of the sheep, goats and cattle reared in South Africa. Nearly all of South African exports of mohair are from the Eastern Cape, which amount to over half of the world export production. Annual production of mohair in South Africa had reached more than 12 million kg by the late 1980s, but fell to 2.3 million kilograms by 2012, reflecting a huge fall in the number of goats in South Africa over the same period (Sender 2016).

It is hard to attribute the change in stock numbers to drier/wetter climate trends or the land-cover change signal at catchment level without longer hydrological and climate timeseries data, as well as stock counts. Reconstructions of past climate back to the 1800s indicate that periods of low rainfall (Vogel 1989), including the influences of the Southern Oscillation (Lindesay & Vogel 1990), have

been a consistent feature in the region. Trade-offs are inherent in the supply of freshwater services (Brauman et al. 2007). In this case, there has been a historical trade-off between the provisioning services supplied by Angora goats (and likely sheep and cattle), and the freshwater services supplied by thicket vegetation.

A view on restoration

Restoration of degraded thicket does not occur spontaneously within a reasonable period of time (Sigwela et al. 2009; Vlok et al. 2003), even with complete resting from browsing (Lechmere-Oertel et al. 2005). In recent years several programs have been initiated with the aim of restoring indigenous *P. afra* dominated thicket, with a principle motivation being the capture and storage of atmospheric CO₂ as a climate change mitigation measure (Marais et al. 2009, Mills et al. 2015). The results of this study suggest that restoration towards an intact state could improve freshwater services as well. This conclusion is an inference, given the ‘quasi-paired’ nature of the experimental design. In other words, we cannot be absolutely sure that the catchments we compared differed only in their land use history: they may have had inherent differences in their flow characteristics due to climate, geomorphology or soil differences, despite our best attempts to control for these factors.

Recent work in West Africa reveals that it is intermediate levels of cover which see the best trade-off between water percolation (and hence groundwater recharge) and plant water use (Ilstedt et al. 2016). An analysis of the stream flow data provided by gauge network, in terms of both overall catchment canopy cover and *P. afra* canopy contribution, could offer interesting insights as to whether there is an optimum tree cover density for the semi-arid thickets.

The ecosystem service assessment approach

Many coupled social-ecological systems are thought to be able to occupy qualitatively different states (Walker and Meyers 2004; Reynolds et al. 2007, 2011), and some of the best examples are drawn from drylands (Fraser et al. 2011). Taking an ecosystem service approach to dryland management allows a shift to a more holistic view of the benefits delivered by the different ecosystem states (Reynolds et al. 2007; Verstraete et al. 2009). Moreover, freshwater services and the way land cover changes affect hydrological attributes is a particularly effective approach for leveraging traditional science into decision making (Brauman et al. 2007).

Conclusions

The methods outlined in this paper provide a first approximation of the impact of land cover change on freshwater ecosystem service provision in this water-limited landscape, and can be included in the a broader assessment of the bundles of ecosystem services delivered by different landscapes.

Our results suggest, within the limitations of a retrospective, non-randomized design, that there is a clear and quantifiable streamflow response when Eastern Cape thickets are transformed to grassy shrublands. The intact thicket delivers a higher fraction yield, providing more useful water, with more reliable low flows and fewer potentially destructive high flows than transformed former thicket landscapes. It can therefore be inferred that restoration of transformed thicket will improve freshwater ecosystem services associated with useful water yield, sustained supply and flood control.

References

Please see Combined Reference List

Chapter 3 Preface

Restoration with *Portulacaria afra*: Using MISR-HR to analyse process trade-offs to total climate regulation service in a semi-arid landscape.

This chapter quantifies the contribution of albedo change to net radiative forcing following restoration using the new high resolution Multi-angle Imaging SpectroRadiometer (MISR-HR) products, and assesses how this trades-off against carbon sequestration.

It is written as a paper intended for publication. Contributions were made by the following people, and their affiliations at the time their contribution were made are listed below:

R.J. Scholes¹ and Michel Verstraete^{1,2}

1. Global Change and Sustainability Research Institute, University of the Witwatersrand, P.O. Box 2050, Johannesburg, South Africa
2. South African National Space Agency, Enterprise Building, Mark Shuttleworth Street Innovation Hub, Pretoria, 0087, South Africa

M. Verstraete assisted with the remotely sensed data acquisition and an understanding of the data products.

The conceptual outline was generated between R.J. Scholes and the candidate. R.J. Scholes has proof read and commented on the work presented.

Chapter 3: Restoration with *Portulacaria afra*: Using MISR-HR to analyse process trade-offs to total climate regulation service in a semi-arid landscape

Introduction

Within a region, both natural and managed landscapes make important contributions to climate regulation at local, regional and global scales (Snyder et al. 2004; Anderson-Teixeira et al. 2012). The conversion of natural cover to human-modified covers has material impacts on the processes through which the land surface modifies the climate (Charney 1975; Pielke et al. 2007). These land-atmosphere processes are comprised of multiple biogeochemical (greenhouse-gas regulation) and biophysical (regulation of water and energy) feedbacks, some of which work in opposing directions (e.g., Bonan et al. 1992; Betts 2000).

At the global scale the balance between the incoming and the outgoing radiation determines the energy available to drive the Earth's climate system. The incoming radiation is almost all derived from the sun, and is predominantly in the short wavelength portion of the spectrum. The outgoing radiation has two terms: reflected shortwave, and longwave re-radiated from the warm land surface. Land cover change has the potential to strongly affect climate through changes in the surface reflectivity, known as albedo. Albedo is the fraction of incident solar radiation that is reflected by the land surface, aerosols, or clouds. Albedo is represented as a dimensionless number ranging from zero to one. The albedo of the land surface is a biophysical feature of the landscape. It is an additive complex function of the surface and the radiation impinging on it including the amount, wavelength and angle of incident solar radiation; the viewing angle; the presence of snow and ice; landscape topography and chemical composition; phenological changes; vegetation heterogeneity and geometry (including canopy height, complexity, leaf angle, and leaf area index); as well as soil moisture and carbon content (Stoner & Baumgardner 1981; Henderson-Sellers & Wilson 1983; Pielke & Avissar 1990; Graetz 1991; Yin 1998). These characteristics vary at multiple scales in both time and space.

From a landuse/landcover (LULC) perspective, a change in vegetation type and quantity, together with changes in canopy complexity and the amount of soil exposed, directly controls the amount of energy absorbed by the land surface for conversion into sensible heat, latent heat or emission from the warm surface back into the lower atmosphere. In open-canopied ecosystems, which account for 70% of non-ice ecosystems, the fractional canopy cover, the brightness of the exposed soil and the abundance of species with particular canopy properties such as light or dark, small or large, hairy or smooth leaves will influence landscape albedo (Graetz 1991; Díaz et al. 2007). In some circumstances

the magnitude of the potential albedo change associated with LULC change is sufficiently high that it could equal or exceed the radiative forcing changes associated with the net change in fluxes of greenhouse gases. An example comes from the boreal forest (Bonan et al. 1992; Bonan 1995; Baldocchi et al. 2000; Chapin III et al. 2000; Betts 2000; Chambers et al. 2005), where the land surface is dark (low albedo) when intact, but bright (high albedo) when the trees are removed and the underlying snow is revealed. A similar contrast exists in arctic regions when ice-covered or ice-free (the ice-positive feedback, for example see Harvey 1988 and Chapin et al. 2005).

Several studies have shown that even in temperate deciduous forests, the change in surface albedo resulting from land cover changes are of sufficient magnitude to warrant inclusion in calculating the net climate consequences of land use change (Bala et al. 2007; Bonan 2008a). On the other hand, in the wet tropics, the top of atmosphere albedo is principally determined by the presence of bright, low clouds rather than the land surface itself, so albedo changes resulting from land cover changes have a much lesser effect on the regional and global climate (Costa & Foley 2000; Bonan 2008a).

While boreal, temperate, and tropical forests have garnered the majority of albedo-related research, and remain in the spotlight (Li et al 2015), the importance of LULC-related albedo change in arid and semi-arid systems is re-emerging decades after the seminal work by Charney on the Sahel (Charney 1975; Charney et al. 1977). Dryland regions are important because of their areal extent (47% or 6.31 billion ha of the total land surface area, of which 38% is semi-arid; Lal 2001) and the high amounts of incoming solar radiation due to their latitudinal location, which is typically in the relatively cloud-free, but still near-equatorial subtropics. LULC change in these regions have importance consequences for the global energy budget (Rotenberg & Yakir 2010), regional climate dynamics (Rotenberg & Yakir 2011; Raz-Yaseef et al. 2012; Houspanossian et al. 2013) and landscape weather patterns (Chambers 1998), which all underscore the complex feedbacks between vegetation change, albedo, and moisture.

The 'climate regulation ecosystem service' is conventionally calculated entirely on the basis of the uptake of carbon dioxide (CO₂) from the atmosphere. This occurs through photosynthesis and plant growth, and the carbon is stored in the biomass of plants and in the soil. For this reason there is significant interest in planting trees (afforestation and reforestation), or the avoidance of deforestation (REDD+) as a climate change mitigation activity. While plant biomass per unit area is low in dryland systems (about 6 kilograms per square meter) compared with many other terrestrial ecosystems (about 10–18 kilograms), the large area means that sequestration of carbon through primary production can play a part in regulating global climate (Nobel 2003; Safriel et al. 2005; Poulter et al. 2014; Saha et al. 2015). Sub-humid lands also have other substantial effects on the

global climate system, for instance, through the production of methane from fires and enteric fermentation (CH_4) (Scholes & Andreae 2000), the emission of volatile organic carbons (VOCs) from the vegetation, the generation of radiatively-active or cloud condensation nucleating aerosols from soils or fires (Guenther et al. 1996). It seems necessary, therefore, to consider to all the substantive effects on the global climate resulting from a land use change, and not just the change in carbon stocks, when evaluating the net benefits or dis-benefits.

It is now uncontested that land management decisions need to consider the interactions and the tradeoffs between multiple land-atmosphere processes (Randerson et al. 2009). There are multiple metrics for weighting the climatic perturbation of emissions of different greenhouse gases (Shine et al. 2005; Johansson 2011), and for the different feedback processes (Anderson-Teixeira & Delucia 2011; West et al. 2011) to make them functionally equivalent and comparable. The most widely used metrics used to combine climate effects from different sources are radiative forcing (RF, in W m^{-2}) and carbon dioxide equivalents (CO_2e , in tonnes ha^{-1}) which that have been used as common currencies by the United Nations Framework Convention on Climate Change (UNFCCC) and in the Intergovernmental Panel on Climate Change (IPCC) Assessment reports.

We use the degradation through over-browsing, and restoration through planting of succulent trees, of the semi-arid thicket vegetation in the Eastern Cape of South Africa as a case study. The succulent thicket is sensitive to sustained high levels of herbivory, particularly by non-indigenous domestic livestock such as goats (Hoffman & Cowling 1990; Stuart-Hill 1992), which largely replaced indigenous ungulate populations by the early 20th century (Milton & Dean 1995). The drier forms of thicket ($<450 \text{ mm yr}^{-1}$, Vlok et al. (2003)) dominated by the arborescent stem and leaf succulent, *Portulacaria afra* Jacq., are particularly vulnerable to transformation (Stuart-Hill 1992) to a shrubby grassland with a much lower standing biomass (Lechmere-Oertel et al. 2005; Mills et al. 2005). The thicket biome originally covered 105 454 km^2 . Nested within that is 16 942 km^2 of *P. afra* dominated thicket in various states of transformation. In 2002, 46% of the *P. afra* dominated thicket was estimated to be heavily degraded, and a further 36% was considered moderately degraded (Lloyd et al. 2002). Recent work suggests that the transformation is ongoing (Nyamugama & Nyamugama 2015). Historical rates of transformation are not well recorded, with literature referring to '20-80 year' perturbation, 'degradation over the last century', and 'since the early 1900s'. Passive recovery of *P. afra* thicket is virtually non-existent (Milton & Dean 1995; Vlok et al. 2003). Therefore active intervention is required if restoration is to be achieved. A restoration protocol has been developed using *P. afra* truncheons (Swart & Hobson 1994; Mills et al. 2010; van der Vyver et al. 2012; Powell 2009; Mills et al. 2015). The Subtropical Thicket Restoration Programme (STRP), which is

administered by the Working for Woodlands project of the Department of Environmental and Water Affairs, has planted approximately 100 km² using *P. afra* since 2004 and earned 4.7 million carbon credits through *ex ante* accounting methodologies (Mills et al. 2015); in other words 470 tCO₂e per hectare, which would translate to an increase in carbon of 128 tC per hectare, or about twice that in biomass terms.

Against this background we will measure and characterise the albedo of degraded and intact thicket vegetation using the new high resolution Multi-angle Imaging SpectroRadiometer (MISR-HR) products (Verstraete et al. 2012), and use the radiative forcing metric (RF) to evaluate how the albedo change following successful restoration trades-off against carbon sequestration. We hope to illustrate the usefulness of simple RF models in approximating the relative magnitude of biophysical and biogeochemical effects on the global climate system associated with LCLU in semi-arid systems.

Methods

Albedo measurements

Albedo is defined as the reflected radiation, integrated over the full sky hemisphere and over all short wave spectra, divided by the incoming solar radiation, also integrated over the same hemisphere and spectral range. It is sometimes expressed as a percentage, by multiplying by 100. To calculate this value it is necessary to view the reflecting surface from far above, at a range of angles and over a sufficient part of the shortwave spectrum.

Several satellite-derived surface albedo products have been produced since the mid-1990s, e.g. Sea-Viewing Wide Field-of-View Sensor (SeaWiFS, <http://fapar.jrc.ec.europa.eu/>), MEdium Resolution Imaging Spectrometer (MERIS, <http://earth.esa.int/dataproducts>), and the Moderate Resolution Imaging SpectroRadiometer (MODIS, <https://lpdaac.usgs.gov/>). They provide estimates approximately every 10 days in the absence of cloud cover, and at a spatial resolution of 1 to 1.5 km, and approximate the above definition to varying, and often unspecified, degrees.

A suite of known-accuracy 275 m resolution land surface products have recently been derived from the spatially-averaged 1.1 km measurements of the Multi-angle Imaging SpectroRadiometer (MISR) (see Verstraete et al. 2012 for details of the processing system). The various land surface reflectance products are derived from the observations of nine cameras (along-track view directions of 0°, ±26.1°, ±45.6°, ±60.0°, and ±70.5° on the centre line of the swathe) in four spectral bands (446, 558, 672, and 867 nm, and bandwidths from 20-60nm; Diner et al. 1989). This multi-angular distribution together with the multispectral information makes for better constrained and thus more accurate

outputs compared to other satellite-derived products, which have only a nadir-viewing camera, and infer the angular effects from the off-nadir views (Verstraete et al. 2012).

The MISR instrument is carried on the Terra platform and has been in continuous operation since February 2000, providing global coverage on a 9-day repeat. The MISR raw and processed data products and extensive documentation are available from the Atmospheric Science Data Centre (ASDC) of the National Aeronautics and Space Administration (NASA) Langley Research Centre (LaRC). A copy of the archive for the African continent is housed at the South African National Space Agency (SANSA) and the Global Change and Sustainability Research Institute (GCSRI) at Wits University, and a new processing system is being implemented to generate the 275m resolution (MISR-HR) products. Currently MISR-HR products for Africa are distributed on an ad-hoc, request-by-request basis.

For the purpose of this study, the MISR-HR products were generated for block 117 in paths 169, 170, 171 and 172 for all available orbits between February 2000 and December 2012. The entire timeseries was extracted for a select number of precise locations using the “timeseries” IDL routine (*pers comm.* Linda Hunt).

Sampling scheme

Neither the STRP sites currently under restoration, nor the older “fortuitous restoration trial” sites on private land (Mills et al. 2015), were large enough to detect and track through time. Instead we selected areas of intact and degraded thicket vegetation using the Subtropical Thicket Ecosystem Programme (STEP) Maps (Pierce 2006). All sites in intact thicket contained *P. afra*, and all degraded sites did not. We chose intact and degraded sites which were on either side of a fenceline, and included areas used in previous studies (Mills & Fey 2004b; Lechmere-Oertel et al. 2005). One hundred paired sites were selected, and these are considered representative of restoration and degradation end points, rather than the transformation process itself (for an example see Figure 1). Inherent in this is the assumption that a mono-culture stand of *P. afra* created by restoration will eventually return to the multi-species intact condition.

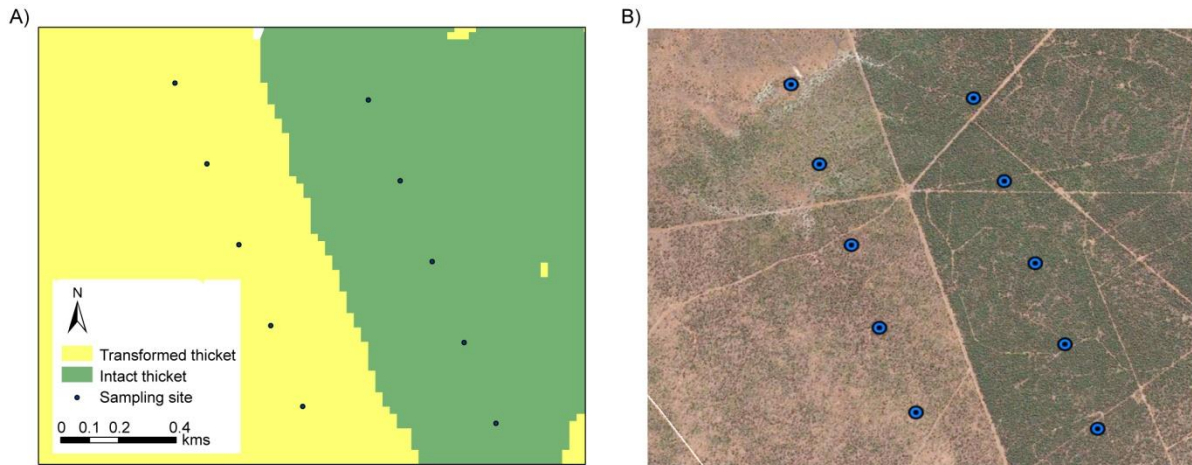


Figure1. A portion of the spatial sampling scheme showing the paired points relative to A) the intact solid thicket containing *P. afra* and transformed thicket boundaries as recorded by the Subtropical Thicket Ecosystem Programme (Pierce 2006), and B) Google Earth (Google Earth 7.1 2015). The dots mark the center of the MISR-HR 275m pixel.

Cleaning the data

For each data point the JRC-TIP (Joint Research Centre - Two-stream Inversion Package) algorithm in the MISR-HR processing system generates a cost function output (Verstraete et al. 2012). This expresses the degree of error propagated through the calculations, due to the presence of clouds and the differential angular sensitivities of the cameras, and can be used to identify outliers (*pers comm.* Michel Verstraete). The extracted data was cleaned using this cost function (Figure 2). Two hundred and five data points were removed from the combined 12-year timeseries (0.37%).

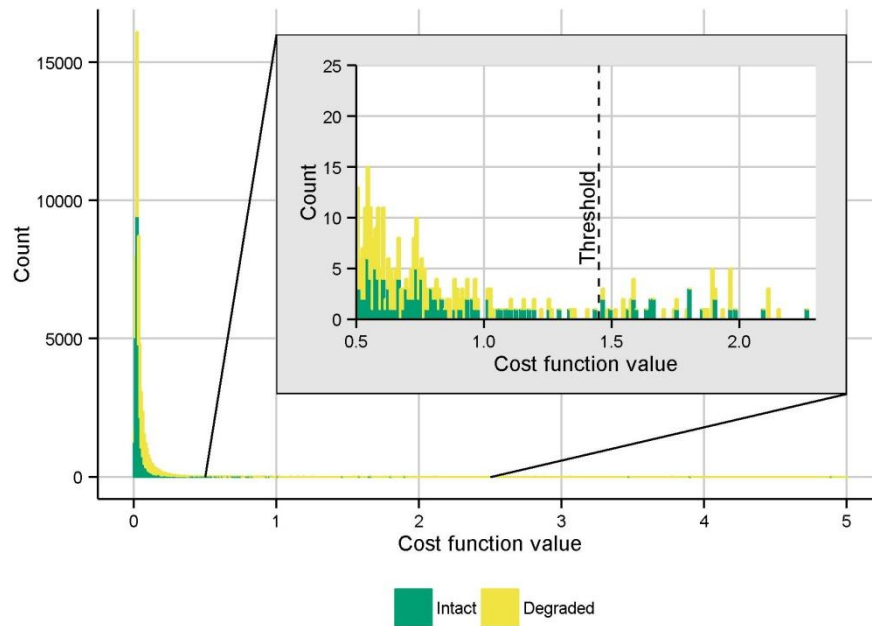


Figure 2. The inverse exponential plot of the cost function values associated with MISR-HR products. X-axis values, which extend to 21, have been truncated at 5 for better visibility. The insert shows the portion of the tail where the beginning of the small mode ($x = 1.5\text{--}2.3$) indicates the threshold value which is used to filter out data points from further analysis. In this case, only data points with a cost function value of 1.45 or less were used.

Selected data products

Ground albedo and top of canopy albedo in the visible and near infrared parts of the electromagnetic spectrum (named 'TrueBkgdAlbedo_VIS', 'TrueBkgdAlbedo_NIR', 'BHR VIS', and 'BHR NIR' respectively) were used to describe the albedo characteristics of intact and degraded thicket states.

Comparison

The interannual mean values for soil albedo and top of canopy albedo in the visible and near infrared were compared with paired t-tests.

Trade-off analysis

For the purposes of analysing the trade-off we used two one-dimensional, simple radiative transfer models by Kirschbaum et al. (2011) and Bird et al. (2008) to calculate the RF resulting from changes to albedo and carbon sequestration. Both models were selected for their simple treatment of

atmospheric aerosols and clouds. Kirschbaum sidestepped the issue of cloud cover by doing the calculations at the land surface (i.e., at the top of the canopy, but below the atmosphere). Bird et al extended their treatment to estimate the albedo at the top of atmosphere (TOA) by using a simple formulation to account for multiple reflections and absorptions by clouds and aerosols.

Radiative forcing changes due to CO₂ uptake or release

Changes in carbon stocks over time resulting from the planting of *P. afra* were taken from the Krompoort restoration site, $0.42 \pm 0.08 \text{ kg C m}^{-2} \text{ yr}^{-1}$ over 27 years, which is the basis of CO₂ credits earned for restoration to date (Mills et al. 2005; Mills et al. 2015).

Both models (Bird et al. 2008; Kirschbaum et al. 2011) begin with the logic:

$$F_{\text{carbon}} = 5.35 \cdot \ln \left(1 + \frac{\Delta C}{C_0} \right) \quad (\text{Equation 1})$$

Where: C_0 is a reference partial pressure (390 ppmv), and

ΔC is the change in atmospheric CO₂ attributable to restoration (ppmv).

The '5.35' is a constant which converts from units of CO₂ to RF, assuming a RF of about 3.75 Wm^{-2} for doubling carbon dioxide concentration (Ramaswamy et al. 2001). This is consistent with previous work (for example, Betts 2000).

Kirschbaum et al. (2011) calculate the RF per meter square of land per day, and scale up to forcing over a year for Earth as a whole with the following equation:

$$F_{\text{carbonKirschbaum}} = 864000 \cdot 5.35 \cdot \ln \left(1 + \frac{\Delta C}{C_0} \right) \cdot A_{\text{Earth}} \times 365 \quad (\text{Equation 2})$$

Where: C_0 is a reference partial pressure (ppmv),

ΔC is the sequestered carbon (tC),

2.123×10^9 converts 1 tC to 1ppm CO₂ (Joos et al. 1996),

A_{Earth} is area of the earth ($5.1 \times 10^{14} \text{ m}^2$),

864 000 is the number seconds to day, and

365 is the number of days in the year.

Bird et al. (2008) use the constant $\left(\frac{3.7}{\ln(2)} \right)$, which approximates 5.34, rather than '5.35', so that

Equation 1 becomes:

$$F_c = \left(\frac{3.7}{\ln(2)}\right) \cdot \ln\left(1 + \frac{\Delta C}{C_0}\right) \quad (\text{Equation 3})$$

For converting carbon sequestered during restoration into the change in atmospheric CO₂ Bird et al. (2008) use:

$$\Delta C = \frac{\Delta C}{M_{CO_2}} \left(\frac{M_{air}}{m_a}\right) \cdot 1.0 \times 10^6 \quad (\text{Equation 4})$$

Where: M_{CO_2} is the molecular mass of carbon (44.0095 g mol⁻¹),

M_{air} is the molecular mass of dry air (28.95 g mol⁻¹),

m_a is the mass of the atmosphere (5.148×10¹⁵ Mg), and

ΔC is the in CO₂ (g).

The term '1.0 × 10⁶' scales the answer to parts per million by volume (ppmv).

Bird et al. (2008) include the decay of atmospheric CO₂ over time (t). Together with a small scale approximation to $\ln(1 + x)$, Equation 3 and 4 become:

$$F_{\text{carbon .Bird}} \approx \frac{3.7}{\ln(2)} \cdot \left(\frac{1.0 \times 10^6 \cdot \Delta C \cdot M_{air}}{C_0 \cdot M_{CO_2} \cdot 1.0 \times 10^6 \cdot m_a}\right) \otimes \left(a_0 + \sum_{i=1}^4 a_i e^{-t/\tau_i}\right) \quad (\text{Equation 5})$$

Where: $\otimes$ represents the convolution operation for annual CO₂ removal, and

a_i and τ_i are decay constants (Archer et al. 1997).

For our purposes, over restoration timescales, we will assume atmospheric CO₂ remains constant.

Radiative forcing due to change in albedo

The change in albedo, delta albedo, was taken as the sum of the differences in top of canopy and soil albedo in the visible and near infrared portions of the electromagnetic spectrum. Using the MISR-HR product nomenclature the equation is:

$$\Delta\alpha = (\text{TrueBkgdAlbedo_NIR}_{\text{degraded}} - \text{TrueBkgdAlbedo_NIR}_{\text{intact}}) + (\text{TrueBkgdAlbedo_VIS}_{\text{degraded}} - \text{TrueBkgdAlbedo_VIS}_{\text{intact}}) + (\text{BHR VIS}_{\text{degraded}} - \text{BHR VIS}_{\text{intact}}) + (\text{BHR NIR}_{\text{degraded}} - \text{BHR NIR}_{\text{intact}}) \quad (\text{Equation 6})$$

A 2002-2011 timeseries for solar radiation was composited from four automatic weather stations (Table 1). Data gaps were filled with modeled solar radiation calculated on a daily basis using seasonal differences in sun-earth geometry (Allen et al. 1998). The long term (1960-2011) mean monthly sunshine hours were composited from the six weather stations (Table 1). Sunshine hours together with modeled daylight hours (N) (Allen et al. 1998) were used to calculate sunshine fraction, which was used in place of the fraction of possible sunshine (S) (Equation 9, below).

Table 1. Long term weather stations used to compile solar radiation and mean monthly sunshine hours used in the radiative forcing calculations. Source: Agricultural Research Council (ARC).

Station name	Station number	Location (Decimal degrees)	Elevation (m asl)	Solar radiation	Sunshine hours
AddoAgric	10561	33.567S, 25.700E	85		x
AddoSitrus NS	20186	33.567S, 25.700E	85		x
AddoOlifantpark	20218	33.450S, 25.750E	152		x
Addo AWS	30561	33.569S, 25.692E	31	x	x
Kirkwood AWS	30787	33.404S, 25.336E	119	x	
Kirkwood Prison	20262	33.400S, 25.350E	96	x	x
Dunbrody AWS	30615	33.472S, 25.545E	61	x	x

Both models (Bird et al. 2008; Kirschbaum et al. 2011) begin with the logic:

$$F_{\text{albedo}} = R \cdot \Delta\alpha \cdot (1 - \alpha_{\text{atm}}) \quad (\text{Equation 7})$$

Where: R is downwelling solar radiation,

$\Delta\alpha$ is the albedo change between degraded and intact thicket, and

α_{atm} is the proportion of shortwave radiation absorbed by the atmosphere (assumed to be 0.165 year-round for this relatively clean-air location, based on the analysis of all available South African data) (Scholes et al. 1999).

Kirschbaum et al. (2011) calculate the daily RF due to a change in albedo for a hectare over the course of a year:

$$F_{\text{albedo .Kirschbaum}} = R \times \Delta\alpha \times (1 - \alpha_{\text{atm}}) \times 10000 \times 365 \quad (\text{Equation 8})$$

Where: R is the daily incident solar radiation ($\text{MJ m}^2 \text{d}^{-1}$),

$\Delta\alpha$ is the difference in surface albedo,

α_{atm} is the proportion of energy absorbed by the atmosphere (0.165, Scholes et al. 1999),

10000 is the number of square metres in a hectare, and

365 is the number of days in the year.

Bird et al. (2008) calculate the RF from albedo changes at the top of atmosphere (TOA). Surface albedo measurements are changed to albedo at the TOA, effective albedo (α_{eff}), by:

$$\alpha_{eff} = \frac{k_c(1-S) \cdot (1-2\alpha_v(1-\alpha_{atm})) + \alpha_v(1-\alpha_{atm})^2}{1-k_c\alpha_v(1-S)} \quad (\text{Equation 9})$$

Where: k_c is the opacity or reflectivity of the clouds (~0.4 is a sunny environment),

S is the fraction of possible sunshine (sunshine hours/daylight hours),

α_v is the surface (vegetation) albedo, and

α_{atm} is the proportion of energy absorbed by clouds (0.165, Scholes et al. 1999).

Similarly, monthly top of atmosphere solar radiation ($R_{TOA,m}$) must be used, and can be estimated:

$$R_{TOA,m} = \frac{R_{annual}}{\pi} \cos\left(\lambda + \eta \cos\left[\frac{(6.5-m)\pi}{6}\right]\right) \quad (\text{Equation 10})$$

Where: R_{annual} is the total annual incoming solar radiation (1360 W m^{-2})

λ is latitude,

η is the inclination of the Earth's axis, and

m is month of the year.

This procedure was used to calculate the forcing on a monthly basis, and then sum to a year. Thus, Equation 7 becomes:

$$F_{\text{albedo .Bird}} = F_{a,m} = -\frac{A}{12A_{Earth}} \sum_m^{12} R_{TOA,m} \cdot \Delta\alpha_{eff,m} \quad (\text{Equation 11})$$

Where: $R_{TOA,m}$ is monthly top of atmosphere radiation (W m^{-2})

A is the area of albedo change between the two landcover types (m^2)

A_{Earth} is area of the earth ($5.1 \times 10^{14} \text{ m}^2$),

$\Delta\alpha_{eff,m}$ is monthly albedo change taking cloud cover into account, and

m is the month of the year.

Comparison of albedo and carbon related radiative forcing

The output of the Kirschbaum models is albedo forcing in $\text{J ha}^{-1} \text{ yr}^{-1}$ and carbon forcing in J tC yr^{-1} .

Multiplying the latter 0.42 will convert it to the same units as the albedo forcing. The forcing components from Bird et al. (2008) are in W m^{-2} and their linear sum gives the change in forcing following restoration.

Data handling

Site selection and generating the sampling scheme was done using ArcGIS® software (Environmental Systems Resource Institute, ESRI, Redlands, California). The MISR-HR data extraction was done using the 'timeseries' routine (*pers comm.* Linda Hunt) in the *Interactive Data Language interface* (IDL 7.1, *Exelis Visual Information Solutions, Boulder, Colorado*). Subsequent data management, calculations, and plotting were preformed in R (R Core Team 2015) using base R functions and the following packages: ggplot2 (Wickham 2009), plyr (Wickham 2011), and cowplot (Wilke 2015).

Results

Surface albedo characteristics

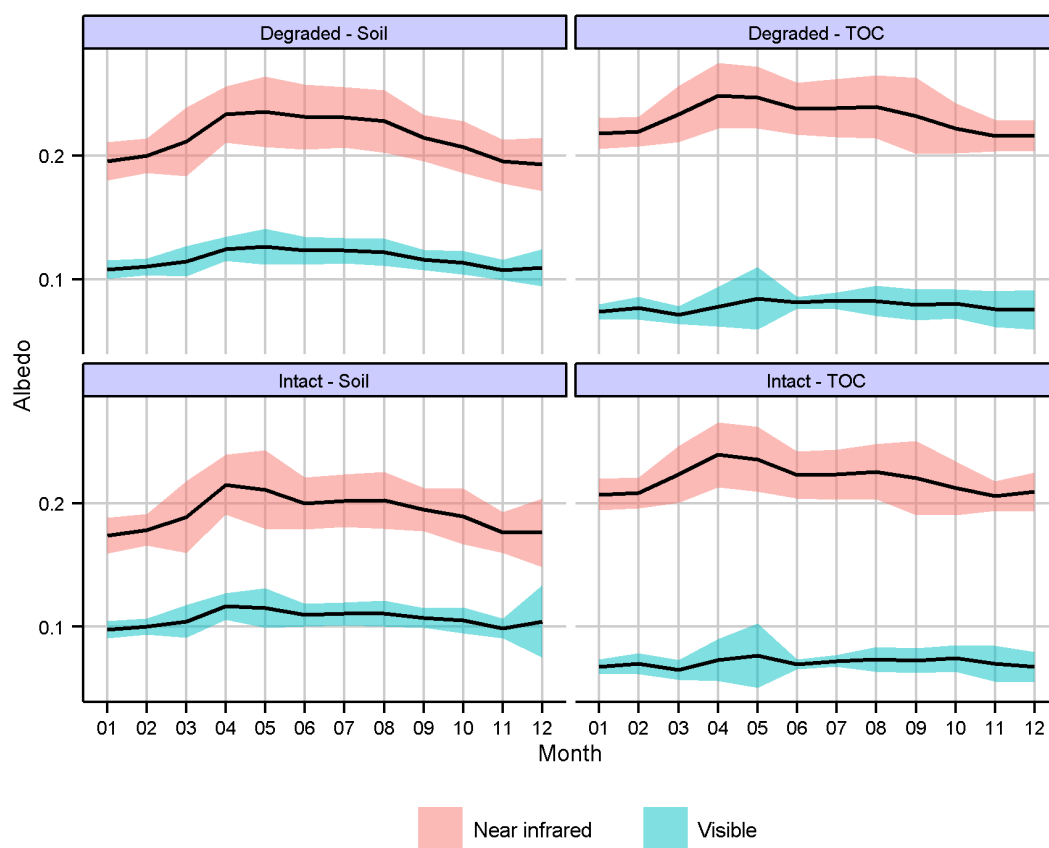


Figure 3. The annual cycle of reflectance for top of canopy (TOC) and soil, separated into the visible (VIS) and near-infrared (NIR) components of the electromagnetic spectrum. Plots for degraded thicket are shown in the top panel, and intact thicket is shown in the bottom panel. The dark lines are the 12 year mean, and the bands show the interannual variation (± 1 SD).

Measured albedo for the thicket follows a slight seasonal cycle (Figure 3). The seasonality of the signal is due to the change in the angle of the incident radiation and due to local rainfall and vegetation growth patterns. The more oblique sun angle in the winter months means a higher

proportion of incoming radiation is reflected by canopies and soil. *A priori* we would expect divergence between the TOC in visible and near-infrared during the rainfall/growing periods due to the absorption by chlorophyll in the visible wavelengths and a higher reflection of the near-infrared of the increasing leaf area index (LAI).

We anticipated a dampened cycle in the intact thicket due to the presence of evergreen succulent species in the canopy, and a stronger seasonal signal in the degraded thickets due to the higher proportion of grass cover. We expected the latter to respond quickly to the onset of rainfall and, later, contribute to an increased albedo by providing standing dry (lighter and more reflective) biomass. This turned out not to be the case. The TOC reflectance cycle is very similar between intact and degraded sites. This perhaps suggests a larger contribution of faster growing vegetation to the intact thicket albedo, or less grass growth in degraded sites, or a dominance by the angular effect, or a combination of all of these factors. Nevertheless, the greater divergence between the NIR and VIS occurs around the peak of first rainfall mode (April) relative to the second mode, which peak in November. This suggests that most growth occurs in this period.

For all albedo characteristics, TOC and soil albedo, in the visible and near infrared, there is a significant different between intact and degraded vegetation (Table 2). The greatest difference is observed soil NIR (Figure 3, Table 2).

Table 2. Summary albedo values for intact and degraded thicket vegetation for the visible (VIS) and near-infrared (NIR) components of the electromagnetic spectrum (interannual monthly mean $\pm$ 1 SD). P-value results from paired t-tests are reported (N=12, df=11).

	Top of Canopy		Soil	
	VIS	NIR	VIS	NIR
Intact vegetation	0.07 $\pm$ 0.01	0.21 $\pm$ 0.02	0.11 $\pm$ 0.01	0.19 $\pm$ 0.02
Degraded vegetation	0.08 $\pm$ 0.02	0.23 $\pm$ 0.02	0.12 $\pm$ 0.01	0.22 $\pm$ 0.02
Mean difference	-0.01	-0.01	-0.01	-0.02
p-value	9.29 $\times 10^{-8}$	4.76 $\times 10^{-9}$	1.59 $\times 10^{-8}$	3.38 $\times 10^{-9}$

Radiative forcing comparison

Intact thickets have a lower albedo than degraded thickets. Restoring to an intact state will result in a mean albedo decrease of 0.05 (Figure 4).

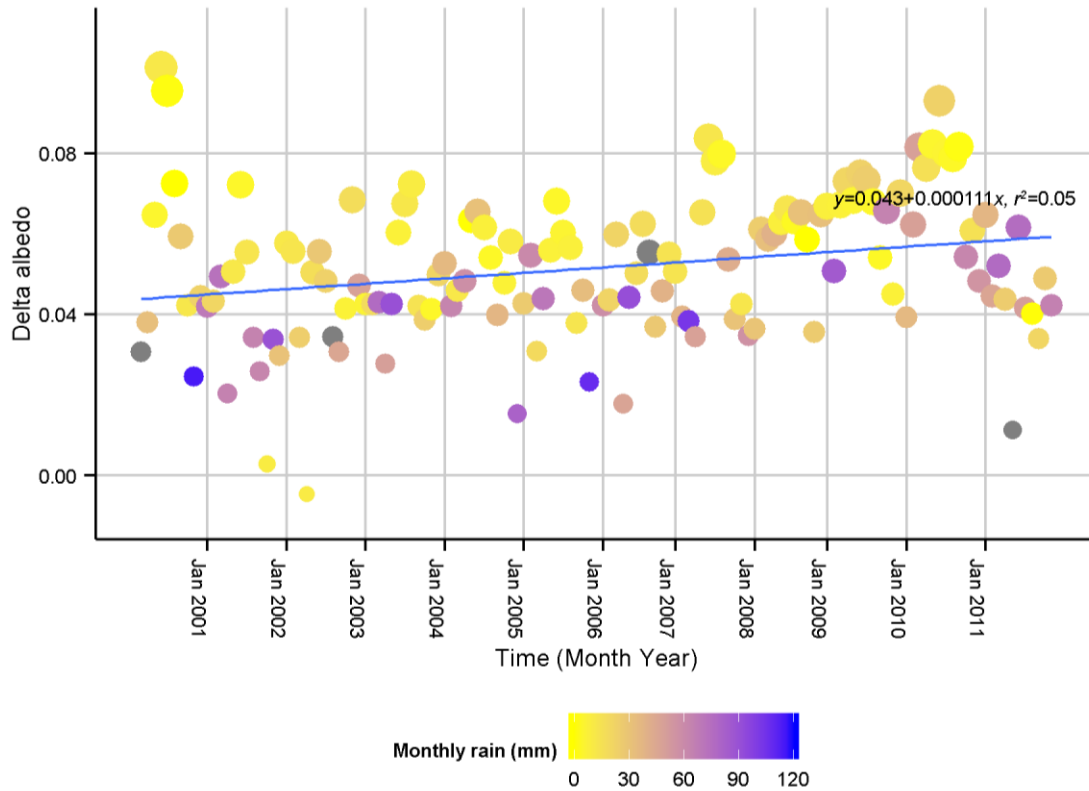


Figure 4. The mean monthly delta albedo for all paired intact and degraded thicket sites over the MISR-HR timeseries March 2000-January 2012. Delta albedo is defined as the albedo of the degraded site minus the albedo of the paired intact site (Equation 6). Note that with a single exception, one month in 2002, the degraded sites have a higher albedo (i.e., brighter and reflecting more solar radiation) than the intact sites. Each point is coloured by the summed monthly rainfall. The linear regression (blue line) shows the trend in delta albedo over the timeseries.

The albedo change following restoration results in an annual positive *global* forcing of 0.019 pWm^{-2} (a pW is 10^{-9} W ; Table 3; Bird et al. 2008). This increased radiation absorption will also have a warming effect on the local environment which is much bigger than this global value. For instance, if the mean incoming solar radiation is 500 W m^{-2} (allowing for the day-night and seasonal cycle, as well as atmospheric absorption and clouds), a change of albedo of 0.05 units would result in 25 W m^{-2} of additional absorbed energy to be dissipated by evaporation (LE), or if water supply is restricted, as SE (warming of the plant, soil and air).

Table 3. Radiative forcing due to carbon sequestration and albedo change associated with restoration from a degraded to intact state. Negative sign indicate a cooling effect, and a positive sign a warming effect.

	Kirschbaum et al. (2011) models	Bird et al. (2008) models
Sequestration rate ¹	4.2 tC ha ⁻¹ yr ⁻¹	420 gC m ⁻² yr ⁻¹
Carbon-related forcing ²	-160.49 GJ ha ⁻¹ yr ⁻¹	-0.0073 pW m ⁻²
Albedo-related forcing ²	+2272.06 GJ ha ⁻¹ yr ⁻¹	+0.019 pW m ⁻²

Notes:

1. Model input. Units reflect the units required by the models and have not been standardised.
2. Model outputs. The carbon-related forcing from the Kirschbaum et al. (2011) model has been multiplied by 0.42 so that it is in the same units as the albedo-related forcing.

The outputs from the two models are in agreement, in sign and the relative magnitude (Table 3). Both models indicate a negative or cooling forcing associated with carbon assimilation, and a positive or warming forcing associated with darkening of the surface albedo. The albedo-related forcing is an order of magnitude larger than the carbon-related forcing.

Discussion

Surface albedo characteristics

The phenological characteristics of intact and degraded vegetation, and the differences between sites dominated by an evergreen species to those dominated by a grassy layer, were not apparent in the TOC albedo measurements.

Moisture and organic content strongly influence spectral reflectance and absorption features in the NIR portion of the electromagnetic spectrum (Stenberg et al. 2010). The greater reflectance in NIR in degraded thicket suggests that there is less moisture in the soil and vegetation. The soil in intact landscapes is masked by a darker layer of leaf mulch and contains more organic matter (Lechmere-Oertel et al. 2008) which will contribute to the large difference in soil NIR between intact and degraded sites. This has important implications for the latent heat flux (LE) which we address later.

A comparison of thicket albedo values to other vegetation types

Comparing the albedo values used in this study with published values is not possible for two reasons. Firstly, single broadband albedo values are more than a linear sum of narrowband observations. Conversion for the MISR instrument is done using a specific set of co-efficients (Liang 2001), and uses all four spectral bands (blue, green, red, near infrared). These bands are not available for the high resolution (MISR-HR) products, nor have conversion co-efficients been created for the VIS and NIR products.

The other main issue complicating a value comparison is that many of the published albedo values, which are often reported at a fairly broad functional group level, are not appropriate for direct comparison to intact thicket, because the ecosystem in question differs in many of the land- and vegetation- characteristics which so critically define albedo. Thicket ecosystems exist elsewhere in the world (Cowling et al. 2005), but no specific studies could be found on them.

Degraded thicket albedo should fall somewhere in between a grassland and shrubland, and reported values are summarized in Table 4. For intact thicket, Matthews (1984) reports albedo values for many vegetation types, and lists an albedo range of 0.15-0.18 for “microphyllous thicket” (Matthews 1984).

Table 4. Summary of published albedo values which form a baseline for comparison to MISR-HR visible (VIS) and near infrared (NIR) values for thicket vegetation.

Vegetation type (author description)	Albedo	Detail	Reference
Semi-arid forest	0.11	Shortwave, eddy covariance (Aubinet et al. 1999)	Rotenberg & Yakir (2010)
Drier woodland	0.11-0.19	Satellite derived radiance flux measurements	Ba et al. (2001)
Evergreen sclerophyllous woodland	0.12-0.15	Seasonal, integrated	Matthews (1984)
Grassland with <10% tree cover or tuft-plant cover	0.14-0.16	Seasonal, integrated	Matthews (1984)
Grassland with 10-40% tree cover or tuft-plant cover	0.14-0.17	Seasonal, integrated	Matthews (1984)
Microphyllous thicket	0.15-0.18	Seasonal, integrated	Matthews (1984)
Grassland	0.18-0.3	Satellite derived radiance flux measurements	Ba et al. (2001)
Semi-arid grassland	0.18-0.21	Shortwave, eddy covariance	Krishnan et al. (2012)
Semi-arid shrubland	0.21	Shortwave, eddy covariance (Aubinet et al. 1999)	Rotenberg & Yakir (2010)
Degraded thicket	0.7, 0.21	VIS, NIR	This study
Intact thicket	0.8, 0.23	VIS, NIR	This study

Radiative forcing trade-offs

The usefulness of the RF metric for exploring the climate regulation service consequences of LULC has been questioned because largely because it does not capture surface heat fluxes (see *Surface heat and latent energy fluxes*, below). However, it remains the standard measure to compare climate forcings (Davin et al. 2007).

Our results indicate that the change in albedo during restoration has a radiative forcing of +0.019 pW m⁻², a factor of 1.6 greater, and in the opposite direction, to the RF related to the removal of atmospheric CO₂ related to *P. afra* growth. Restoration has an overall RF of +0.0046 pW m⁻², and the cooling associated with carbon sequestration will be counteracted by the darkening of the surface.

This pattern is consistent with findings from another semi-arid area. Rotenberg & Yakir (2010) found a delta albedo of 0.1 following a hypothetical change from shrubland to forest (Table 4). Despite being productive, even in the face of drought, there was a 24 factor difference in the carbon- and albedo-related RF.

The assumption that planting *P. afra* truncheons will sequester carbon at the suggested rates is overly optimistic. Newly planted cuttings are likely to shutdown their stomata entirely in order to conserve water (a metabolic state known as CAM-idling (Lüttge 2004; Borland et al. 2011)), but may also have air trapped in their vessels, which ultimately leads to death (embolism). Truncheon die-off under restoration protocols carried out to date is between 20-100% (Mills et al. 2015), largely because it has been planted in front-zones in the landscape (Duker et al. 2015). This may promote the albedo-associated warming with carbon sequestration related cooling at a fraction of the maximum. How much *P. afra* establishes may also be important for the positive benefits to freshwater ecosystem services (see Chapter 2; Ilstedt et al. 2016).

The negative and positive forcing, or cooling and warming effects, will operate over different timelines. Time to a net cooling effect, a radiative forcing tipping point, will depend on *P. afra* growth rates and realized sequestration rates.

Surface heat and latent energy fluxes

It is important to consider the effects of restoration on the radiation budget via fluxes other than just carbon and albedo. Latent energy (LE) and sensible energy (SE) are two important surface flux characteristics which relate to one another, but have contrasting effects on the surface energy budget (Figure 6).

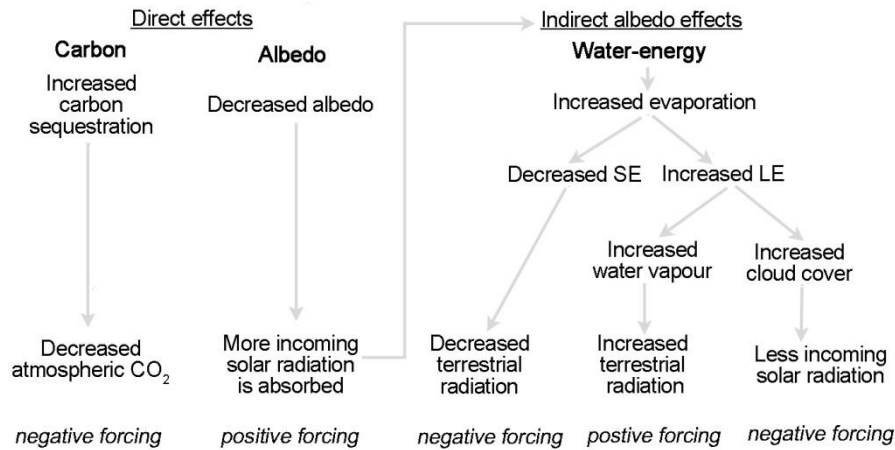


Figure 5. A summary of the land-atmosphere feedback processes affected by thicket restoration using *P. afra*. SE and LE denote sensible energy and latent energy, respectively. Drawn after Findell et al. (2007) and Kirschbaum et al. (2011)

The partitioning between LE and SE is expressed as the ratio SE:LE, and called the Bowen ratio. We would typically expect the restoration would result in a lower Bowen ratio (Bonan 2008b), with a greater portion of energy going towards latent heat and contributing to cloud formation and rainfall (right hand side, Figure 5). However, the influence of *P. afra* succulence and the species' ability to employ water-conserving CAM photosynthetic behaviour is likely to impact on this typical interpretation in unknown ways.

One of the impacts of global climate change in the drylands is in the projected increase in evapotranspiration and reduced precipitation (Safriel 2009). This would lead to future conditions of reduced soil moisture – which is already low in this semi-arid environment. This reduced water availability for primary production could reduce carbon sequestration and enhance the delta albedo – exacerbating the post-restoration feedbacks (Figure 4 and 5).

The links between regional land cover change and rainfall are complex. They have been explored for South Africa in a scenario of widespread forestation in the Eastern Cape using two regional climate models under the representative concentration pathway 4.5 ('RCP 4.5' which stabilises radiative forcing in the year 2100 at 4.5 W m^{-2} ; Thomson et al. 2011). Naik & Abiodun (2016) show mixed results, with wet and dry conditions being induced in different parts of the country.

Conclusions

The change in albedo following restoration constitutes a direct radiative forcing of $+2272.06 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ or $+0.019 \text{ pW m}^{-2}$. This warming effect overwhelms the climate benefit derived from carbon

sequestration by a factor of 1.6. This highlights the need to include other land-atmosphere feedbacks when assessing the climate service delivered by restoration. The simple models outlined in Bird et al. (2008) and Kirschbaum et al. (2011) will make an important addition to the tools available to ecologists studying the impacts of land cover change.

In the context of climate change, the land cover change feedback to the rainfall needs to be given particular attention, due to the *P. afra*'s characteristics of stem and leaf succulence and ability to employ CAM metabolism.

References

See Combined Reference List

Chapter 4 Preface

Carbon assimilation rates in *Portulacaria afra* dominated landscapes of the Eastern Cape

This chapter quantifies the rate of carbon assimilation using radiocarbon and stable isotope analysis, growth ring analysis, dendrometry, water use efficiency and eddy covariance data.

This chapter was written with contributions from the following people, and their affiliations at the time their contribution were made are listed below:

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A breakdown of the author contributions is as follows:

The conceptual outline was generated between R.J. Scholes and the candidate. The water balance model was developed by R.J. Scholes and is detailed in Appendix 1. R.J. Scholes has also proof read and commented on the work presented.

Stable isotope analysis was performed by S. Woodbourne.

Chapter 4: Carbon assimilation rates in *Portulacaria afra* dominated landscapes of the Eastern Cape

Introduction

In their undegraded state (hereafter called 'intact', meaning having a canopy cover >75%), the subtropical thickets of the Eastern Cape, South Africa are an extremely dense, multi-stemmed, low-growing, evergreen, species-rich vegetation type which is thought to have covered an area of two million hectares (Lloyd et al. 2002) in pre-colonial times. Clearing for agriculture, rural and urban human settlement, forestry, historical mining activities and rock quarries; combined with degradation through over-browsing by domestic livestock - goats in particular - are the main factors thought responsible for reducing the areal extent of the various thicket types by 31 - 88% (Lloyd et al. 2002).

For an environment which is generally arid (436 mm per year mean annual rainfall, MAR, with a spatial standard deviation of ± 128 mm per year; Hijmans et al. 2005), the carbon density of intact thickets is high (averaging about 130 tC ha^{-1} , of which 33 tC ha^{-1} is in aboveground biomass, 7.4 tC ha^{-1} is in litter, 14.9 tC ha^{-1} is in belowground biomass, and 72.6 tC ha^{-1} is in soil organic carbon; Mills & Cowling 2010; Mills et al. 2005; Powell 2009). It has been suggested that re-establishing dense thickets on formerly degraded lands will meet several demands: the restoration of a biodiverse habitat (van der Vyver et al. 2013), the re-creation of a browsing resource (Stuart-Hill & Aucamp 1993; Bothma et al. 2002; Sims-Castley 2002); the improvement of landscape hydrology (van Luijk et al. 2013), and the sequestration of carbon as a measure to mitigate climate change (Mills & Cowling 2006). The sale of carbon credits has been seen as the main way to finance the restoration (Mills et al. 2007; Mills et al. 2015; www.ercap.co.za; www.r3g.co.za).

Carbon credits accrue from proven increases in the carbon density of the landscape. In other words, they do not accrue from how much carbon is present, but rather from how much the carbon has increased over a given period of time; thus, they are related to the carbon assimilation rate rather than the carbon stock *per se*. Since there are high fixed costs for carbon projects, including the costs of proving (certifying) the presence of the carbon and recurrent costs related to land management to ensure the carbon is taken up and protected (Wise et al. 2009; Thomas et al. 2010), the economic viability of land-based carbon sequestration projects is critically dependent on the net carbon uptake rate. To avoid competition with food, fibre or bioenergy crops on prime land, marginal lands (usually degraded or arid lands) have been suggested as potential places to store carbon (Scurlock & Hall 1998; Rosenberg et al. 1999; Safriel et al. 2005; Lal 2001; Witt et al. 2011). Such lands typically also

have low net carbon uptake rates (less than $1.5\text{tCha}^{-1}\text{y}^{-1}$), not only due to aridity and erratic rainfall, but also due to prevailing land management practices (Lal 2009). However, the combination of their large spatial extent (47% of the global land area; FAO 2004; Lal 2009) and Millennium Development Goal (MDG) co-benefits, earn arid-land restoration projects further consideration (Niamir-Fuller et al. 2007). Recent work shows that semi-arid systems can make an important contribution to the global carbon cycle (Poulter et al. 2014), and increasingly so, if the positive trends in productivity indicated by remotely sensed vegetation indices continue (Saha et al. 2015).

The arid intact thickets of the Eastern Cape often have a succulent tree species, *Portulacaria afra* Jacq., as a conspicuous component (Lloyd et al. 2002). *P. afra* has a relatively high establishment success rate when planted from truncheons, making it the key species in restoration protocols (Swart & Hobson 1994; Mills et al. 2010; van der Vyver et al. 2012; Powell 2009). Estimates of the sequestration rates of pure *P. afra* stands have suggested that they are sufficiently high to make restoration schemes viable (Mills et al. 2007). The indicated carbon uptake rates are substantially higher than would be expected from such an arid environment (Mills et al. 2005). This has been attributed to the facultative Crassulacean Acid Metabolism (CAM) carbon assimilation pathway exhibited by this species, which allows it to have a high water use efficiency (g C assimilated per g H_2O transpired). *P. afra* is also a highly palatable browse species (Aucamp et al. 1978; Stuart-Hill 1992; Lloyd et al. 2002). However, all the published data are derived from very small plots, often in unusual locations, and relying on inferences regarding their initial carbon densities. There are as yet no long-term growth rate data (Turpie et al. 2003; Marais et al. 2009; Mills et al. 2010), from a representative environment, and at landscape scale.

This chapter sets out to estimate growth rates and water use efficiencies values of *P. afra* under field conditions, from which realistic carbon assimilation rates can be estimated for succulent tropical thickets in the Eastern Cape containing a large fraction of *P. afra*. It does so by applying a variety of different approaches – radiocarbon and stable isotope analysis, growth ring analysis, dendrometry, water use efficiency and eddy covariance. In doing so, we reveal and explore some of the physiological traits of *P. afra* and, more broadly, of intact thicket ecosystems.

Site and Methods

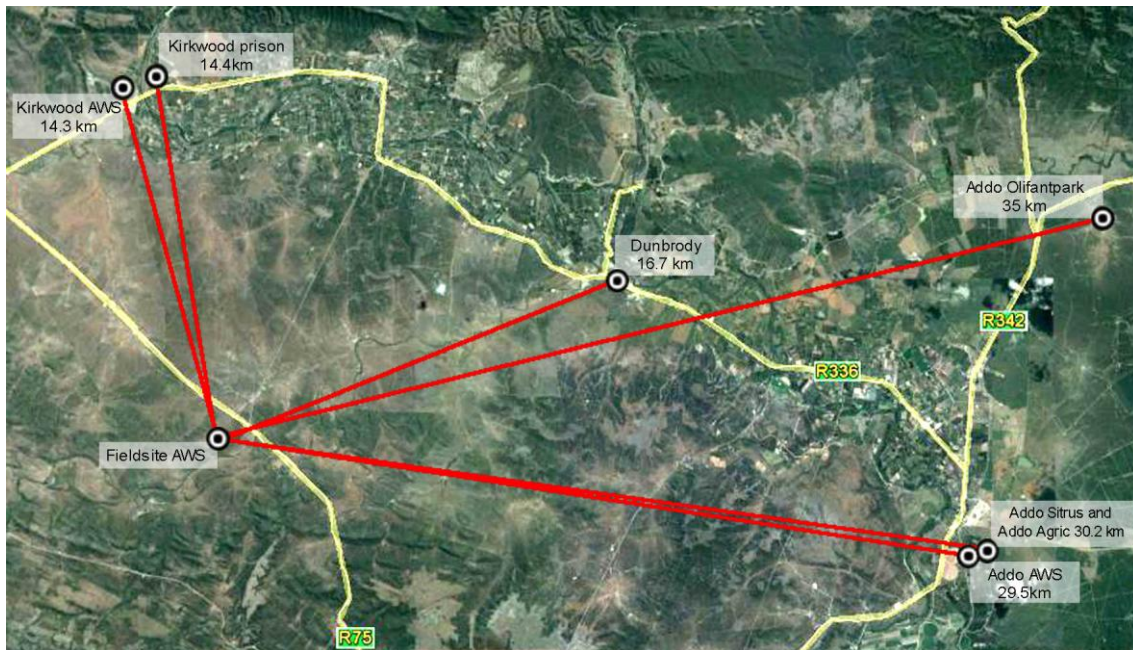


Figure 1. Map showing the core experimental site and the surrounding long term weather stations. The annotations show the respective distances, as the crow flies (Google Earth 7.1 2015).

The core experimental site was situated at 33.5276° S 25.3776° E, 15 km south-west of the town of Kirkwood in the Eastern Cape, South Africa (Figure 1). Daily weather data from stations at a distance of 14 to 35 km from this field site were available for the period 1960 to the present, with varying temporal gaps. The data from the closest weather station with available data for each period was used. The long-term mean monthly and annual precipitation, maximum and minimum temperatures are shown in Table 1.

Table 1. Mean climate data for the period 1960 to 2010 compiled from seven long term weather stations (altitudes are above sea level): AddoAgric (10561) 33.5667°S, 25.7000°E, 85m (years 1960-2002), AddoSitusNS (20186) 33.5667°S, 25.7000°E, 85 m (1976-1993), AddoOlifantpark (20218), 33.4500°S, 25.7500°E, 152 m (1994-2003), Addo AWS (30561) 33.5685°S, 25.6922°E, 31m (2002-2007), Kirkwood AWS (30787), 33.4038°S, 25.3361°E, 119 m (2007-2010); Kirkwood Prison (20262) 33.4000°S, 25.3500°E, 96 m (1990-2002); Dunbrody AWS (30615) 33.4721°S, 25.5449°E, 61 m (2003-2010). Source: Agricultural Research Council (ARC).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Rain (mm)	31.3	37.3	43.6	37.00	22.7	20.8	20.4	31.2	26.5	38.0	39.6	32.0	380.4
T _{min} (°C)	16.8	17.1	15.6	12.2	8.8	6.1	5.4	6.8	8.8	11.2	13.36	15.2	11.3
T _{max} (°C)	29.6	29.8	28.6	26.3	24.2	22.0	21.9	22.9	24.1	25.0	26.62	28.4	25.78
E ₀ ¹ (mm/d)	4.37	3.88	3.04	2.07	1.32	0.95	1.09	1.69	2.43	3.23	3.94	4.40	2.69

Notes:

1. Calculated using an atmospheric transmissivity of 0.835 (Scholes et al. 1999), cloud cover data from Addo (not reported here), an albedo of 0.23, and an elevation of 220 m asl, following the Penman-Monteith formulation (McMahon et al. 2013).

The site consisted of an approximately 200 ha fenced patch (a ‘camp’ in local parlance) of thicket, with *P. afra* conspicuous, on a privately-owned farm used primarily for hunting of the indigenous browser, kudu (*Tragelaphus strepsiceros*), and some Angora goat (*Capra aegagrus*) husbandry. Adjacent camps had little thicket, as a result either of deliberate clearing or past over-browsing. The site is located towards the top of a gently rolling landscape (220 m asl) on shale geology, yielding a shallow, gravelly clay-loam soil (Table 2).

Table 2. Soil properties from a soil pit at 33.5281°S, 25.3781°E. The saturated hydraulic conductivity was estimated to be 82 mm d⁻¹, using Schaap et al (2001). The texture class is clay loam.

Depth	Gravel ¹	Sand ²	Clay ²	Bulk density ³	θFC ⁴	θWP ⁴	θAD ⁵
mm	Mass % whole dry soil (g per100 g)	% by mass of oven-dry, gravel free soil		Of the soil matrix excluding gravel	m/m		
0-260	90.5	48.6	19.8	1.99	0.24	0.07	0.03
260-460	88.4	46.4	22.8	1.81	0.31	0.08	0.04
460-530	91.9	44.2	27	1.81	0.31	0.08	0.04

Notes:

1. By sieving dried soil through 2 mm sieve and weighing fractions. The bulk density of gravel pieces (generally shale fragments) was measured to be 2.30 Mg m⁻³.
2. By hydrometer method after dispersion with sodium hexametaphosphate and shaking.
3. Of the soil matrix, determined by measuring the dry mass and volume of an undisturbed ped, followed by correction for the gravel content and its known density.
4. Estimation of the water retention curve using the ROSETTA programme (v1.0) (Schaap et al. 2001) using the third level (H3) Pedo-Transfer Functions (PDFs), and correcting for the volume fraction occupied by gravel. Field capacity was assumed to be at -0.01 MPa and wilting point at -1.5 MPa.
5. From the difference between air-dried and oven-dried soils; corresponds to -9 MPa.

Determining the fraction of P. afra in the landscape

Vegetation transects

Vegetation structure and composition based on projected cover was determined using line intercept transects conducted in October 2009 following the methodology in Kutsch et al. (2004). In brief, the canopy width and height for biomass above 0.5 m in height was measured over ten 50 m transects, 10 m apart, and following the fenceline that divided the *P. afra* camp. The percent contribution by each species to biomass volume was calculated following Equation 1.

$$\text{Species contribution} = \frac{\sum_{\text{species}} (D_{\text{end}} - D_{\text{start}}) \cdot (H_{\text{max}} - H_{\text{min}})}{\sum \text{for all species}} \times 100 \quad (\text{Equation 1})$$

Where: D_{end} is the distance measurement along the transect at the end of the plant canopy,

D_{start} is the distance measurement at the beginning of the plant canopy,

H_{max} is the highest point of the canopy, and

H_{min} is the lowest point of the canopy.

P. afra leaf sampling and analysis for $\delta^{13}\text{C}$

Leaf samples were collected during two site visits in October 2009 and July 2010. On each occasion a single tree per vegetation transect was selected for sampling. From each individual leaves were collected from the north facing side of the plant; one well-exposed leaf, and one shaded leaf toward the main stem. The leaves were wrapped in tinfoil and stored in a cooler box upon collection, and upon return to the lab the samples were frozen until they could be oven dried and ground.

Samples were weighed out into tin capsules (D1008, Microelemental Analysis) and used in carbon isotope analyses. Aquilots ranged from approximately 0.25 -1 mg ($\pm 1 \mu\text{g}$ accuracy, Mettler Toledo MX5) due to a change in sample delivery system within the spectrometer (details below).

Contribution of *P. afra* to soil organic carbon—sampling and analysis for $\delta^{13}\text{C}$

Soil samples were collected during two site visits in March 2009 and July 2010. A soil auger was used to sample soil at 5 cm intervals to depths of between 20 and 45 cm from under *P. afra* cover, under herbaceous cover and of exposed soil.

In October 2009 a soil pit was dug to a depth of 53 cm in the soil between several large *P. afra* plants. Samples from the vertical profile were taken every 10 cm, apart from the final sample between depths of 45-53 cm (8 cm). Following sieving and grinding the soils were given an acid-pre-treatment (1% Hydrochloric acid burn) followed by washing with distilled water until a pH between 3-4 was reached (Merck Universal Indicator strips). Dry aquilots of approximately 20 mg were weighed out ($\pm 1 \mu\text{g}$ accuracy, Mettler Toledo MX5) to tin capsules (D1008, Microelemental Analysis) and used in carbon isotope analyses (details below).

Determining the age of *P. afra* stems

Growth ring analysis

Ten live main stems (numbered S1 to S10) of *P. afra* were cut from near the base of separate plants in October 2009 at the experimental site. Cross-sectional disks were cut from the stems near their

base and the wet circumference measured before they were oven dried. Each disk was halved transversely, forming two complete disks, with one half stored as a witness and the second half prepared for sampling. The formerly joined cut surface of each disk was smoothed using sandpaper until the outermost ring structures were apparent under low magnification. The dry circumference measurements were taken, and average diameter was determined by measuring two diameters (perpendicular to one another) across the center of the stem disk.

The ring structures were separated one from another using repeated dry-wet stress. When the rings began to separate, they were physically divided using the back end of a scalpel. The widths of the ten outermost rings (R1-10), below the bark, were measured using an electronic digital verniercaliper (± 0.01 mm accuracy, Omni-Tech). Aliquots were pre-treated by a toluene-ethanol (2:1, v/v) Soxhlet distillation to remove all mobile constituents (Hall 2010), for instance recently-produced sugars or starches, leaving the cellulose and lignin cell walls for analysis.

The carbon isotope content of the plant tissue and soil samples were measured at the CSIR, Pretoria, South Africa, on a Thermoquest EA 1110 elemental analyser integrated with a VG Isogas SIRA 24 stable isotope ratio mass spectrometer. Isotope results are expressed in delta (δ) notation on a per mille (‰) scale relative to the Vienna PeeDee Belemnite (VPDB) standard.

P. afra does not exhibit simple annual growth ring production. The rings were linked to periods of growth opportunity (i.e., periods when the soil profile contained plant-available water) interspersed by periods too dry to support growth, as inferred from a simplified plate water balance model (Appendix 1). Typically, several such episodes occurred per year. The absolute dates were constrained by radiocarbon dating (below).

Radiocarbon dating

From a single stem (S1) of wet diameter 79 mm, three samples were taken: one from the ring immediately below the bark cambium, one from the centre of the stem, and one from a point approximately midway between the two. After pre-treatment as described above, >20 mg aliquots were sent to Beta Analytic Inc. (USA) for ^{14}C activity measurements by Accelerator Mass Spectroscopy (AMS). All samples exhibited post-bomb radiocarbon activities (Table 3). The ^{14}C values were converted to a radiocarbon date using the CALIBomb programme (Reimer & Reimer 2011) calibrated with the southern hemisphere atmosphere datasets for the bomb pulse (SHCal13 Southern Hemisphere Zone 1-2) (Hua et al. 2013; Hogg et al. 2013). These dates compared well those estimated using the ^{14}C curve from Pretoria, South Africa (Vogel et al. 2002) (Table 3). The age model was determined by plotting the number of rings against the absolute calendar dates.

Dendrometry

Two plants of *P. afra* were equipped near the base of the stem with electronic band dendrometers ($\pm 2\mu\text{m}$ accuracy, DC2, Ecomatik, Germany) to measure circumference variation over the period 26 March 2009 to 17 April 2011, recording at 30 minute intervals. An automatic weather station located about 2 meters away recorded rainfall (Tipping bucket rain gauge, TR-525M, Texas Electronics, Inc., USA); wind speed (± 0.5 m/s accuracy) and direction ($\pm 5^\circ$ accuracy, 03001 R. M. Young Wind Sentry, Campbell Scientific, Inc., USA); atmospheric temperature ($\pm 0.3^\circ\text{C}$ accuracy at 0°C) and relative humidity ($\pm 3\%$ accuracy, 0-90% range; $\pm 5\%$ accuracy, 90-98% range) (HMP50 probe, Vaisala Inc., Finland); and Photosynthetically Active Radiation (PAR) (LI190SB, Li-COR, USA) over the same period. This meteorological data was stored on a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) at 30 minute intervals.

Eddy covariance

A tower with an eddy covariance sensor mounted at 5 m was operated for 3 short-duration campaigns: 17 September to 10 October 2008 (23 days), 11 to 22 March 2009 (11 days), and 27 January to 3 February 2010 (7 days). Ancillary meteorological data included rainfall, wind speed and direction, atmospheric temperature, relative humidity, and solar net radiation recorded every 30 minutes. The 30-minute fluxes of CO_2 and H_2O were calculated using ECOFLUX software (Grelle & Lindroth 1996) using a Flux Computer (In Situ Flux Systems AB, Sweden). Further details of the system can be found in Clulow et al. (2015).

The eddy covariance technique measures net ecosystem exchange (NEE). NEE is related to plant production as follows (Kirschbaum et al. 2001):

$$GPP \approx NEE + R_a + R_h \quad (\text{Equation 2})$$

Where: *NEE* is Net Ecosystem Exchange (all values follow the convention of fluxes into the atmosphere being expressed as positive values and fluxes out of the atmosphere negative),

GPP is Gross Primary Production, the amount of CO_2 assimilated by plants through photosynthesis,

R_a is the carbon returned to the atmosphere during autotrophic respiration, the plant's own metabolism, and

R_h is heterotrophic respiration, carbon returned via the decomposition of plant matter.

Over the course of a year, in the absence of disturbance or lateral transfers, NEE approximates the Net Ecosystem Production (NEP), the annual change in carbon stored in an ecosystem. NEP can be negative or positive, which indicates whether the ecosystem is a carbon sink (-ve) or source (+ve) for CO₂ relative to the atmosphere (Kirschbaum et al. 2001).

For the purposes of estimating *P. afra* growth rates the ideal “carbon accounting” term to have would be Net Primary Productivity (NPP). NPP measures the actual production of new plant biomass over a given time period (usually a year), and if respiration losses occur only from carbon assimilated during the measurement period (Roxburgh et al. 2005) then:

$$NPP = GPP - R_a \quad (\text{Equation 3})$$

By combining Equation 2 and Equation 3, we can estimate the rate of ecosystem biomass production:

$$NPP \approx NEP - R_h \approx NEE - R_h \quad (\text{Equation 4})$$

Field measurements of soil respiration, which is the dominant term in R_h in thickets not being heavily browsed were taken during the third period campaign (27 January to 3 February 2010) using respiration rings inserted into the soil by a depth of 3 cm. If we assume they adequately represent the annual soil respiration, then using Equation 4 we can constrain *P. afra* growth rates (NPP).

Water use efficiency calculations

Water use efficiency (WUE) was calculated using two approaches. The first made use of carbon isotope values and the second made use of the eddy covariance data (described above).

WUE is the ratio of carbon gain during CO₂ fixation (assimilation rate, A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the loss of water (H₂O) during transpiration (transpiration rate, E , $\text{mmol m}^{-2} \text{s}^{-1}$), and is described for C₃ plants as (Farquhar et al 1989):

$$WUE = \frac{A}{E} = \frac{c_a(1 - c_i/c_a)}{1.6} \quad (\text{Equation 5})$$

Where: c_a is the atmospheric concentration of CO₂ ($\mu\text{mol mol}^{-1}$),

c_i/c_a is the ratio of atmospheric and intercellular CO₂ concentrations,

1.6 is the ratio of diffusion coefficients for H₂O and CO₂ in the air (Farquhar et al 1989).

To account for the effect of evaporative demand on water loss and hence over all WUE (Ehleringer & Monson 1993; Seibt et al. 2008), we can include v in the denominator of Equation 5.

$$WUE = \frac{A}{E} = \frac{c_a(1 - c_i/c_a)}{1.6v} \quad (\text{Equation 6})$$

Where v is the difference between water vapour concentration between intercellular spaces and the atmosphere. If we assume that the leaf intercellular spaces are at water vapour saturation, and leaf temperature was identical to air temperature, then the value of v is the ratio of vapour pressure deficit (kPa) to atmospheric pressure (kPa) (Ponton et al. 2006; Brien et al. 2011). We calculated the vapour pressure deficit and atmospheric pressure following Allen et al. (1998).

The value of c_i/c_a was determined using the model of Farquhar et al. (1982):

$$c_i/c_a = \frac{\Delta - a}{b - a} \quad (\text{Equation 7})$$

Where: a is the isotopic fractionation during the diffusion of CO_2 into the leaf (4.4‰),

b is the net isotopic fractionation associated with carboxylation (27‰), caused by the preference of Rubisco for $^{12}\text{CO}_2$ over $^{13}\text{CO}_2$, and

Δ is photosynthetic ^{13}C discrimination.

Δ distinguishes between the variations in the $\delta^{13}\text{C}$ of atmospheric CO_2 due to fossil fuel combustion and biomass burning from the effects of plant metabolic processes (Seibt et al. 2008). The linear version for this photosynthetic discrimination is:

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C_m}{1 + (\delta^{13}C_m/1000)} \quad (\text{Equation 8})$$

Where: $\delta^{13}C_a$ is the isotopic value of atmospheric CO_2 , and

$\delta^{13}C_m$ is the isotopic value of organic matter.

Isotopic values and CO_2 concentrations for the atmosphere were taken from the Manua Loa data set (<http://cdiac.ornl.gov>, see Appendix 2).

For the first approach both Equation 5 and 6 were applied to the analysed carbon isotope samples from intact thicket soils and *P. afra* tissue (leaves and stems) to calculate intrinsic WUE and instantaneous WUE, respectively.

For our second approach, ecosystem WUE was calculated using the Webb-corrected H₂O and CO₂ measurements (Webb et al. 1980) from eddy covariance data. WUE was calculated as the ratio of NEE and ET, and called WUE_{NEE}. The calculation of WUE_{NEE} was made on a subset of the data. Following Parton et al. (2006) records were removed from the timeseries if they met the following criteria: days with recorded rainfall; two days following rainfall days, if the rainfall exceeded 5mm; periods of low water vapour fluxes ($<0.05 \text{ mmol mol}^{-2} \text{ s}^{-1}$); or periods of low turbulence ($u^* < 0.10 \text{ m s}^{-1}$). Typically, measurements during low levels of incoming solar radiation are also removed, but because of the high presence of plant species with a CAM metabolism in the landscape, this criterion was not included.

Data management

Data management, calculations and plotting were performed in R (R Core Team 2015) using base R functions and the following packages: ggplot2 (Wickham 2009), plyr (Wickham 2011), and cowplot (Wilke 2015).

Results

Vegetation transects

The survey data confirmed that the field site is dominated by *P. afra* in the canopy and contributed 54% of the canopy. Spinescent species, *Gymnosporia polyacantha*, *Putterlickia pyracantha*, *Rhigozum obovatum*, *Lycium* sp. and *Rhus longispina*, dominated thereafter, contributing roughly 5-7% of the canopy. *Crassula tomentosa*, *C. muscosa*, *C. perforata* and *Euphorbia hamata* fell below the 0.5 m height threshold, but were noted as prevelant sub canopy species.

Growth rings and radiocarbon dating

Stem 1 (S1) is estimated from radiocarbon dating to have started growth in 1964 (Table 3). Age estimates based on this method can be 'aliased': in other words, sometimes two dates could correspond to the same observed $\delta^{14}\text{C}$, as occurred with the stem centre measurement.

Table 3. Radiocarbon estimates of the age of Stem 1 (S1)

Sample	$\delta^{14}\text{C}$ (‰)	Fraction Modern	Calendar age ¹ Two sigma	Calendar age ²
Outermost ring	53.7 ± 3.9	1.0537 ± 0.0039	2007-2009 (modern)	2009 (known)
Mid-point between outer and centre	177.1 ± 4.4	1.1771 ± 0.0044	1987-1991	approx. 1988
Centre of stem	561.5 ± 5.8	1.5615 ± 0.0058	1964,1967-1969	approx. 1969

Notes:

1. CALIBomb by Queens University Belfast, SH Zone 1-2, SHCal13 calibration datasets, smoothing in years = 1 (Hua et al. 2013; Hogg et al. 2013).
2. Vogel et al. 2002.

We used the midpoint measurement (Table 3), which is non-aliased, for our age model (Figure 2A). From this mapping, we can assume that an average of 2 growth rings are laid down annually. Therefore, the annual stem diameter increment for approximately 5 years preceding harvest could be estimated for each of the ten stems (S1-10) in which the ten outermost rings were sampled (Table 4).

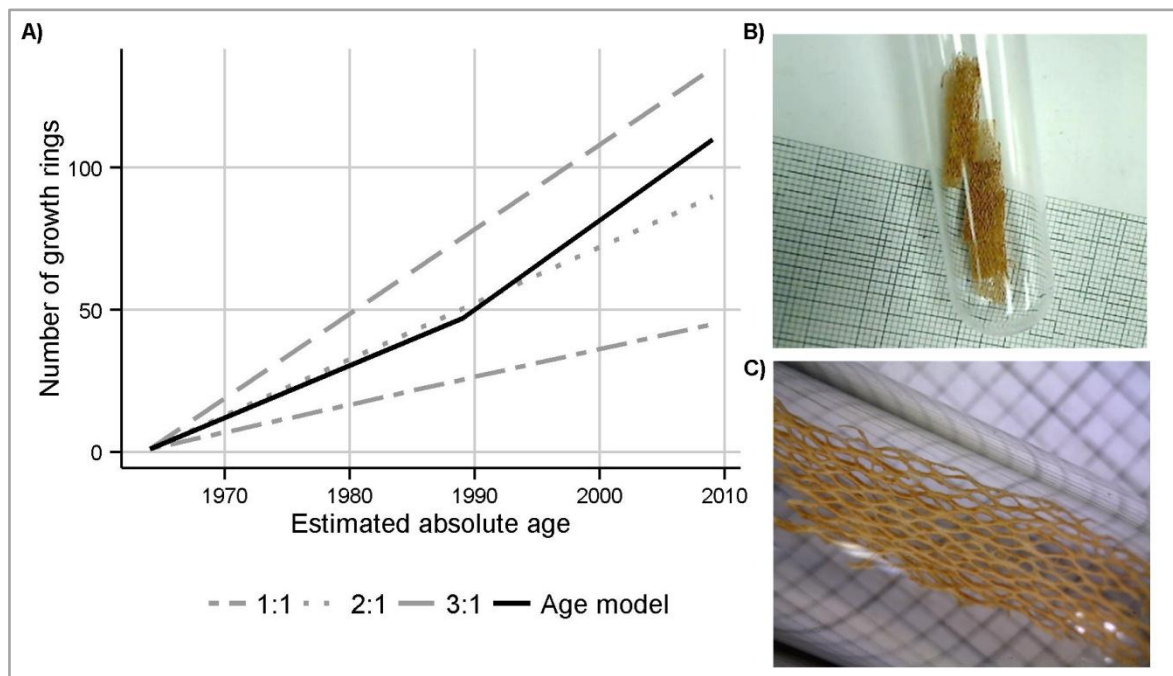


Figure 2.A) The age model constructed using radiocarbon dating on three samples from Stem 1 (S1), outer, mid-point, and centre, corresponding to absolute dates of 2009, 1989 and 1964 respectively. The grey lines show ring production of one, two and three rings per year. Sections B) and C) show photographs of the mid-point ring aquilot which was sent to Beta Analytic.

Table 4. Annual stem diameter increment for S1-10 based on the measured widths of the first ten growth rings, R1-10; as well as the derived diameter at the end of each year, back calculated on the harvest diameter. Measurements are in mm.

Stem	2005		2006		2007		2008		2009		
	Sum R9 and R10	Diameter (dry)	Sum R7 and R8	Diameter (dry)	Sum R5 and R6	Diameter (dry)	Sum R3 and R4	Diameter (dry)	Sum R1 and R2	Harvest diameter (wet)	Harvest diameter (dry)
S1	0.48	69.35	0.86	71.07	0.65	72.36	0.64	73.64	0.74	93.4	75.12
S2	0.50	48.37	0.84	50.04	0.64	51.31	0.45	52.20	0.51	67.84	53.21
S3	0.71	45.80	0.38	46.56	0.53	47.61	0.91	49.43	0.79	64.84	51.01
S4	0.71	47.96	0.61	49.18	0.40	49.98	0.36	50.70	0.40	53.62	51.49
S5	0.49	41.62	0.61	42.83	0.62	44.07	0.74	45.55	0.41	55.06	46.36
S6	0.71	49.17	0.76	50.69	0.30	51.28	0.90	53.09	0.63	62.06	54.35
S7	0.51	41.41	0.30	42.00	0.34	42.68	0.77	44.22	0.43	58.88	45.08
S8	0.51	48.16	0.58	49.31	0.45	50.20	0.22	50.64	0.89	63.70	52.41
S9	0.92	47.08	0.39	47.85	0.78	49.40	0.71	50.81	0.72	60.20	52.24
S10	0.73	38.18	0.52	39.22	0.62	40.45	0.55	41.55	0.27	53.69	42.08

Our age model was used infer the growth rate over the period 1989-2009 (2.3 mm diameter increment per year, or 2.5 % per year, and diameter growth rate over the period 1964 to 1989 was 1.8 mm per year (2 % per year). If approximately two rings grow annually (Figure 1A) then, over both periods, the average growth ring was 0.4 mm (wet) or 0.3 mm (dry) in width.

Stem increment from growth rings and dendrometry

Analysis of the stem diameter fluctuations at the sub-daily scale provide clues as to when the plant is in CAM mode and when it is functioning more like a C₃ plant (Table 5). In full CAM mode the stomata are open at night and in the early morning, and closed during most of the daylight hours. Therefore the diameter of this succulent tree shrinks during the night when in CAM mode, and is stable or swelling during the day. Conversely, when the stomata are open during the day, indicating C₃ photosynthesis, the stem shrinks during the day and recovers at night. C₃ and CAM are now considered to be endpoints on a spectrum, rather than an either-or binary switch (Silvera et al. 2010). A “weak CAM” state exists between C₃ and CAM, named CAM-cycling; and a “very strong CAM” state exists beyond the classical CAM mode, named CAM-idling. CAM-idling is adopted in periods of prolonged stress conditions, during which the stomata are closed for the entire diel cycle,

and water and CO₂ are internally recycled. When a plant is in CAM-cycling, the stomata are open throughout the diel cycle, and the plant has CAM-like acid fluctuations during the daylight hours.

Table 5. Conditional arguments for defining the photosynthetic pathway used by *P. afra* based on changes in stem size. Changes in stem size are denoted by: + for swelling, - for shrinkage, and 0 (zero) for stable periods. The diel cycle was split seasonally between night and day using sunrise and sunset times.

Photosynthetic pathway	Period of stomatal opening	Night	Day	C ₃ to CAM spectrum More C ₃ ↓ More CAM
C ₃	Day only	0	-	
		0	+	
CAM-cycling	Day and night	+	+	
		+	-	
		-	-	
		-	+	
Classical CAM	Night only	-	0	
		+	0	
CAM-idling	Neither day nor night	0	0	

From Figure 3 it can be calculated that the diameter growth rate of the larger stem over the 753 days of measurement was 0.0003 mm per day, equivalent to about 0.093 mm per year; while the smaller stem grew at 0.001 mm per day, or 0.482 mm per year. Both stems responded to low profile water content (PWC), and shrunk dramatically when PWC dropped below about 40 mm (Figure 3).

Changes in stem diameter from the growth rings (Table 4) and from the dendrometer bands (Figure 1) can be converted to aboveground relative growth rates (RGR, gDM per gDM per year) by estimating the dry mass at time 1 (DM₁) and time 2 (DM₂) (Equation 10) using allometric equations for aboveground biomass in *P. afra* (Equation 9; Powell 2009).

$$\log_{10}(DM) = a + b(\log_{10} BA) \quad (\text{Equation 9})$$

Where: *DM* is dry mass (kg),

BA is basal area (m²),

a is 2.4464, and

b is 1.1043.

$$RGR = \frac{DM_2 - DM_1}{t_2 - t_1} \quad (\text{Equation 10})$$

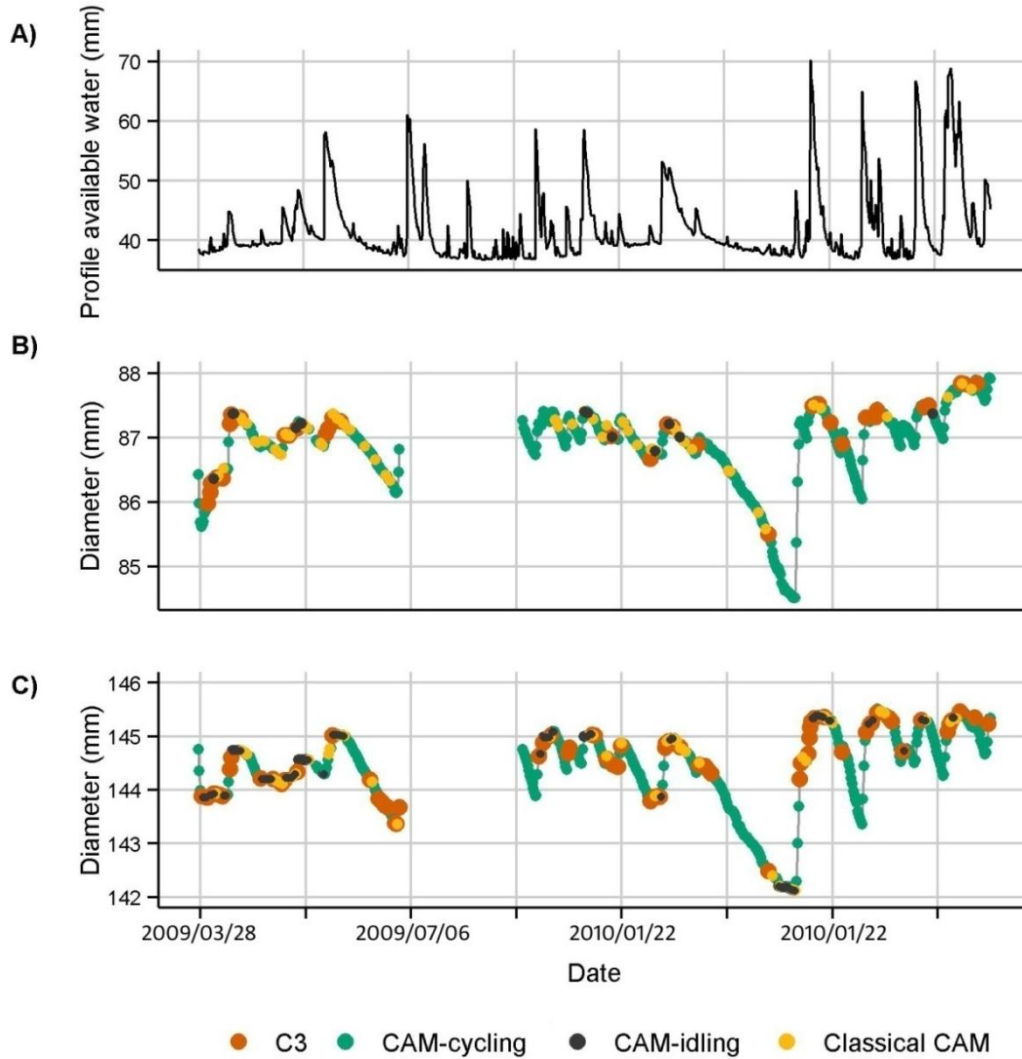


Figure 3. Stem diameter fluctuations measured by the dendrometer bands, in relation to the daily profile available water content calculated from daily climate data, over the period 26 March 2009 to 17 April 2011. The colours of the dots relate to the inferred photosynthetic modes (method described in the text and Table 5). A) Rainfall events, B) diameter as measured by dendrometer 2, C) diameter as measured by dendrometer 1. Diel-cycle stem dynamics are defined by daily sunset and sunset times and calculated as the sum of hourly diameter changes rounded to two decimal places.

From Table 6, the multi-year and multi-source aboveground relative growth rate (RGR) mean is 0.006 g DM per g DM per year ± 0.005 g DM per g DM per year (1 SD). For S1-S10, R1-10, this is about 1.1% per year.

Table 6. The aboveground relative growth rates (g DM per g DM per year) of *P. afra* in recent years.
Growth ring widths were scaled from dry to wet values using the individual wet:dry ratio for each
stem (Table 4, S1-10 mean ratio=1.21 ± 0.08 1 SD).

	2011 (for data days)	2010	2009	2008	2007	2006	2005	1989-2010 average	1964-1988 average
Rainfall (mm)	655 (185)	319	274	267	385	522	358	371	394
Growth days ¹ [n, (%)]	293 (59%)	154 (42%)	145 (31%)	149 (41%)	197 (54%)	261 (72%)	185 (51%)	189 (52%)	210 (58%)
Dendro 1 ²	-	0.001	-	-	-	-	-	-	-
Dendro2 ²	0.009	0.00003	0.002	-	-	-	-	-	-
S1	-	-	0.003	0.013	0.006	0.006	0.009	0.018 ³	0.010 ³
S2	-	-	0.003	0.014	0.007	0.002	0.003	-	-
S3	-	-	0.009	0.002	0.004	0.018	0.012	-	-
S4	-	-	0.005	0.003	0.001	0.001	0.001	-	-
S5	-	-	0.003	0.005	0.005	0.008	0.002	-	-
S6	-	-	0.006	0.008	0.001	0.013	0.005	-	-
S7	-	-	0.004	0.001	0.001	0.012	0.002	-	-
S8	-	-	0.003	0.004	0.002	0.000	0.014	-	-
S9	-	-	0.014	0.001	0.009	0.007	0.007	-	-
S10	-	-	0.009	0.004	0.006	0.004	0.001	-	-

Notes:

1. Growth days occur when the profile water content ≥40mm.
2. RGR calculations made on a daily basis using the data days available and multiplied to an annual value. Where the stem was shrinking the RGR could not be calculated.
3. Calculated using half the harvest wet diameter.

Guided by the stem response to soil water content recorded by the dendrometers (Figure 2) and the radiocarbon ages (Figure 1A), the sub-annual diameter increments were matched to favourable periods for growth for the ten sampled stems (Figure 4). Years were divided according to the bimodal distribution of rainfall into January-June and July-December periods, and called “mode 1” and “mode 2”, respectively. There are distinct differences between plants over time (Figure 3, Figure 4, Table 6). This becomes more apparent as the time integral becomes greater – i.e. from daily to monthly to 6 monthly to annually, and moving from water to carbon related measurements, i.e., from responses to soil water content to growth ring widths. This variation could be an age- or size-dependant effect, as tree physiology and photosynthetic capacity has been shown to change with

age or size in some species (Vieira et al 2009), or it could occur at the individual level as a result of microclimate effects.

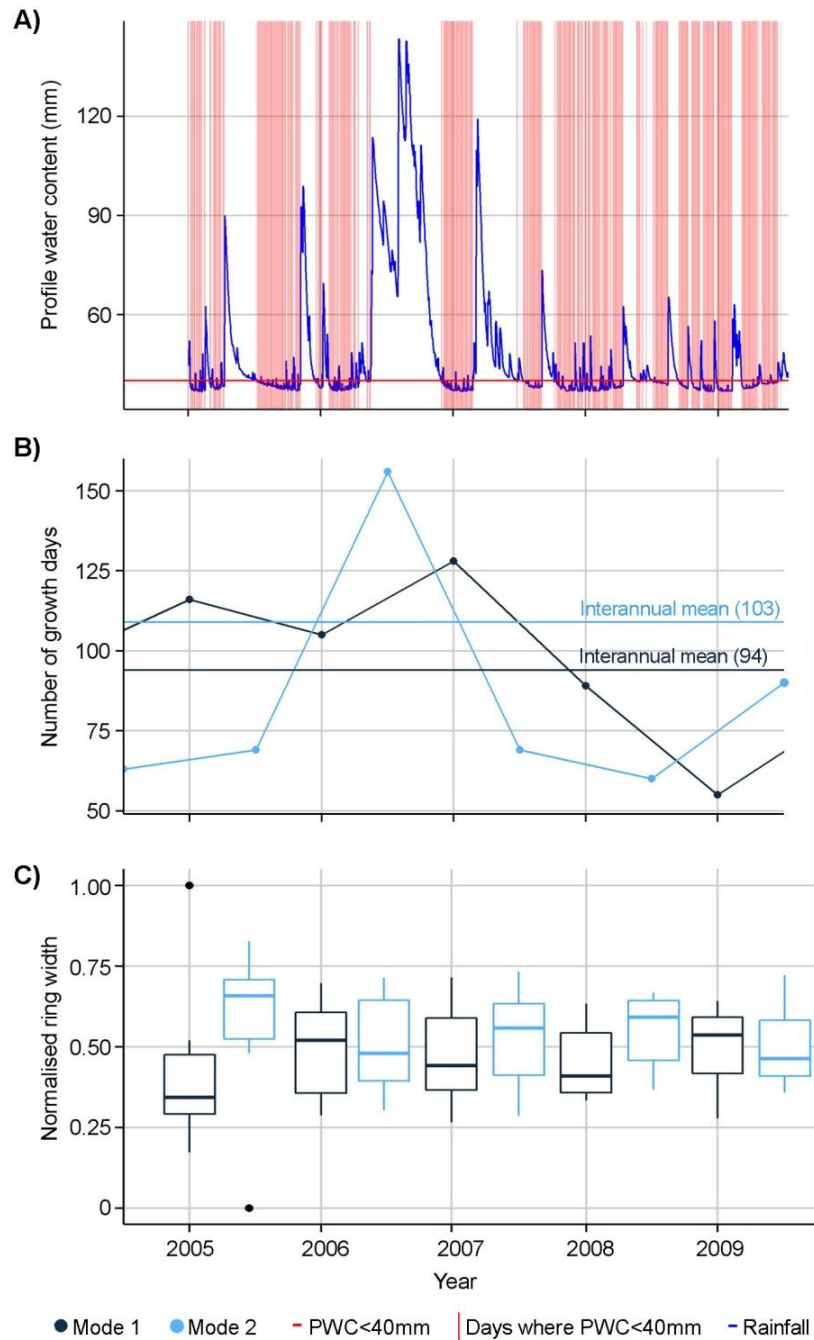


Figure 4. The relationship between growth ring width and profile water content (PWC): A) The sequence of wet and dry periods over the period 2005-2009, where the red horizontal line indicates the 40 mm PWC growth threshold, and the vertical red lines indicates periods when the PWC is below this threshold; B) the shows number of growth days, defined as when PWC is greater than 40 mm, for the January-June ('mode 1') and July-December ('mode 2') periods, as well as the 1960-2010 mean values; and C) shows the normalised widths of R1-10 for S1-10 versus mode, where R1 occurs in mode 1, R2 in mode 2, R3 in mode 1, and so forth.

Net Ecosystem Exchange by eddy covariance

At an ecosystem scale, there is a drawdown of atmospheric CO₂ during the early hours of the morning due to photosynthetic assimilation (Figure 5A), which is pattern is consistent over the months of the eddy covariance campaigns (Figure 5B). There is a noticeable increase in assimilation during late summer/early April when higher rainfall coincides with cooler temperatures; as well as increased carbon uptake in the early evening hours at beginning of spring (Figure 5B).

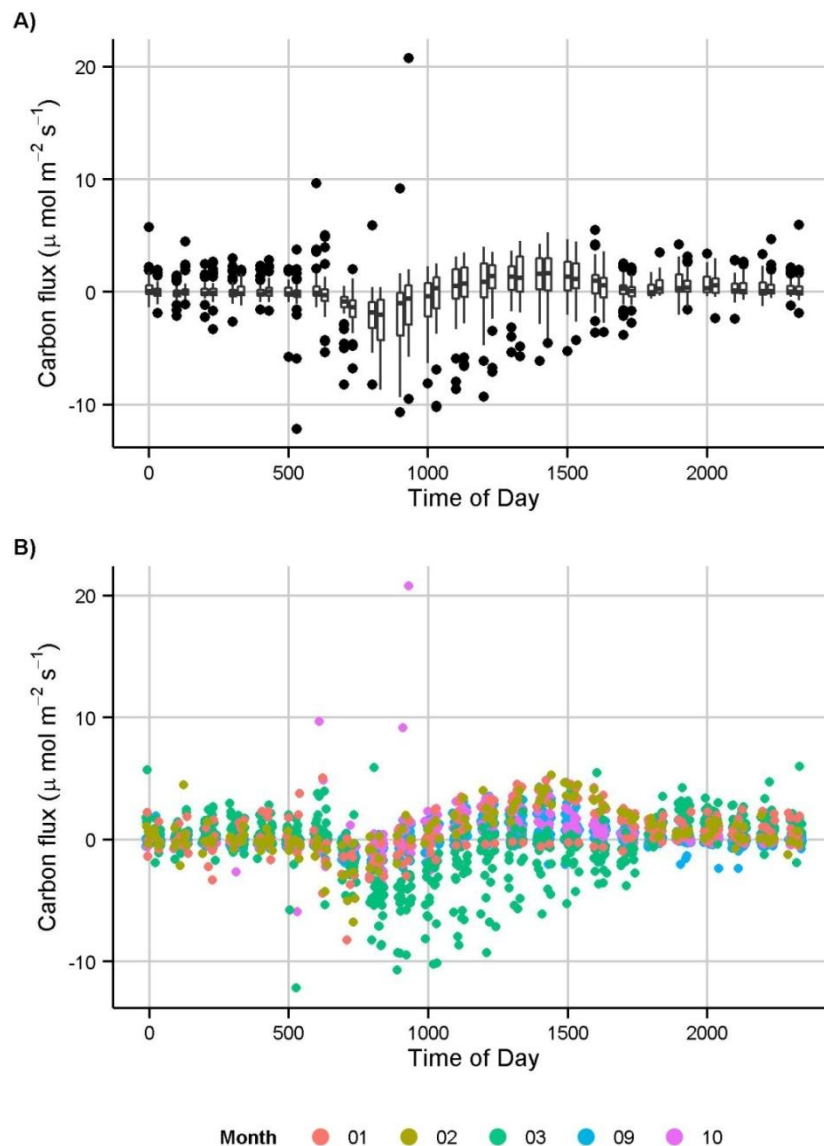


Figure 5. The Webb-corrected half hourly carbon flux measurements for the three eddy covariance campaigns: 17 September to 10 October 2008 (22 days), 11 to 22 March 2009 (11 days), and 27 January to 3 February 2010 (7 days). A) Shows the range of values by time of day, and B) shows the variation in range by month. Note: the horizontal positions of the points in part B) are slightly jittered to avoid over plotting.

On average, efflux from the land to the atmosphere dominates the NEE signal, and intact *P. afra* thicket vegetation, as measured during the three short-duration field campaigns, is a net source of carbon to the atmosphere of $0.11 \mu \text{mol m}^{-2} \text{s}^{-1}$, or $0.018 \text{gC m}^{-2} \text{hr}^{-1}$.

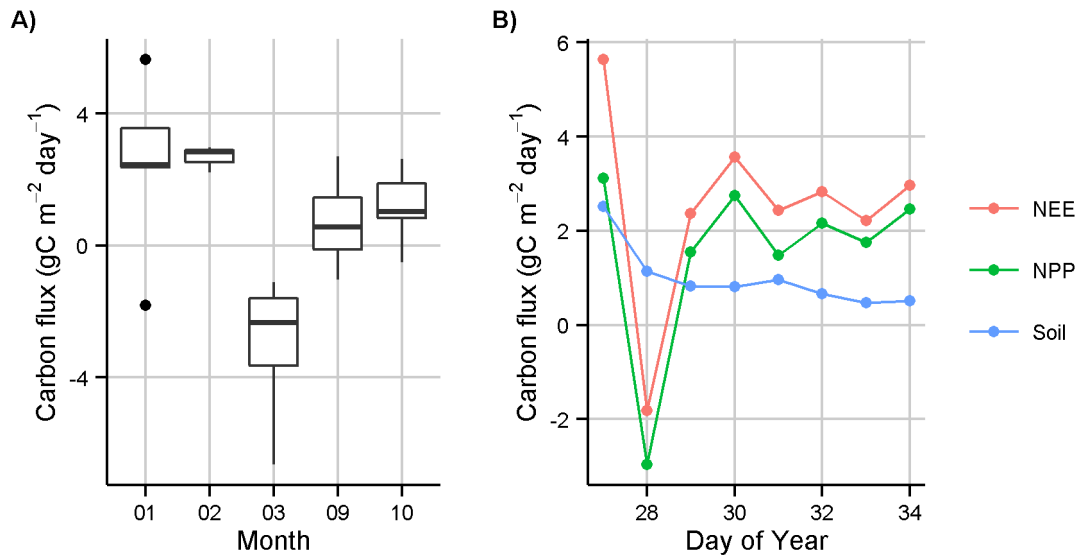


Figure 6.A) the daily Net Ecosystem Exchange (NEE) by month, and B) the daily measurements for the eddy covariance campaign period 27 January to 3 February 2010 for which there are NEE and soil respiration measurements from which Net Primary Productivity (NPP) can be approximated.

Soil respiration between for the seven days between 27 January and 3 February 2010 was $0.99 \text{gC m}^{-2} \text{day}^{-1} \pm 0.66 \text{gC m}^{-2} \text{day}^{-1}$. The approximate Net Primary Productivity over the same period is $1.53 \text{gC m}^{-2} \text{day}^{-1} \pm 1.91 \text{gC m}^{-2} \text{day}^{-1}$ (positive values denote a loss of CO₂ to the atmosphere).

The NEE in January is toward the upper end of the measured range (Figure 6A). Nevertheless, if we apply the proportional difference established between NEE and NPP (Figure 5B) over the measurement period (Figure 7), then we have a value of $-1.83 \text{gC m}^{-2} \text{day}^{-1}$ (negative for CO₂ uptake by vegetation; mean $0.22 \pm 2.05 \text{gC m}^{-2} \text{day}^{-1}$ (1 SD)) with which we can constrain the growth rates from other data sets.

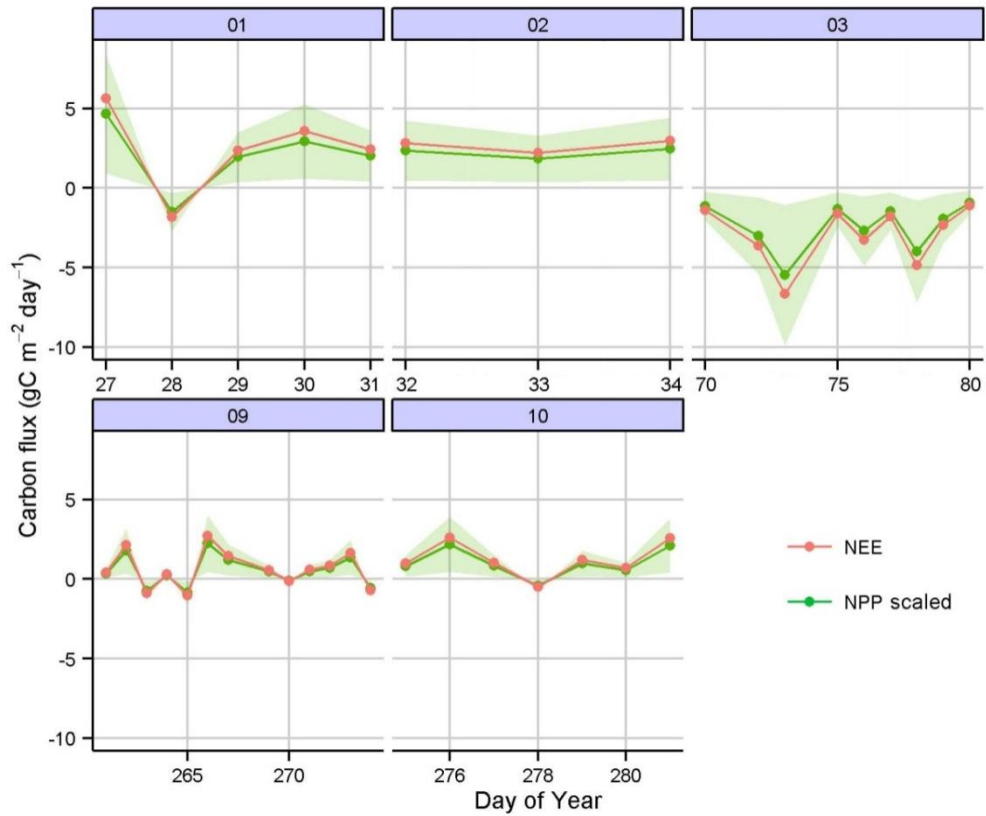


Figure 7. Net Ecosystem Exchange (NEE) and derived Net Primary Productivity (NPP) over the course of the short-term eddy covariance campaigns. The derived NPP is proportional to NEE (cf. Equation 4) established for the campaign period 27 January to 3 February 2010. The shaded area shows the NPP (1 SD).

Water Use Efficiency

In a landscape where the canopy is currently 54% *P. afra*, the isotope record reflects a changing contribution of CAM-, C_3 - and C_4 -derived carbon to the ecosystem. At the plant level, more carbon is acquired through C_3 photosynthesis (red points) than reflects in the stems (blue points), and we can see this leaf $\delta^{13}C$ signal the top soil layers (green point) (Figure 8A).

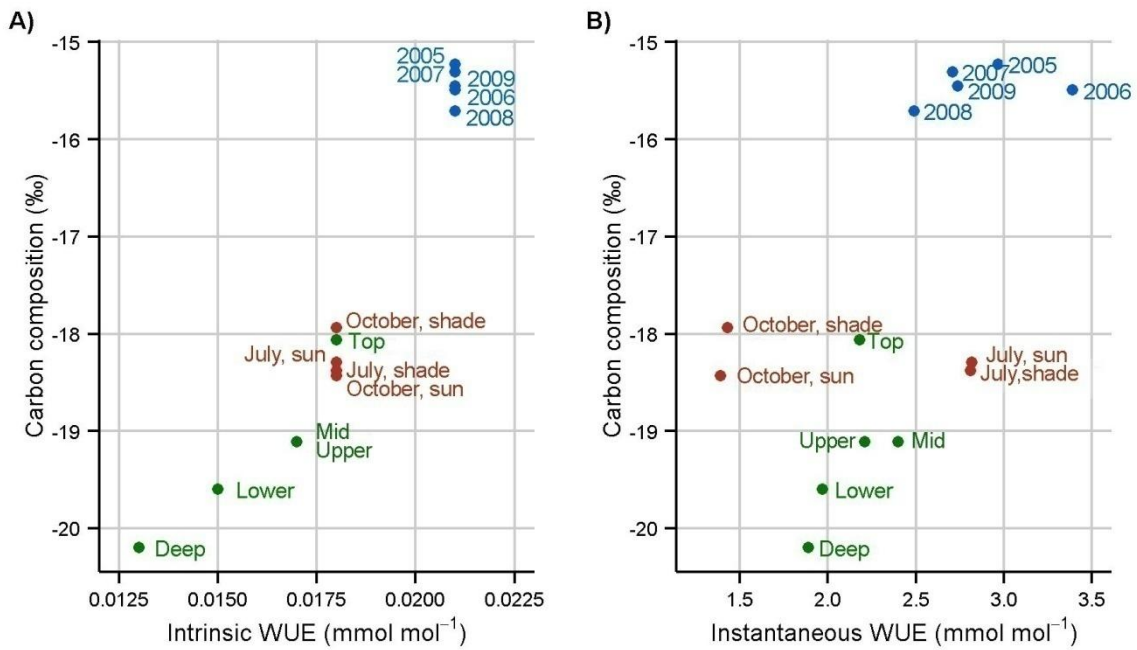


Figure 8. The mean isotopic and water use efficiency values for *P. afra* tissue and thicket soils. The points are coloured by the source of the carbon: soil in green, *P. afra* leaf tissue in red, and the *P. afra* tree rings combined across stems in blue; the labels correspond to Table 5. A) shows intrinsic WUE values (cf. Equation 5), and B) instantaneous WUE values (cf. Equation 6).

Instantaneous WUE captures changing responses to water availability and evaporative demand. At a leaf-level, *P. afra* has a higher WUE in July, when rainfall and temperatures are lowest (Table 1), which is two times higher than the WUE in October when temperatures are higher, but the second mode of rainfall has begun (Table 7).

Table 7. Comparison of WUE determined by eddy covariance and estimated from stem and leaf stable isotope discrimination. All values are given as mean $\pm$ 1 SD, reported to at least one significant figure. Note that WUE from eddy covariance is at the landscape level (i.e., the carbon term includes respiration as well as photosynthesis, and the water term includes evaporation as well as transpiration), whereas the isotopic estimates are at the leaf or whole plant level. Thus the expectation is that landscape WUE estimates are lower than isotopic WUE estimates, as shown here.

	Carbon composition (‰)	Intrinsic WUE (mmol mol ⁻¹)	Instantaneous WUE (mmol mol ⁻¹)	InstantaneousWUE (gC per gH ₂ O)
Leaf isotopes (n=40) ¹				
October shade	-17.94 $\pm$ 0.87	0.018 $\pm$ 0.0009	1.43 $\pm$ 0.08	0.0035 $\pm$ 0.0002
October sun	-18.42 $\pm$ 0.49	0.018 $\pm$ 0.0005	1.39 $\pm$ 0.04	0.0034 $\pm$ 0.0001
July shade	-18.38 $\pm$ 1.30	0.018 $\pm$ 0.0014	2.81 $\pm$ 0.22	0.0069 $\pm$ 0.0005
July sun	-18.29 $\pm$ 1.19	0.018 $\pm$ 0.0013	2.82 $\pm$ 0.20	0.0069 $\pm$ 0.0005
Growth ring isotopes (n=40) ²				
2005	-15.23 $\pm$ 0.77	0.021 $\pm$ 0.0008	2.97 $\pm$ 0.12	0.0073 $\pm$ 0.0003
2006	-15.49 $\pm$ 1.29	0.021 $\pm$ 0.0014	3.39 $\pm$ 0.23	0.0083 $\pm$ 0.0006
2007	-15.31 $\pm$ 0.74	0.021 $\pm$ 0.0008	2.71 $\pm$ 0.10	0.0066 $\pm$ 0.0003
2008	-15.71 $\pm$ 1.22	0.021 $\pm$ 0.0013	2.49 $\pm$ 0.16	0.0061 $\pm$ 0.0004
2009	-15.45 $\pm$ 0.83	0.021 $\pm$ 0.0009	2.74 $\pm$ 0.12	0.0067 $\pm$ 0.0003
Soil isotopes ³				
Top, 0-5cm (n=13)	-18.06 $\pm$ 1.95	0.013 $\pm$ 0.0007	1.89 $\pm$ 0.10	0.0046 $\pm$ 0.0003
Upper, 5-10 and 5-15cm (n=15)	-19.11 $\pm$ 0.95	0.015 $\pm$ 0.0013	1.97 $\pm$ 0.16	0.0048 $\pm$ 0.0004
Mid, 10-15 cm (n=12)	-19.11 $\pm$ 1.04	0.017 $\pm$ 0.0011	2.40 $\pm$ 0.16	0.0059 $\pm$ 0.0004
Lower, 15-20cm(n=12)	-19.60 $\pm$ 1.21	0.018 $\pm$ 0.0021	2.18 $\pm$ 0.26	0.0053 $\pm$ 0.0006
Deep, >20cm (n=18)	-20.20 $\pm$ 0.74	0.017 $\pm$ 0.0011	2.21 $\pm$ 0.14	0.0054 $\pm$ 0.0003
Eddy covariance				
Sep-Oct 2008 WUE _{NEE} (n= 22 days)	-	-	1.61 $\pm$ 1.93	0.0039 $\pm$ 0.0047
March 2009 WUE _{NEE} (n= 11 days)	-	-	-1.33 $\pm$ 2.22	-0.0032 $\pm$ 0.0054
Jan-Feb 2010 WUE _{NEE} (n= 7 days)	-	-	0.99 $\pm$ 0.88	0.0024 $\pm$ 0.0021

Notes:

1. Two isotope samples per leaf, ten leaves per month and sun 'treatment'.
2. Two growth rings per year, across 10 stem, two isotope samples per ring.
3. Soil data were binned due to the different sampling depths.

Discussion

Landscape-scale assimilation rates based on stem RGR

In order to estimate area-based Net Primary Production (NPP) from the annual stem increment (Table 6), further steps are needed. An expansion factor is applied to account for belowground production, assuming that the allocation to stem and root is in proportion to their biomass. An expansion factor of 0.49 is derived from the below:above ground biomass for intact thicket canopy sites (Mills and Cowling 2006). The estimated NPP per stem is plotted against stem basal area in Figure 9. The slope of the relation between stem NPP and stem diameter can be used to express the NPP by *P. afra* on a land area basis, using the stem diameters of *P. afra* measured within plots of known size.

To express growth in terms of carbon gain, it is necessary to multiply the dry mass by the C content of the *P. afra* isotope samples (stem C = 45.14% $\pm$ 1.2%; 1 SD, n=138). This is slightly lower than the 48% used by Mills & Cowling (2006).

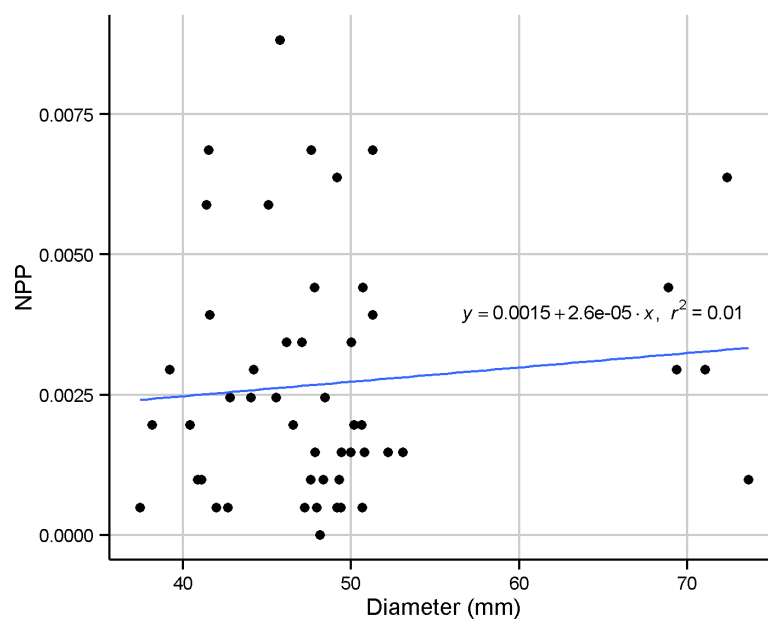


Figure 9. The estimated Net Primary Productivity (NPP) against stem diameter (mm) for S1-10.

The vegetation sampling conducted at the field site recorded canopy measurements. The mismatch meant that an area-based measurement for Net Primary Production (NPP) could not be obtained for this study. There is potential to derive NPP and carbon gain for restored landscape patches which use truncheons of specified sizes, typically 20-50 mm diameter, although smaller cuttings are now being explored (Thicket Forum 2016). Further data points for the stems diameters less than 30 mm

and greater than 80 mm should improve the strength of the observed relationship, which is statically weak ($r^2 = 0.01$, Figure 9).

Water Use Efficiency

If we view the leaf, stem, soil and ecosystem WUE values as an indicator of trends in carbon uptake and water loss over different integrals of time, an interesting picture emerges.

The soil carbon suggests that whole ecosystem WUE has decreased, a pattern emerging globally across different vegetation functional types between 2000 and 2013 (Tang et al. 2014). The soil record reflects a changing contribution of CAM-, C_3 - and C_4 -derived carbon to the ecosystem and suggests that either *P. afra* spent the majority of its time in C_3 mode (Winter & Holtum 2002) or that plant community composition has changed.

Comparative studies of WUE show systematic variation among plant functional groups. (grasses>forbs, annuals>perennials, broad leaf>fine leaf, CAM> C_4 > C_3 ; for instance see Palmer et al. 2010). The isotope record could suggest that the plant community which contributed to the soil carbon in the past was predominantly C_3 , and perhaps not dominated by *P. afra*. This hypothetical plant community would have more C_3 woody shrubs (a $\delta^{13}C$ signature of -33 to -24 ‰), which might be a signal of disturbance because browsing has been shown to increase the proportion of C_3 woody shrubs in drier thicket types (Hoffman & Cowling 1990).

CAM is a mechanism of providing increased water use efficiency (CO_2 fixed per unit water lost) by reducing daytime stomatal conductance and, therefore, transpiration water loss during the period of greatest evaporative demand. CAM increases the WUE of facultative CAM species from approximately 300 gH₂O per gDM in C_3 mode to approx. 100 g H₂O per gDM in CAM (Winter et al. 2005; replotted in Herrera 2009). Our instantaneous WUE estimates from the carbon discrimination in *P. afra* tissue (mean 0.0025 mol CO_2 per mol H₂O) are just outside of this range. At the leaf level, *P. afra* WUE changes seasonally, responding to evaporative demand. Over annual integrals whole plant WUE changes. The growth rings indicate that over the period 2005-2009 there was a decline in WUE. This might suggest a greater proportion of time spent in C_3 mode, however trends from other C_3 species indicate long term increases in WUE (Brienen et al. 2011; Xu et al. 2013).

Eddy covariance results

The negative NPP value from the eddy covariance data means that our assumption that autotrophic respiration losses occur from biomass accrued in the measurement period only is invalid. This is an assumption from which many NPP values are made, and does not reflect an error in the

methodology, but is rather a subjective issue relating to the bounds of the system (Kirschbaum et al. 2001).

Estimates of NPP as a source of carbon to the atmosphere have been reported from monthly and annual integrals (Kicklighter et al. 1999; Cramer et al. 2001) and are common in conditions of high temperature and low water availability (Adams et al. 2004). However, only the 2010 eddy covariance campaign sampled soil respiration, which is known to be highly variable (Zhou et al. 2009). A better understanding of the seasonal change in temperature sensitivity (Q_{10}) of soil respiration is key to describing the carbon efflux from the system.

Caveats arising from methodology and datasets

Isotopic measurements

The radiocarbon dating was done on three samples taken from one individual. While a middle sample was taken to avoid aliasing, further samples from multiple individuals would create a more robust measure of age.

The stable carbon isotopes measured for the leaves and stems may be influenced at post-carboxylation kinetic fractionation, in other words fractionation due to metabolic processes occurring after assimilation (Badeck et al. 2005; Werner et al. 2011). The degree to which this may occur has not been established for *P. afra*. However, if we apply a mean post-photosynthetic depletion of 1.91‰ between leaves and woody stems (Badeck et al. 2005), the possibility of a changing contribution of CAM- and C_3 - derived carbon remains.

Synchronicity of multiple datasets

The opportunity to include eddy covariance data in this study came about fortuitously. The sampling campaigns were planned and executed by the CSIR Ecophysiology Unit, and were not explicitly designed to complement the rest of the sampling and data collection. The campaigns took place in the same landscape to ensure proximity to the automatic weather station (described in *Methods*, above) established at the field site. The eddy covariance data does not capture seasonal or annual behaviour, but it does serve to highlight the variability in this system.

Conclusions

Our age model two rings grow annually with the average growth ring was 0.4 mm (wet) or 0.3 mm (dry) in width. The multi-year and multi-source aboveground relative growth rate (RGR) mean is 0.006 g DM per g DM per year $\pm$ 0.005 g DM per g DM per year (1 SD), which is about 1.1% per year.

For the short period investigated, the eddy covariance data highlighted the variability in the system, measuring intact *P. afra* thicket vegetation a net source of carbon to the atmosphere of $0.11 \mu \text{ mol m}^{-2} \text{ s}^{-1}$, or $0.018 \text{ gC m}^{-2} \text{ hr}^{-1}$.

The trend in isotopic signatures and WUE should be explored to assess the affect of climate change on carbon and energy budgets on thicket systems .These patterns should be explored to reconcile the variation in the values with thicket carbon and water dynamics.

References

See Combined Reference List

Chapter 5 Preface

The mix of photosynthetic pathways in *Portulacaria afra* growing in its natural habitat

This chapter explores the contribution of C₃- and CAM-derived carbon to *P. afra* carbon sequestration. Stable carbon isotopes, dendrometry and infrared thermometry are used to assess the amount of time the species spends different photosynthetic modes.

This chapter was written with contributions from the following people, and their affiliations at the time their contribution were made are listed below:

R.J. Scholes^{1, 2} and Stephan Woodborne^{1, 3}

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2. Global Change and Sustainability Research Institute, University of the Witwatersrand, P.O. Box 2050, Johannesburg, South Africa
3. iThemba Labs (Gauteng), Private Bag 11, Wits 2050, Johannesburg, South Africa

A breakdown of the author contributions is as follows:

The conceptual outline was generated between R.J. Scholes and the candidate. The water balance model was developed by R.J. Scholes and is detailed in Appendix 1. R.J. Scholes has also proof read and commented on the work presented.

Stable isotope analysis was performed by S. Woodbourne.

Introduction

Crassulacean Acid Metabolism (CAM) is a physiological system for carbon assimilation, thought to have evolved multiple times from ancestral C_3 plants, primarily in response to declining atmospheric CO_2 concentrations in the distant past (Pearson & Palmer 2000), perhaps in the late Tertiary Period, with the most diversification in the early-mid Miocene epoch (Ehleringer & Monson 1993; Raven & Spicer 1996). CAM is seen as a CO_2 concentrating mechanism conferring a higher carboxylation efficiency (Winter & Smith 1996) during periods with a reduced CO_2 diffusion gradient. It also confers significant water conservation benefits in the warmer, water-stressed environments which may have accompanied these global atmospheric changes (Ehleringer & Monson 1993; Raven & Spicer 1996). CAM is found in phylogenetically unrelated families, including the Crassulaceae, Cactaceae, Bromeliaceae and more than 30 other (Silvera et al. 2010), including the Portulacaceae (Guralnick & Jackson 2001).

In the C_3 photosynthetic system carbon assimilation occurs during the daytime, and the enzyme responsible for the key assimilatory step is ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). In CAM plants, the diel cycle carboxylation-decarboxylation processes are separated into four phases. Carbon fixation typically occurs at night (Phase 1) and is mediated by the enzyme phosphoenolpyruvate carboxylase (PEPC) (Lüttge 1987). The nocturnally fixed carbon is stored in vacuoles as organic acids, mostly malic acid. During the day the organic acids are decarboxylated, leading to a high internal CO_2 concentration, permitting photosynthesis to occur with closed stomata (Phase 3). Keeping the stomata closed during the hottest and driest part of the diel cycle and open in the coolest and most humid part of the night - when the diffusion gradient that drives the loss of water through the stomata is least - conserves water. This allows high water use efficiencies; approximately 100 gH_2O per g DM growth compared to approximately 300 gH_2O per g DM in C_3 (Winter et al. 2005, re-plotted in Herrera 2009). The widespread presence of CAM in the succulent sub-tropical thickets of the Eastern Cape, South Africa, has been invoked to explain why this vegetation achieves apparently anomalously high net primary productivity in such a dry environment (Mills et al. 2005).

However, CAM carries a cost – the peak assimilation rates are restricted partly by low stomatal and mesophyll conductances, and partly by the storage capacity for organic acids in the mesophyll vacuoles (Cushman et al. 2008). There are also physiological limits to the amount of acidity that can be accumulated during the night without damaging the leaf tissue (Raven & Spicer 1996; Lüttge

2002). The quantum light use efficiency (the efficiency with which absorbed light is converted to fixed carbon), while poorly characterised for CAM species, is lower and more variable than that of either C₃ or C₄ photosynthesis ($0.033 \pm 0.017 \text{ mol mol}^{-1}$ [n=6], compared to $0.052 \pm 0.003 \text{ mol mol}^{-1}$ [n=61], and $0.057 \pm 0.006 \text{ mol mol}^{-1}$ [n=56], respectively; Skillman (2008)). The fact that CAM plants are largely confined to two very specific niches (arid lands and epiphytes in tropical forests) suggests that the pathway is not competitive with C₃ except under water-limited circumstances.

Many species are facultatively CAM, allowing them to switch to C₃ when circumstances permit. In fact, there is a wide spectrum of CAM dependence, from CAM-idling (using CAM to service periods of extreme water stress, during which the CO₂ is derived from respiration and Phase 1 CO₂ uptake is eliminated), through obligate CAM (CAM is the main photosynthetic pathway at all times), facultative CAM (able to switch from C₃ to CAM when water stressed to maintain photosynthetic integrity and sometimes productivity) to CAM-cycling (species which show brief periods of CAM at particular times of day or under special circumstances) (Lüttge 2004; Borland et al. 2011). The duration of stress-induced CAM metabolism varies widely, from months to days and even hours (Herrera 2009). Induced CAM may also be easily reversed or, once induced, a plant may remain in CAM for the rest of its lifecycle (Herrera 2009).

Since calculation of the Net Primary Productivity (NPP) of ecosystems dominated by CAM-capable plants requires knowing the proportions of time in which the individual plants spend in C₃ or CAM it is also necessary to know under what circumstances the switch between photosynthetic systems occurs. No matter which approach to production modelling is adopted –photosynthetic efficiency; water use efficiency; or the assimilation-carbon concentration curve – the parameters differ depending on which metabolic pathway is active. At a landscape level, it is not enough to know what fraction of the plants are CAM-capable. It is also necessary to know when in the diel cycle and when in the year they are actually using the CAM pathway.

Portulacaria afra Jacq. is a facultative CAM plant in the Portulacaceae family, widespread in the eastern parts of southern Africa and often dominant in the subtropical thickets of the Eastern Cape (Lloyd et al. 2002). It switches from C₃ to CAM photosynthetic modes under high water stress conditions (Ting & Hanscom 1977). *P. afra* has been widely promoted as a species for use in carbon sequestration projects in semi-arid lands (Swart & Hobson 1994; Mills et al. 2009; Powell 2009; Mills et al. 2010; van der Vyver et al. 2012), partly because it can be vegetatively propagated from truncheons, and partly because it is able to survive dry periods. The question of how productive it is, particularly during periods of drought and in relation to C₃ species, remains open. Here we use infrared thermometry, dendrometry and stable isotopes to explore the photosynthetic switching

between C_3 and CAM in *P. afra*, on multiple temporal scales, in response to environmental variables, including soil moisture variability. We also propose a set of decision rules for determining and classifying the time spent by *P. afra* in each mode.

Methods

The core experimental site was situated at 33.5276° S 25.3776° E, 15 km south-west of the town of Kirkwood in the Eastern Cape, South Africa. It falls in the sub-tropical thicket biome which is defined by several characteristics: (1) the grass component is noticeably sparse in closed canopy thicket; (2) the system is not fire prone (Kerley et al. 1995); (3) rainfall is low, erratic and non-seasonal; and (4) the presence of succulents. The annual distribution of rainfall in the region is typically bimodal, with peaks in spring and autumn (Figure 1c). See Cowling et al. (2005) for a description of the vegetation and its history.

Thicket vegetation has many variants and subtypes (Vlok et al. 2003; Lloyd et al. 2002). One of the defining features of the succulent thicket subtypes is the presence of *P. afra*. Depending on the landscape circumstances and the mix of surrounding plant species, the absence of *P. afra* may indicate a prior history of degradation through heavy browsing, or it may simply be a natural part of that community. The experimental site and surrounding area is a mosaic of Sundays Valley Thicket (Lloyd et al. 2002) with various levels of utilization and transformation. The area immediately around the experimental site is intact thicket with *P. afra* dominating the vegetation cover.

Climate data and soil moisture modelling

The rainfall record since 1960

Long term daily rainfall and temperature data for the region were sourced from seven Agricultural Research Council (ARC) weather stations (Table 1).

Table 1. Long term weather stations used to compile a single weather history for Kirkwood, Eastern Cape. Source: Agricultural Research Council (ARC).

Station name	Station number	Location (decimal degrees)	Elevation (m asl)	Duration of record used	Distance from site (km)
AddoAgricultural	10561	33.567°S, 25.700°E	85	1960-2002	30.2
AddoSitus NS	20186	33.567°S, 25.700°E	85	1976-1993	30.2
AddoOlifantpark	20218	33.450°S, 25.75°E	152	1994-2003	35
Addo AWS	30561	33.569°S, 25.692°E	31	2002-2007	29.5
Kirkwood AWS	30787	33.404°S, 25.336°E	119	2007-2010	14.3
Kirkwood Prison	20262	33.400°S, 25.350°E	96	1990-2002	14.4
Dunbrody AWS	30615	33.472°S, 25.545°E	61	2003-2010	16.7

These seven datasets were compiled into a single composite dataset representing the likely rainfall at the experiment site, giving preference to the closest available weather station at each time. The result was a 50 year climate dataset for use in interpreting the growth and physiological patterns observed. The rainfall record shows the distinct highly variable and bimodal pattern associated with the region (Figure 1).

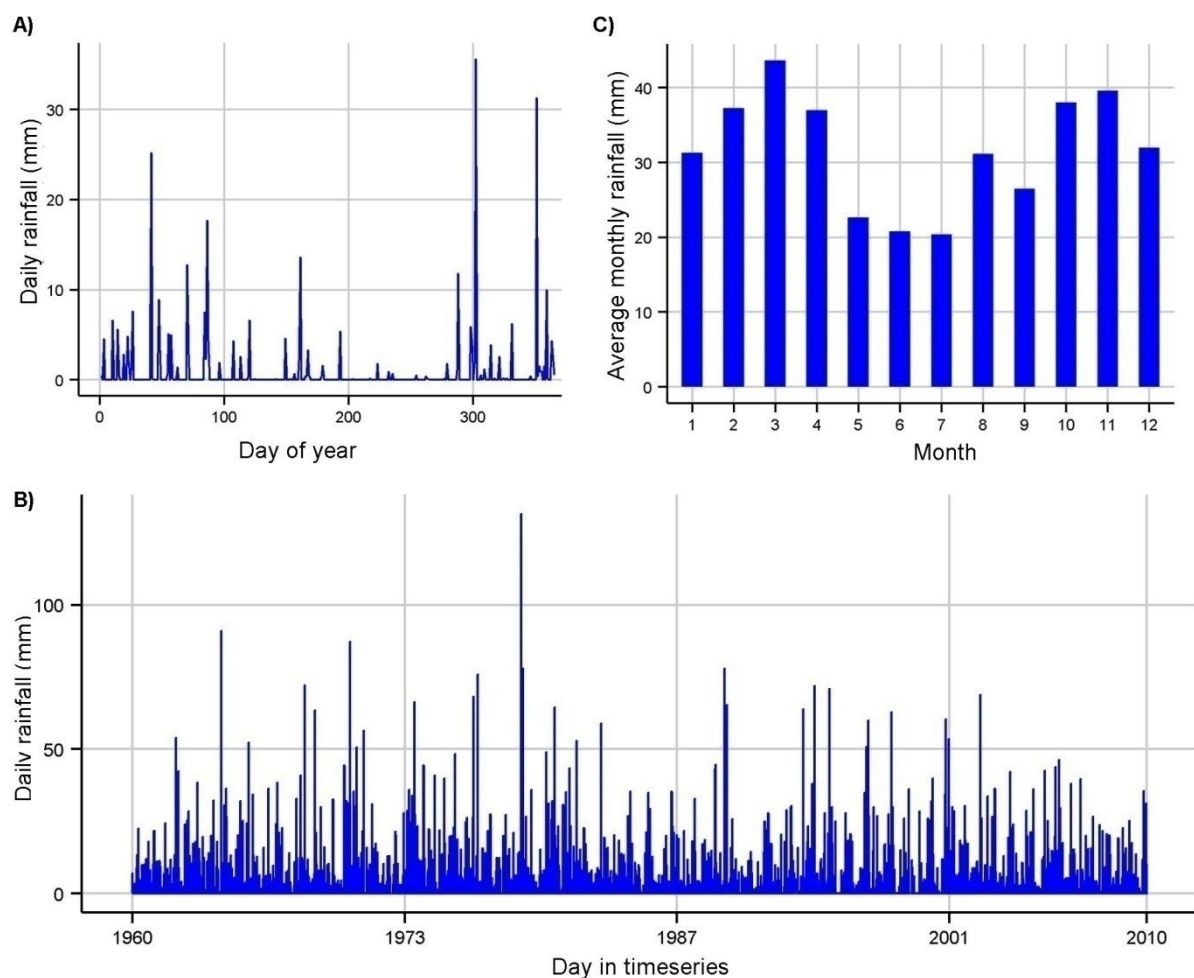


Figure 1. Long term rainfall record for showing A) the daily time series for 2010, B) daily time series from 1960 to 2010, and C) monthly average rainfall. This record was compiled from seven weather stations, the details of which are given in Table 1.

Water balance model

A 'plate model' consisting of a large number of 'bucket models' stacked above one another, was used model soil moisture for the site (Appendix 1). This kind of model has sufficient realism to represent the partitioning of water between interception, evaporation from the soil surface, transpiration, runoff drainage and changes in volume stored in the profile, but can be robustly parameterised for these shallow, variable and stoney soils. The model was driven by daily weather

(Table1). Other inputs included the average monthly fraction of absorbed photosynthetically active radiation (FAPAR), extracted for intact thicket sites from MISR-HR (Verstraete et al. 2012), as a representation of the seasonal display of leaf area; an estimated daily crop factor (K_c), being the relationship between actual and potential evapotranspiration (Allen et al. 1998) and calibrated using data from several brief eddy covariance measurement campaigns in the region (see Chapter 4); and canopy interception volume (Cowling & Mills 2011).

Collection and treatment of sample material

Stem cross-sections

Ten live main stems (numbered S1 to S10) of *P. afra* were cut from near the base of separate plants in October 2009 at the experimental site. After measuring the live circumference, disks were cut from the stems near their base and oven dried and the circumference and largest and smallest diameters remeasured to determine the shrinkage caused by drying. Each disk was halved transversely, with one half stored as a witness and the second half prepared for ring counting and tissue sampling for isotope determination.

The joined cut surface of each half of the disk was smoothed using sandpaper until the outermost ring structures were apparent under low magnification (Figure 2). In the disk from which the tissue samples were taken the ring structures were separated one from another using repeated dry-wet stress. When the rings began to separate they were physically divided using the back end of a scalpel.

The widths of the ten outermost rings, below the bark, were measured using an electronic digital Vernier calliper (± 0.01 mm accuracy, Omni-Tech). Aliquots of sampled tissue from each ring were pre-treated by a toluene-ethanol (2:1, v/v) Soxhlet distillation to remove all mobile constituents (Hall 2010).

For a single stem (S1) tissue aliquots were taken for *all* distinct ring structures from the outermost ring below the bark to the central core of the stem, totaling 110 samples. All aliquots were pre-treated by a toluene-ethanol (2:1, v/v) Soxhlet distillation to remove all mobile constituents (Hall 2010).



Figure 2. The polished witness disks. Top row: S1-S3, middle row: S4-S6, bottom row: S8-S10. The witness for S7 cracked radially from the pith outward and handling was kept to a minimum; it is not included in this image. 'S' is used to denote stem.

Stable carbon isotope analysis

The ^{15}N and stable carbon isotopes (^{12}C and ^{13}C) for all growth ring samples (R1-10 in S1-10) and were measured at the CSIR, Pretoria, South Africa, on a Thermoquest EA 1110 elemental analyser integrated with a VG Isogas SIRA 24 stable isotope ratio mass spectrometer. Isotope results are expressed in delta (δ) notation on a per mille (‰) scale relative to the Vienna PeeDee Belemnite (VPDB) standard.

The relationship between environmental variables (both modeled and measured) and carbon isotope values were explored with principal components analysis. On an individual stem basis the relationship between modelled soil moisture and isotopic values was assessed with a linear regression.

Field instruments for detecting CAM behaviour

Weather station

An automatic weather station located about 2 meters from the plant recorded rainfall (Tipping bucket rain gauge, TR-525M, Texas Electronics, Inc., USA), wind speed (± 0.5 m/s) and direction ($\pm 5^\circ$) (03001 R. M. Young Wind Sentry, Campbell Scientific, Inc., USA), atmospheric temperature ($\pm 0.3^\circ\text{C}$ at 0°C) and relative humidity ($\pm 3\%$, 0-90% range; $\pm 5\%$, 90-98% range) (HMP50 probe, Vaisala Inc., Finland) and Photosynthetically Active Radiation (PAR) (LI190SB, Li-Cor, USA) over the same period. The outputs from all the instruments and dendrometer were stored on a CR1000 data logger (Campbell Scientific Inc., USA) at 30 minute intervals. The meteorological sensors were installed according to recommendations of the World Meteorological Organisation (WMO 2008).

The relationship between the environmental variables and the photosynthetic mode of behaviour were explored using Principle Components Analysis (PCA). The environmental variables were scaled and centered using the mean and standard deviation before exploration using PCA.

Infra-Red Thermometry

Canopy temperature of *P. afra* plants was measured using a SI-100 series infrared radiometer ($\pm 0.2^\circ\text{C}$ between -10 and 65°C , Apogee Instruments Inc., United States) mounted at a height of 1.5 m in a radiation-shielding PVC pipe and pointed southwards, 55° from nadir. The sensor, which has a field of view of approximately 22° , was positioned at a distance of ~ 30 cm from the target portion of the canopy, thus viewing only the leaves of *P. afra* and excluding signal from the soil or sky. A north-facing portion of the plant was chosen, and the sensor was positioned to prevent any shading of the observed area by neighbouring plants.

The measured leaf temperatures were compared to a modelled leaf temperature based on energy balance in order to determine whether the stomata were open. The ‘Gates model’ (Campbell and Norman, 1998) was used to calculate the theoretical leaf temperature:

$$T_{leaf} = T_{air} + \frac{R_{net} - \lambda \cdot G_v \cdot \frac{D}{P_a}}{c_p \cdot G_{hr} + \lambda \cdot S \cdot G_v} \quad (\text{Equation 1})$$

Where: T_{leaf} is the temperature of the leaf ($^\circ\text{C}$)

T_a is the average air temperature (°C)

R_{net} is the net incoming solar radiation (W m^{-2})

λ is the latent heat of vaporisation of water (kJ mol^{-1})

G_v is the conductance of vapour ($\text{mol m}^{-2}\text{s}^{-1}$)

D is the vapour pressure deficient (kPa)

P_a is the atmospheric pressure (kPa)

c_p is the specific heat of air at constant pressure ($\text{J mol}^{-1}\text{C}^{-1}$)

G_{hr} is the sum of boundary layer heat conductance and radiative conductances, and

s is the slope of saturation mole fraction function Δ/P_a (C^{-1}).

The calculation was made for conditions of zero transpiration ($G_v = 0$) for a leaf width of 11.1 mm.

The effective equation is then:

$$T_{expected} = T_a + \frac{R_{net}}{c_p \cdot G_{hr}} \quad (\text{Equation 2})$$

Dendrometry

The same plant that on which leaf temperature was observed, and another small plant, were equipped near the base of the stem with an electronic band dendrometer ($\pm 2 \mu\text{m}$ accuracy, DC2, Ecomatik, Germany) to measure stem size variation over the period 25 March 2009 to 17 April 2011. These dendrometers are referred to as 'D1' and 'D2', respectively. Both individuals had an arborescent growth structure and rooted nodes where the side branches touched the ground.

Determining photosynthetic modes

Two classification approaches were used: a 'four phase framework' using all possible CAM phases; and a "minimalist framework" based only on Phase 1 and 3 (Lüttge 1987). For the four phase framework, hourly data was used, while for the minimalist framework the hourly data was binned into night and day-time, corresponding to Phases 1 and 3 only. For each night and day period the average hourly difference in modelled and measured leaf temperature ($T_{expected} - T_{actual}$) was calculated, and the hourly change in circumference was summed (Figure 3).

Four phase framework				
Hourly dendrometer data	1 stomata open	2 stomata open	3 stomata closed	4 stomata open
Minimalist framework				
Binned hourly data, IRT and dendrometer	1 stomata open	3 stomata closed		
	Night	Day		

Figure 3. Schematic of the two classification approaches used in this study, both of which draw on the phases of CAM defined by Lüttge (1987).

Comparison of the four phase and minimalist classifications confirmed that the latter was sufficient for *P. afra* in this ecosystem. No fine detail – stomatal opening in Phase 2 and 4 – was lost in using the simpler scheme rather than the more elaborate scheme (see Results).

Dendrometer and IRT values are reported to three decimal points, which corresponds to one significant digit and is consistent with the resolution of the instruments and the diel variability they exhibit. In comparing the IRT-derived classification with the dendrometer-derived classification, there was a better match when using this level of precision. Ultimately, both datasets were used to distinguish between photosynthetic modes. The decision rules are presented in ‘Results’.

Data management

Calculations and plotting were performed in R (R Core Team 2015) using base R functions and the following packages: ggbiplot (Vu 2013, <https://github.com/vqv/ggbiplot>), ggplot2 (Wickham 2009), plyr (Wickham 2011), and cowplot (Wilke 2015).

Results

Variation in $\delta^{13}\text{C}$ between growth rings

There is a bimodal distribution to the stable carbon isotope ratios found in the growth rings with the majority clustered around -15.3‰ (outer rings) and -15.8‰ (full S1 disk) and a second peak at -17.7‰ and -19‰ (Figure 4).

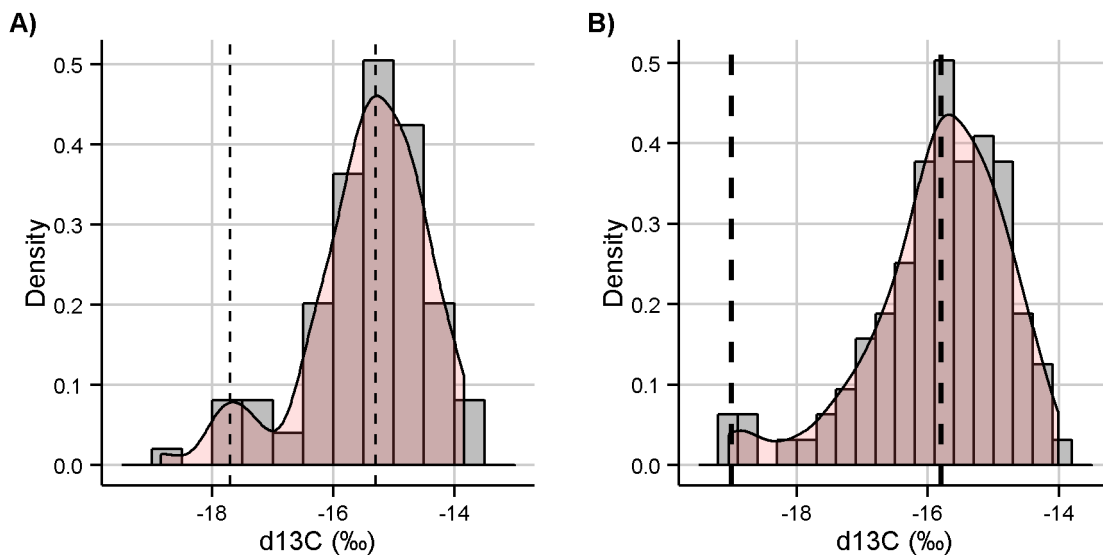


Figure 4. A histogram overlaid with a kernel density plot of the ratio of stable carbon isotope discrimination ($\delta^{13}\text{C}$) for A) rings (R1-10) from stems (S1-10), and B) rings 1-110 for S1. Note the assymetric bimodal distribution. Mode means are indicated by dashed lines (---)

If we explore each stem separately we see that individual plants display unique carbon assimilation behaviour over time (Figure 5). There is no consistent response to the number of growth days, even if the effect of stem size is accounted for by expressing the ring widths as relative values (Figure 6). The $\delta^{13}\text{C}$ values show occasional excursions to more negative values (for example S07 and S03 in 2008 Figure 5). The discrimination between ^{12}C and ^{13}C is greatest during periods when stomatal conductance is high, therefore more negative $\delta^{13}\text{C}$ values are conventionally interpreted as revealing periods of a greater predominance of C_3 photosynthesis.

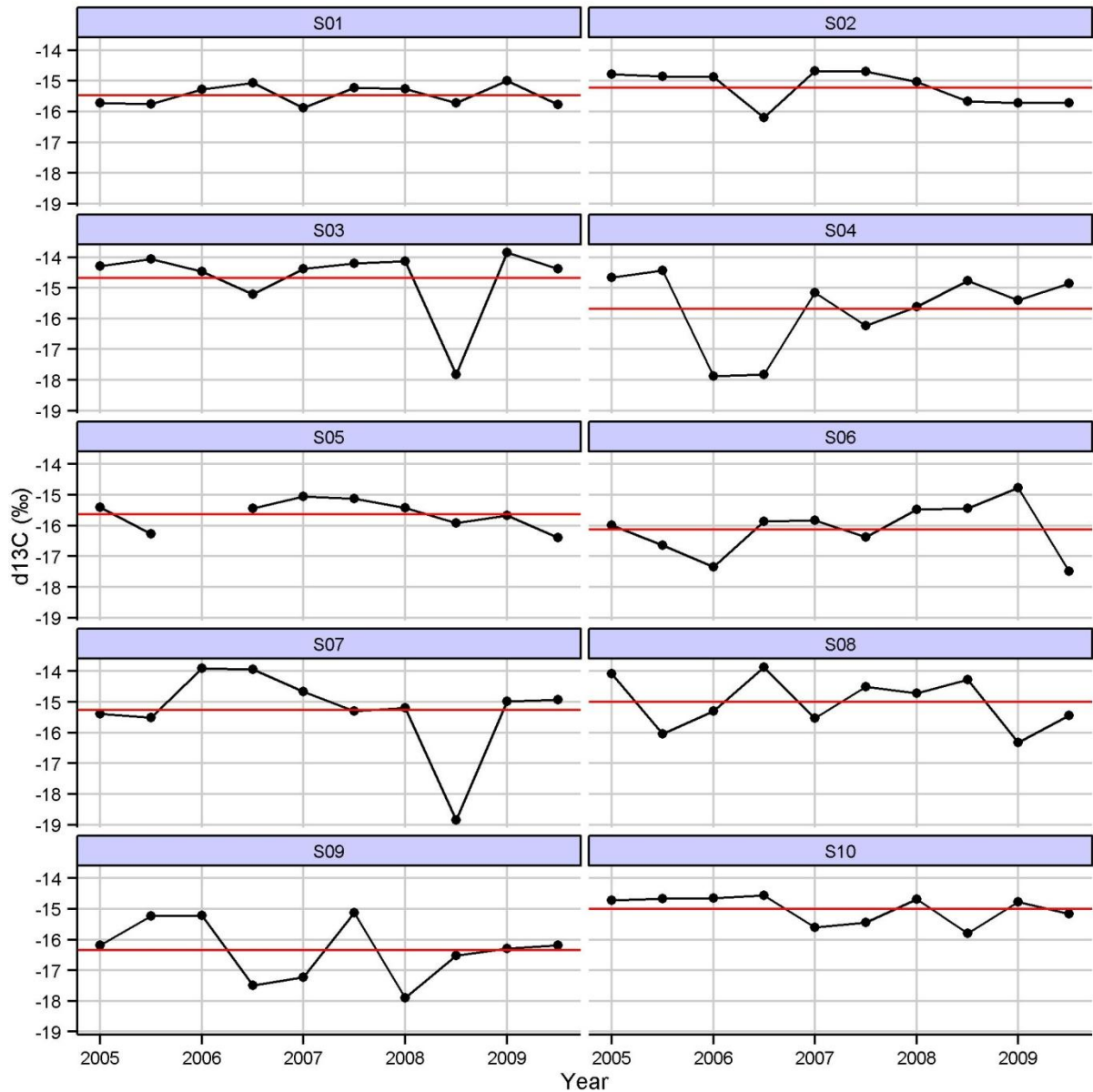


Figure 5. The $\delta^{13}\text{C}$ time series measured in successive growth rings (R1-10) on ten *P. afra* stems (S1-10), with the mean $\delta^{13}\text{C}$ value indicated by a solid red line. Our growth model, derived from dendrometry and radiocarbon aging (Chapter 4), suggests that on average two growth rings are produced annually, which is concordant with the typically bimodal rainfall distribution. The ten rings sampled therefore cover a five year period from the date of harvest in late 2009; i.e., from 2005 to 2009.

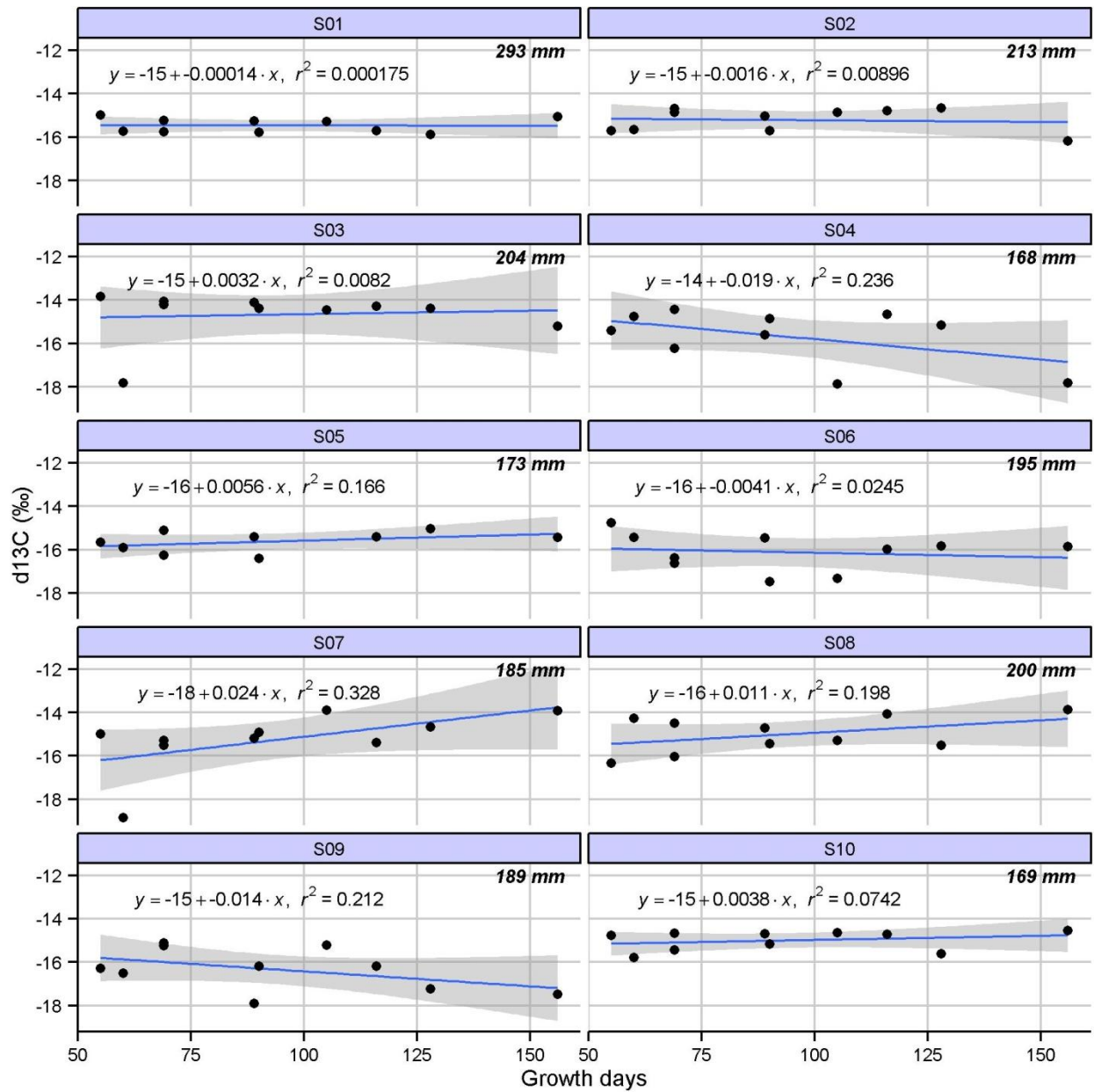


Figure 6. The $\delta^{13}\text{C}$ measured in successive growth rings (R1-10) on ten *P. afra* stems (S1-10) in relation to the number of days in a 6-month period with a profile available water content greater or equal to 40 mm, and the linear regression (blue line) showing the 95% confidence interval (grey shading). Stem circumference is annotated in the upper left hand corner in bold italic font. The rings are thought to be sub-annual, corresponding to the two annual rainfall modes. Thus, the days of profile available water content were calculated for the January-June and July-December periods.

There is a weak statistical relationship showing that rings with a stronger C_3 isotopic signal (more negative) are wider (Figure 7).

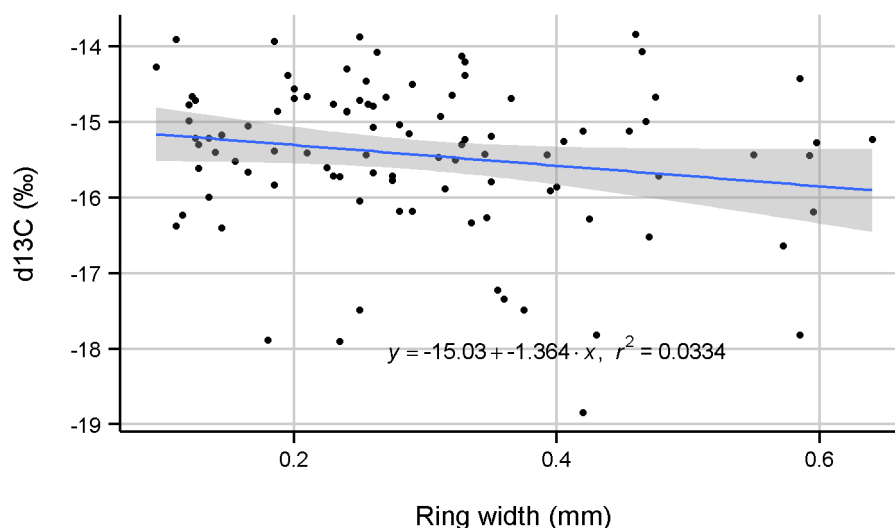


Figure 7. Ring $\delta^{13}\text{C}$ versus ring width for stems S1-S10, and the linear regression (blue line) showing the 95% confidence interval (grey shading).

Classification framework

For the duration of the IRT and dendrometer observation period, *P. afra* did not display the full complement of the 4 phases over a 24 hour period. At no point during the time series did the stomata remain closed for the duration of Phase 3 (i.e., midday).

Table 2. An hour-by-hour analysis of *P. afra* stomatal behaviour against the traditional 4 phase CAM framework (Lüttge 1987). Stomatal aperture was inferred from the difference between actual leaf temperature as measured by the IRT, and expected leaf temperature as modelled by the Gates equation (Campbell and Norman, 1998). Two CAM frameworks were used, in which phase 2 and 4 were both assigned either one or two hours duration.

	Phase 1		Phase 2		Phase 3		Phase 4	
	1 hour	2 hours	1 hour	2 hours	1 hour	2 hours	1 hour	2 hours
Expected occurrence (count)	7200		634	1267	6728	5462	634	1267
Actual occurrence* (count and percent)	4246 (59%)		270 (43%)	599 (47%)	1275 (19%)	929 (17%)	594 (94%)	1185 (94%)

Notes:

- * The actual phase occurrence was not conditional on the expected phase occurring in the preceding hour.

On an hour-by-hour basis, *P. afra* is operating Phase 4 and Phase 1 most often (Table 2). The occurrence of Phase 2 and Phase 4 is artificially high and an artefact of C_3 photosynthesis employed during the day, which corresponds to low occurrence of Phase 3. Phase 3 occurred for only a few hours, most frequently in early morning (peak frequency at 08:00) and during winter when day length was shortest and rainfall is at its lowest (Figure 8). There are instances when the stomatal approximates the 4 phase CAM framework (Figure 10b).

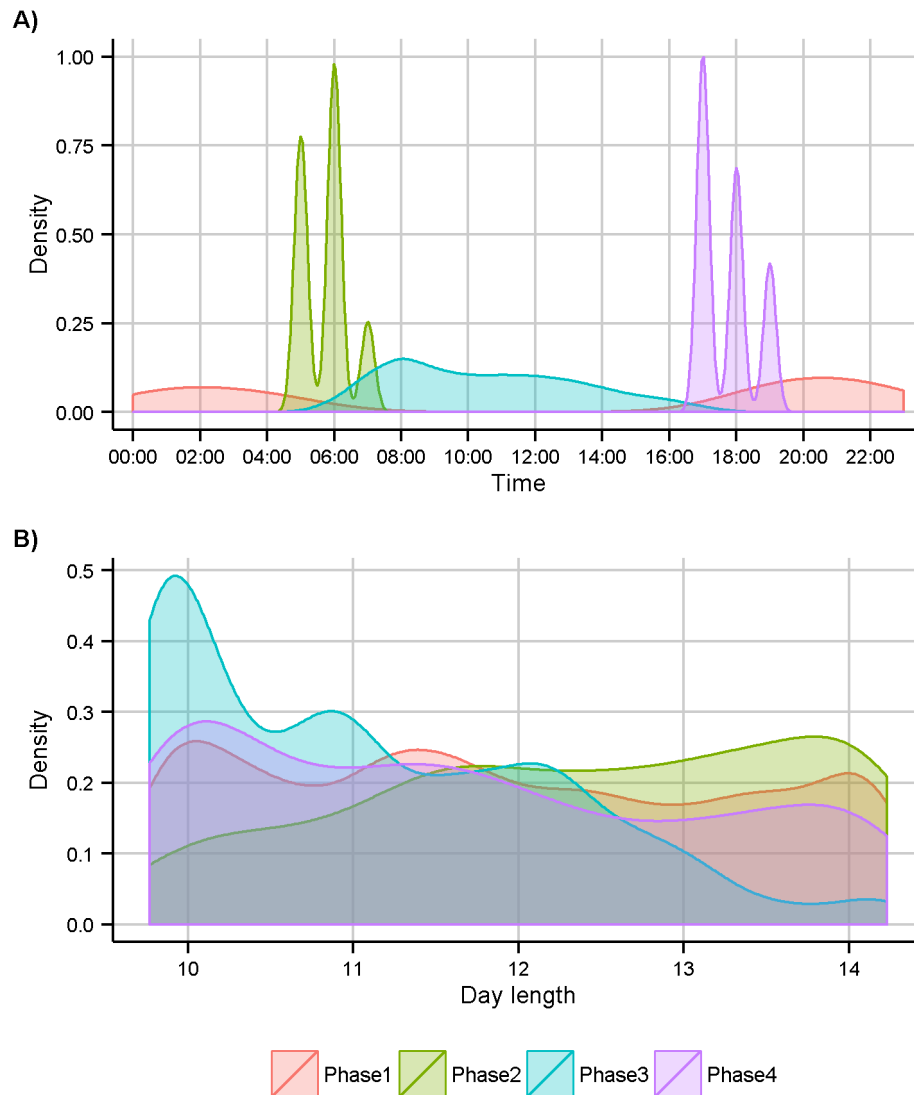


Figure 8. Kernel density plot showing the distribution of the occurrence of the 4 CAM phases (Lüttge 1987) in relation to A) time of day, and B) length of day.

When the decision rules for the expression of each phase included the expression of the expected phase in the previous hour, the match between actual expected occurrences dropped to less than 0.2% for all phases. Therefore the minimalist framework was used for classification, as described under methods.

C₃ and CAM from leaf temperature

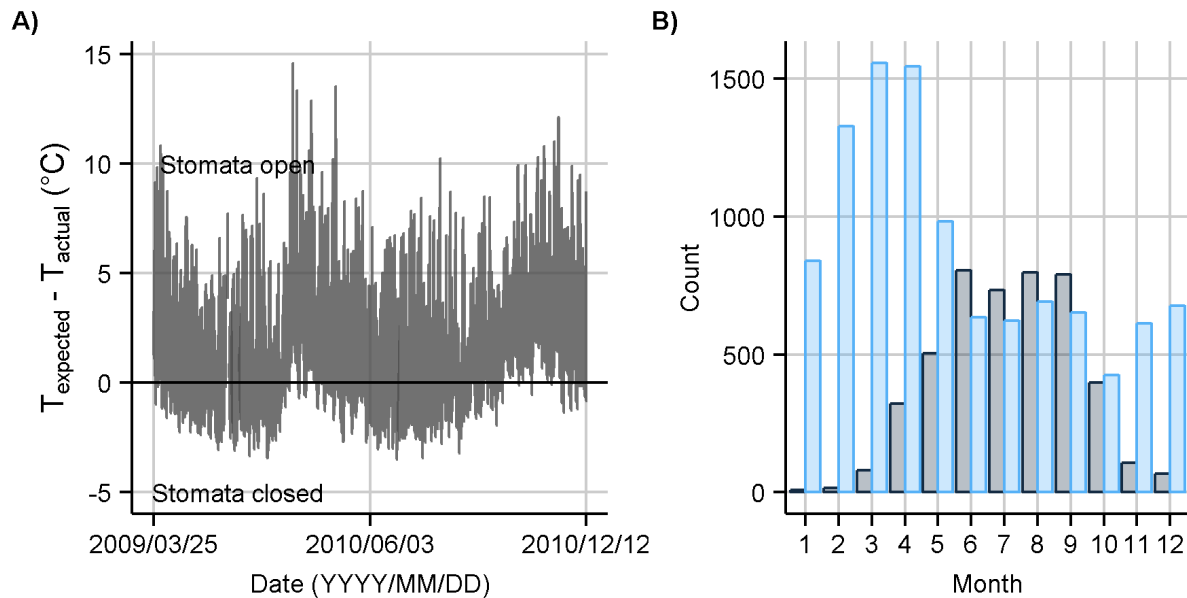


Figure 9. The difference between expected leaf temperature, i.e. with zero transpiration from the Gates model (Campbell and Norman, 1998), and the observed leaf temperature as recorded by the IRT for A) the entire timeseries. The temporal spread of stomatal aperture is shown in B) where light blue indicates open stomata and grey indicates closed stomata.

P. afra shows flexible stomatal behavior on a range of timescales (Figures 9 and 10). For the majority of the timeseries the stomata are open (Figure 9). There is variation in stomatal closure over the year, which appears strongly seasonal, and suggests a link to the bimodal rainfall pattern experienced in the region (Figures 1C and 9B). There are instances when stomatal behaviour approximates the 4 phase CAM framework (Figure 10B), and clear instances of CAM-idling where stomata are closed over multiple diel cycles (Figure 10C).

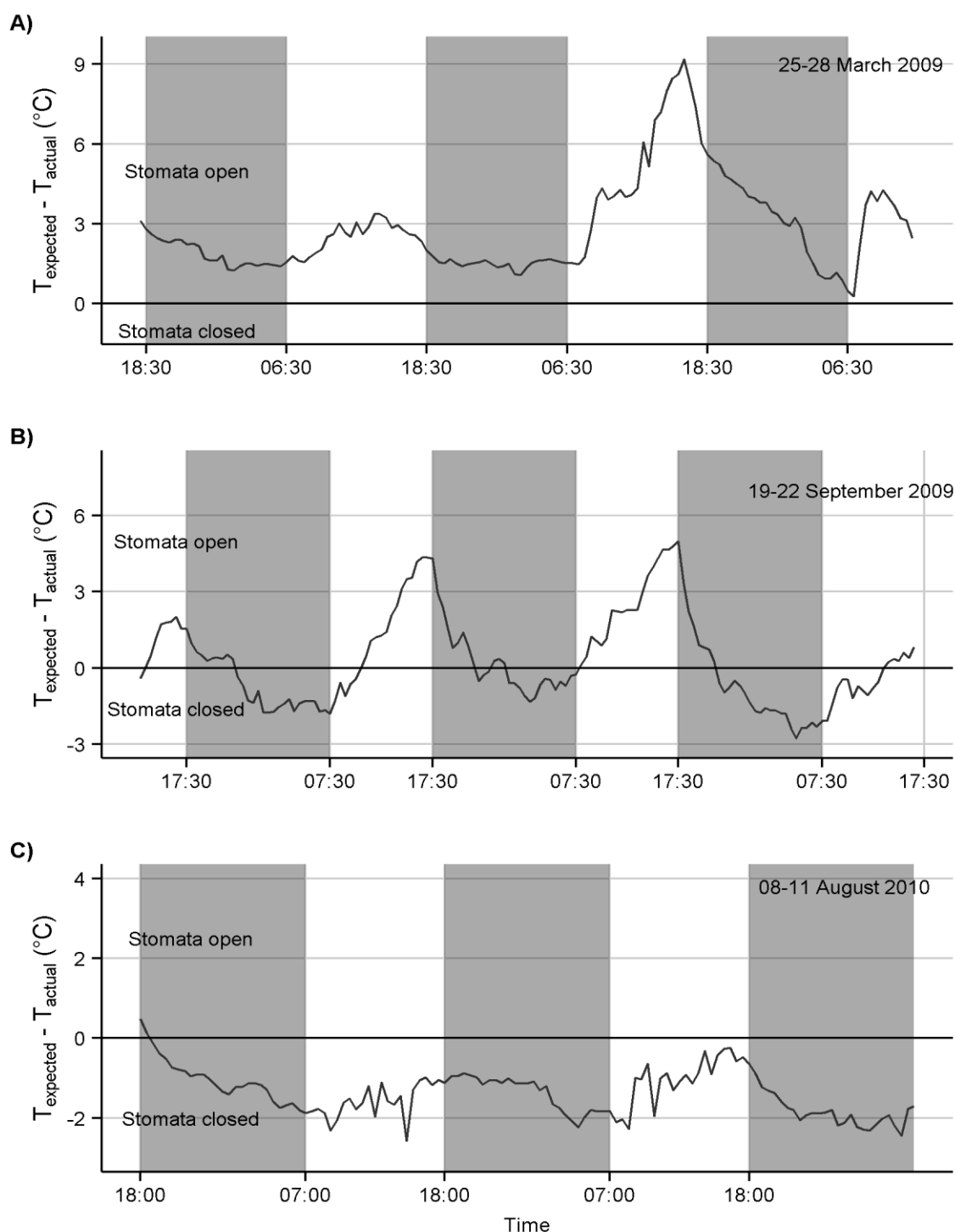


Figure 10. The difference between expected leaf temperature, with zero transpiration from the Gates model (Campbell and Norman, 1998), and the observed leaf temperature as recorded by the IRT for A) 25-28 March, B) 19-22 September, and C) 8-11 August 2010. The vertical gray bars indicate night time. Where leaf temperature (T_{actual}) is less than modelled temperature (T_{expected}) the stomata are open and evapotranspirational cooling is occurring.

The variation between C_3 and CAM periods according to dendrometry

Table 3. Stem starting and endpoint circumferences, and details of shrinking and swelling behavior.

Means are given with 1 SD in brackets.

Dendrometer	Starting circumference (mm)*	End circumference (mm)*	Average shrinkage (mm)			Average swelling (mm)		
			Daily	Night	Day	Daily	Night	Day
D1	454.76	456.61	-0.12 (0.13)	-0.07 (0.06)	-0.07 (0.07)	0.33 (0.47)	0.25 (0.25)	0.28 (0.33)
D2	271.52	276.16	-0.09 (0.12)	-0.05 (0.06)	-0.06 (0.08)	0.31 (0.44)	0.17 (0.25)	0.11 (0.28)

Note:

* The last and first viable readings from the dendrometers were used. After installing the dendrometer some settling time is advised before the data is used.

Interpretation of the dendrometry data is as follows. When these succulent-stemmed plants are transpiring, the stem circumference shrinks. When the stomata are closed, the stem swells as it rehydrates. The change in overall circumference over the two year measurement period due to growth was relatively small, and the short-term fluctuations due to hydration and dehydration were clear and distinct from any sensor noise.

Both measured stems experienced more instances of shrinkage than swelling (Figure 11A). Shrinking through the same day and night is the most frequent change in stem size, but these are relatively small changes (bottom left hand quadrant, Figure 11B). Less frequent but much larger gains occur, predominantly through concurrent day and night periods, which result in a net increase in stem size over the period of the study (upper right hand quadrant Figure 11B, and Table 3). The plants are in a weak CAM mode (CAM-cycling), the majority of the time (Figure 11C).

The smaller stem (D2) displays more instances of shrinking, and spends the more time in CAM-cycling; keeping stomata open during the day and night (Figure 11B and C). It also displays no incidence of CAM-idling. This is in contrast to the larger stem (D1) which seems to spend a greater fraction of its time in water conserving modes of CAM-idling and 'classical CAM' – and relative to D2, it spends less time shrinking (Figure 11 B and C). D1 shows larger absolute changes in circumference, both in shrinking and swelling, while the relative changes are larger for D2 (Table 3). While the sample size is too small to establish a clear pattern, the differences between stems suggest there may be age- or size dependant effects on physiology related either to threshold after which CAM-

idling can be employed, or differentiated trade-offs between carbon gain and water loss, or perhaps a combination of the two.

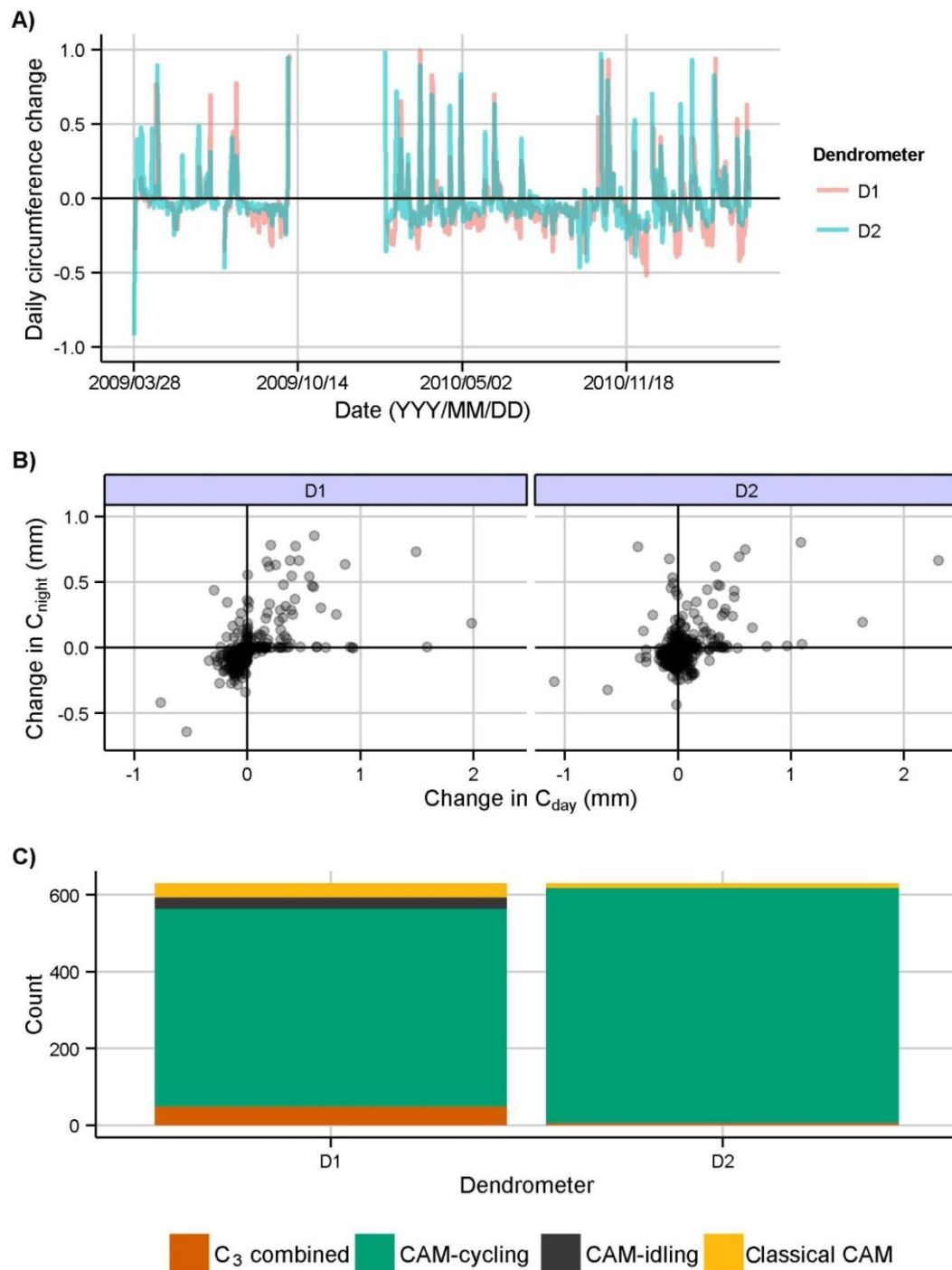


Figure 11. The change in circumference from both dendrometers (D1 and D2) for A) the entire timeseries, B) the night- versus day-time changes, and C) the inferred carbon assimilation modes. Change in circumference (mm) was taken as the sum of the hourly change in circumference over night- and day-time periods, reported to three decimal points. Night and day were determined daily based on sunset and sunrise times.

Combined classification of CAM state using IRT and dendrometer

Initially we used the same stem dynamics as the dendrometer-derived classification and added stomatal aperture as a conditional argument (Table 4). Where previously the all days were classified as either C₃/CAM-cycling/Classical CAM/CAM-idling, now just under 60% of the data days were classified after the application of the decision criteria. In other words, rather than simply acting as classification confirmation, the IRT data significantly refined the distinction between modes.

Table 4. Conditional arguments for defining the photosynthetic pathway used by *P. afra* based on changes in stem size and stomatal aperture. Changes in stem size are denoted by: + for swelling, - for shrinkage, and 0 (zero) for periods which were not clearly shrinking or swelling, but showing no variation, or simply changes in the range of instrument noise. The diel cycle was split seasonally between night and day using sunrise and sunset times. The *a priori* classification is marked in black, the *post priori* additions are marked in red.

Photosynthetic metabolism	Period of stomatal opening**	Stem size change*		
		Night	Day	
C ₃	Day only	0	-	C ₃ to CAM spectrum More C ₃
		0	+	
		-	+	
		-	-	
		+	+	
		+	0	
		0	0	
		-	0	
CAM-cycling	Day and night	+	+	↓ More CAM
		+	-	
		-	-	
		-	+	
		0	0	
Classical CAM	Night only	-	0	
		+	0	
		0	-	
		-	-	
CAM-idling	Neither day nor night	0	0	
		-	-	
		+	+	
		+	-	
		0	-	
		-	+	
		-	0	
		+	0	

Notes:

* Sum of the hourly change in circumference

** Average hourly difference in leaf temperature between modeled and measured values

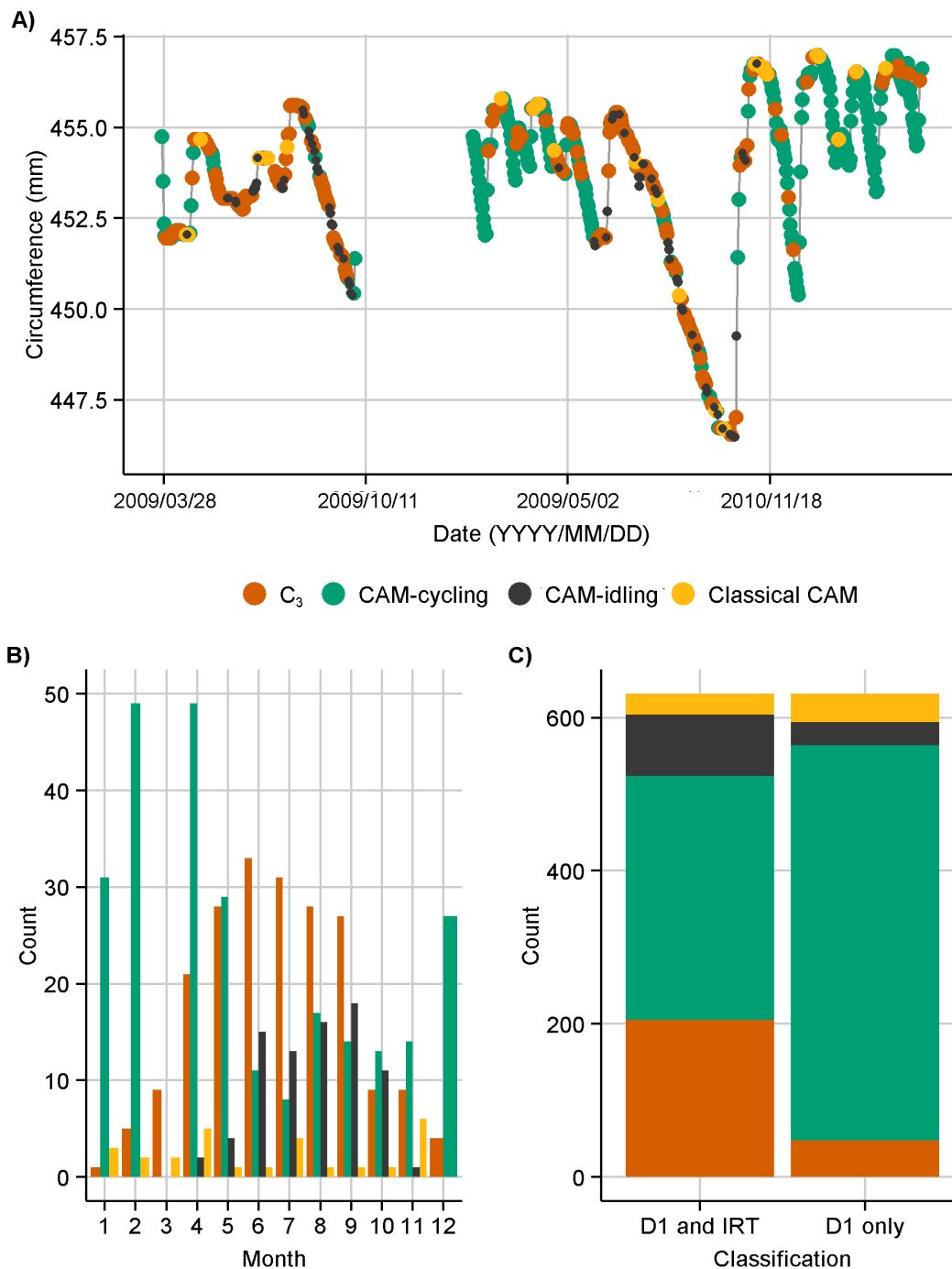


Figure 12. Final mix of modes from a combined IRT- and dendrometer-derived classification approaches, with A) showing the classification on a daily timestep, B) the occurrence of modes on a monthly basis, and C) the difference in classification outcomes when only dendrometer data is used, and when both IRT and dendrometer data are used.

Between the two classifications, each based on one set of instrument readings, there was a 53% agreement for D1. The majority of the errors were distinguishing between CAM-cycling and C₃. The

dendrometer-derived decision rules were over-representing CAM, and under-classifying C_3 and CAM-idling (Figure 12C).

Based on the IRT- and dendrometer-derived classification, *P. afra* employs CAM-cycling ('weak CAM') most of the time (51 %), followed by C_3 mode (32%) and CAM-idling (18%) (Figure 12). Classical CAM is employed least often (4%) which, interestingly, occurs at the turning points and some inflection points in the timeseries (Figure 12A). CAM-idling occurs during the dry season and when the stem goes through massive water-loss related shrinkage (Figure 12 A and B).

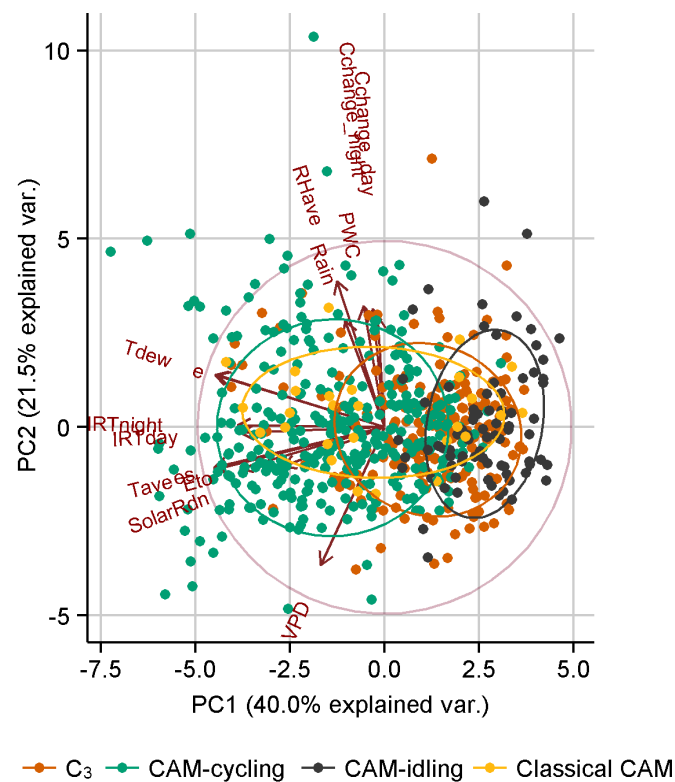


Figure 13. A biplot of the first two components of the PCA on environmental variables, average IRT values for night and day, and hourly stem circumference changes summed over night and day. The multi-coloured ellipses show a normal contour line with a probability of 68% (1 SD), and the correlation circle indicates a probability of 95% (2 SD).

The PCA on the scaled environmental variables binned into January-June and July-December periods reveals a large number of variables contributing to the variation (Figure 13) with lots of overlap between the photosynthetic modes. In the first principal component (PC1) the largest loadings are for average air temperature (T_{ave}), then vapour pressure (e and es), followed by dew temperature (T_{dew}). In the second principal component that largest loading is on average relative humidity and (RH_{ave}), followed by vapour pressure deficit (VPD), and profile water content (PWC). An analysis on

un-scaled data shows both PC1 and PC2 dominated by summed rainfall and the number of growth days (days in which the profile water content exceeded 40 mm).

Discussion

Fraction of P. afra growth contributed by C₃ and CAM

Differences in the ratio of stable carbon isotope discrimination during carbon assimilation are due to the fractionation characteristics of PEPC and Rubisco, and are indicative of how much CO₂ was fixed during the day (by Rubisco) and at night (by PEPC) (Osmond et al. 1973). These differences occur in whole tissue carbon isotopic ratios (Ehleringer & Osmond 1989), and there are clear modes for C₃ and C₄/CAM carboxylation processes.

Plants with a C₃ photosynthetic system have a $\delta^{13}\text{C}$ signature of -33 to -24 ‰ while the CAM plant signature is -20 to -10 ‰ (Ehleringer & Osmond 1989). 'Strong' CAM (i.e. obligate CAM and facultative CAM predominantly in CAM mode) has a signal of -16.1 ± 2.6 (Silvera et al. 2010). Our stems, averaged across all rings, had a signature of -15.8 ± 1.0 ‰ (1 SD).

Extrapolation of a laboratory-derived relationship in seven CAM and two C₃ species between $\delta^{13}\text{C}$ signal and the fraction of the time for which plants are in CAM mode indicates that the pure C₃ end member is -26.9‰ and the pure CAM end member is -8.7‰ (Winter & Holtum 2002). The equation for the proportion of time that assimilation occurred as CAM is thus $y = -5.4909x - 47.94$. This suggests that the *P. afra* plants in this locality over the past decades derived 61% of their carbon through the CAM pathway and 39% through the C₃ pathway. Previously reported values of -17 to -17.5‰ for field grown *P. afra* (Guralnick et al. 1984a; Guralnick et al. 1984b; Mooney et al. 1977) which suggests a different C₃-CAM mode mix; with the plants previously documented fixing 6.6-10% more carbon via Rubisco than those measured in this study.

In the stem cross section S1 there are occasional large excursions, always in a single ring, towards more negative $\delta^{13}\text{C}$ values (-19.0‰); in other words towards the C₃ range. We speculate that these are related to prolonged periods of adequate soil water.

Fraction of time spent in CAM mode

Relying on isotopic signatures to distinguish photosynthetic modes has given rise to the phenomenon of 'hidden CAM' (Zots 2002), where isotopic signatures indicate a C₃ plant, but other techniques show clear CAM behaviour (e.g., diurnal acid fluctuations in the Bromeliaceae; Pierce et al. 2002). In this case the opposite is true: our isotopic signatures suggest a strongly CAM plant, while our classification indicates very little time spent in classical CAM mode. Based on our classified

time series we would anticipate a more negative $\delta^{13}\text{C}$ as a result of the large proportion of daytime CO_2 uptake occurring during C_3 and CAM-cycling.

One possible resolution is to consider at how *P. afra* might potentially partition assimilated carbon. Analysis of $\delta^{13}\text{C}$ of seeds, seedlings, flowers and new shoots might reveal whether carbon fixed via Rubisco makes a contribution to reproductive success rather than vegetative growth (for instance see Winter & Ziegler (1992) and Cushman & Borland (2002)).

From personal observations we have noted a huge investment to the seedset, but with very little to no seedling survival. This is supported by observations of the slow to absent recovery to *P. afra* following over browsing and removal from the landscape (Lechmere-Oertel 2003) which may, in turn, reflect a stem-size or age related ability to employ CAM pathway (note the difference in CAM employment in D1 and D2).

It has also been noted that not all individual plants flower at the same time. If individual plants have a unique switching behaviour it might give rise to unique mix of C_3 - and CAM-derived carbon available for maintenance and growth. If an individual does not flower in a season the carbon accrued through C_3 photosynthesis might go towards growth – which may explain the more negative isotopic excursions noted in our 10 stem time series.

Nevertheless, it is clear that carbon derived from CAM photosynthesis plays an important role in contributing to net carbon gain.

Triggers for switching mode

P. afra switches photosynthetic mode on a daily or sub-daily timescale, a pattern which is clear regardless of the classification decision-rules used. The differences in dendrometer- and IRT-derived classification might be expected, since changes in stem size is driven by the daily rhythm of changing water potential gradients, but as *P. afra* is a succulent plant, this signal is confounded by the stem water storage.

Previous work on stem diameter variation in facultative CAM plants indicates a strong relationship to VPD (Matimati et al. 2012). Our PCA findings indicate that the trigger for switching between modes is caused by multiple factors rather than a single dominant factor. This is consistent with findings for strongly CAM plants (Lüttge 2004). We believe the multiple water-temperature interactions along soil-plant-atmosphere continuum are integrated by profile available water content.

CAM requires low variability of water supply– it is found in succulents, not xerophytes – and there needs to be hydrated tissue in order to store the malic acid. Our trace (Figure 12A) and plot of the

monthly occurrence (Figure 12B) of mode switching suggests that there is insufficient replenishment of internal water reserves to allow prolonged employment of classical CAM. The majority of CAM cycling occurs during high rainfall, high temperature conditions; and CAM-idling during conditions of low-moderate temperatures and low rainfall (Figure 12B). The net is slow growth (Chapter 4).

Insights for restoration

Microclimate effects have been found to have significant effects on plant survivorship and growth rates in semi-arid environments (del Campo et al. 2006). It has also been noted that opposite leaves in the facultative CAM *Clusia minor* (formerly *Clusia rosea*) have been found to employ different metabolic pathways depending on relative humidity of the air immediately surrounding them (Schmitt 1988). This micro-habitat effect may have to the restoration protocol using *P. afra*. Restoration trials have found that inter-truncheon planting distance may play a role in truncheon survival (Mills et al. 2015). This maybe a case of intra-canopy shading creating a stomatal response to microclimate and leaf-specific differences in photosynthetic modes, which would ultimately affect net carbon balance, growth and survival.

Photosynthetic modes: separate paths or one axis?

The value of the distinction between C_3 and CAM has been questioned (Zots 2002), with some calling in an outdated impediment to understanding CAM. But viewing C_3 and CAM on a spectrum has a different suite of issues. Some researchers report difficulty in distinguishing between CAM and CAM-cycling (Martin et al. 1990).

What remains unquestioned is that CAM metabolism, and particularly facultative CAM metabolism, is very plastic (Cushman & Borland 2002; Dodd et al. 2002, Herrera 2009). In order to capture this 'plasticity' long term *in situ* studies of facultative CAM plants have been called for (Herrera 2009; Zots 2002). To that end we feel our approach provides a solution; a continuous and non-destructive method which can run for periods much longer than studies typically done to date (which cover on the order of days to weeks).

Caveats arising from methodology and datasets

Isotopic fractionation

Post-photosynthetic fractionation has been shown to influence the measurement of stable carbon isotopes in the stems of woody species (Badeck et al. 2005). This level of kinetic fractionation has not been explored for *P. afra*. However, if we apply the woody stem depletion values of 1.91‰

(Badeck et al. 2005) to our mean growth ring signature of -15.8 ± 1.0 ‰, *P. afra* would still be considered a strong CAM species (-16.1 ± 2.6 ‰; Silvera et al. 2010).

Dendrometry and influence of rooting

The variable growth morphology of *P. afra* (Stuart-Hill, 1992) could potentially influence the applicability of the dendrometer results. The individuals in this study had an arborescent-like structure rather than the sprawling growth pattern that is also observed, and in both individuals rooted side branches were noted. Further proof-of-concept needs to include stem diameter variations recorded for arborescent individuals with rooted nodes and individuals with roots at the main stem only. The node roots may influence the stem water potential and therefore the size, pattern and duration of radial shrinkage and swelling.

Reconciling the datasets

Further exploratory analyses of the state space of the system may identifying key environmental variables and help reconcile the data sets. Derivative analysis approach has proved useful for revealing key environmental triggers linking dendrometry measurements of shrinkage and gain. (Cocoza et al. 2012).

The notion that the leaves are acting independently (see *Insights for restoration*, above) could account for some of the unique individual behaviour noted. Leaf malic acid concentrations sampled for all over in individual would yield insights into the leaf dynamics, and perhaps provide a means to reconcile the data sets (see Matimati et al. 2012).

Conclusions

Patterns in carbon gain from multiple species using stable carbon isotopes suggest that *P. afra* in the wild in the core of the thicket biome is deriving about 60% of its carbon from the CAM pathway. Our data suggest that it is spending only 4% of the time in classical CAM mode, and the majority as CAM-cycling. This is a 'weak CAM' mode which we would have expected to have resulted in a signature closer to that of a weak CAM plant (i.e., more negative $\delta^{13}\text{C}$), rather the than values reported, which are more consistent with a relatively 'strong CAM' plant. We believe that the $\delta^{13}\text{C}$ from grow rings provide a good integral over time, and marry well with the non-typical instrumental data used, to capture the variation in switching behaviour over long timescales.

References

See Combined Reference List

A summary of the key findings

Global scale

At a global scale, the climate regulation service provided by terrestrial ecosystems is substantial, although it varies with locality. Importantly, the portion of this service provided by carbon is finite, and land management decisions may increase the vulnerability of the service. This highlights the need to understand other non-carbon related service benefits and how they trade-off against carbon.

Landscape scale

In the thicket, at a landscape scale, there is stream flow response to land cover change and presence of *P. afra* in the vegetation canopy. Simple metrics based on river gauge data can distinguish different aspects of freshwater ecosystem services, which show that intact vegetation reduces floods and provides more steady flow than degraded vegetation. The restoration of thickets is likely to improve the range of ecosystem services based on the reliable provision of fresh water and the attenuation of floods.

The net impact of thicket restoration on the surface energy budget and net radiative forcing is also clear, but differs in this study from the conventional wisdom that afforestation or reforestation is a net climate benefit. The albedo characteristics of intact and degraded thicket were described using the new Multi-angle Imaging SpectroRadiometer High Resolution (MISR-HR) products. The difference in mean annual albedo between (a well-established) intact *P. afra* thicket and that of degraded thicket was observed to be 0.05, with the thicket being the darker, more radiation-absorbing surface. Following restoration, this difference results in positive (warming) radiative forcing which is an order of magnitude bigger than (cooling) radiative forcing inferred from published increased in carbon stocks for the area.

This underscores the need for robust measurements of carbon assimilation for restoration projects and the importance of considering the full suite of substantive land-atmosphere interaction processes, including albedo changes and potential climate impacts via non-CO₂ greenhouse gases and aerosols. In the context of climate change, the land cover change feedback to the rainfall needs to be given particular attention, due to the *P. afra*'s characteristics of stem and leaf succulence and ability to employ CAM metabolism.

Plant level

The ecophysiology and photosynthetic physiology of *P. afra* was examined in order to better understand the contribution by this “service providing” species (Martin-Lopez et al. 2009) to the carbon sequestration and climate regulation services provided by thickets. Patterns in carbon gain from stable carbon isotopes suggest that *P. afra* is deriving about 60% of its carbon from the CAM pathway, while water and temperatures fluctuations at stem and leaf level suggest that it is spending only 4% of the time in classical CAM mode.

What remains unquestioned is that the photosynthetic behaviour of *P. afra* very plastic (Cushman & Borland 2002; Dodd et al. 2002, Herrera 2009) and datasets which cover long timescale are required to explore the dynamics of the switching (Herrera 2009; Zots 2002). To that end we feel our approach provides a solution: a continuous and non-destructive method which can run *in situ* for periods much longer than studies typically done to date (which cover on the order of days to weeks).

Critical thoughts: room for improvement and an opinion on the datasets required

Perhaps the most interesting ‘story’ emerging from Chapters 4 and 5 is the difference in the classification and occurrence of photosynthetic modes from the dendrometry, infrared thermometry and stable carbon isotopes datasets. Further work on the classification proof of concept is required. Further work to explore the state space of the system will provide new insights into the essential properties, thresholds and dynamics of the system.

Future research – fresh insights

This work has highlighted a range of areas which could be further explored which I summarise in Table 1. Some of which are evident in the chapters themselves, some which became apparent while working on this, and others emerged from my discourse with other students and colleagues.

Table 1. Top future research directions emerging from this thesis.

Topic	Area	Specifics	Related relevant chapter(s)
1	<i>P. afra</i> growth ring, widths, carbon isotopes and $c_i:c_a$ ratios.	Understanding plant and ecosystem carbon and water dynamics in conditions of climate change. Understanding how c_i and WUE relate to atmospheric CO ₂ concentrations and climate change.	3,4 and 5
2	Surface energy balance.	The partitioning between latent and sensible heat fluxes.	3
3	Albedo characteristics for South African vegetation types.	Inclusion MISR-HR in land-atmosphere model	3
4	Histological understanding the <i>P. afra</i> growth ring formation.	Vessel density and size and their relationship to climatic variables; growth ring delineation.	4 and 5
5		Assess how physiological responses affect growth – i.e. age and size related growth trends.	4 and 5
5	<i>P.afra</i> allometric equations and an understanding of the different growth patterns.	Allometric relationships based on measurements other than basal stem diameter; perhaps stratified by growth form.	4

Topic 1 explores the response of *P. afra* to changing climate conditions, future ecosystem water and carbon dynamics, and the magnitude of the climate regulation services delivered. This work can be started with the data currently in hand.

I believe topics 2 and 3 are particularly important and topical. Global Climate Models (GCMs) are sensitive to albedo. The GCM run out of the CSIR, a Conformal-Cubic Atmospheric Model (CCAM; Engelbrecht et al. 2009), has yet to have a sensitivity test to albedo (*pers comm.* F. Engelbrecht, 2016). Topic 3 requires a small increment of work on the foundation laid in Chapter 3 to generate a detailed albedo surface for South Africa which would assist in the parameterization of inputs for the next Coupled Model Intercomparison Project (CMIP) phase.

The other MISR-HR products (Verstraete et al. 2011) should be explored for as a resource for improving the representation and categorization of our biomes and landcover, which could

considerably improve the current dynamic vegetation models (DGVMs) over South Africa (Moncrieff et al. 2015). Both albedo and vegetation layers would assist in the evolution of GCMs toward closing the interaction between the land surface and the atmosphere.

Our understanding of the surface energy balance is complicated by the partitioning of absorbed radiative energy into latent heat (evaporation of water) and sensible heat. To effectively plan for and manage future ecological change - including for agriculture/food security or species conservation - requires a substantial improvement in this regard (Topic 2). There is strong consensus among the Coupled Model Intercomparison Project phase 5 (CMIP5) (Taylor et al. 2012) that the pattern of precipitation minus evaporation (P-E) will be enhanced in the warming climate.

Parting thoughts

In the time it has taken to finish this thesis, the international interest in the contribution of semi-arid systems to global energy budget and climate regulation has increased, and so too has the interest in land-use change on the land-atmosphere feedbacks within global and South African ecological community. The large scale restoration of the thickets has also begun. Interest in, and the mainstreaming of, ecosystem services continues with the establishment of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services in 2012 (IPBES, <http://www.ipbes.net/>). This makes working in this interdisciplinary space very exciting indeed.

References

See Combined Reference List

Appendix 1

Plate Model Manual

RJ Scholes, Wits October 2015

Description

The plate model consists of a stack of bucket models, arranged so that the overflow from each runs into the bucket below. The buckets can be any volume (expressed as mm equivalent depth). One approach is to define one plate per soil horizon. Another is to define the top plate to be that depth which represents the soil from which water can be evaporated (i.e. to 5 cm in sands, 30 cm in clays), the next deeper one the layer which contains both tree and grass roots, a deeper one with tree roots only, and a yet deeper one representing water below the rooting depth. A third strategy is to arbitrarily make the plates a fixed real thickness (say 1 cm), and have as many as are needed to occupy the full profile. Since the algorithms to solve a plate model are so simple, the model executes extremely fast. Unlike full physics models, having a large number of layers is not a big drawback. Thus the ability to simulate soil moisture and root distribution with high vertical spatial resolution is a unique feature of this class of model.

Table 1. Each plate is represented by the following variables in SiteName.lay.

Variable	Units	Description
Zlower	mm	Depth of the bottom of the plate below the soil surface
ThetaSat	mm	Water depth equivalent of soil porosity ($1-\sigma/2.64$)
ThetaFC	mm	Water depth equivalent at field capacity ($\psi = -0.001$ MPa)
ThetaWP	mm	Water depth equivalent at 'wilting point' ($\psi = -1.5$ MPa)
ThetaAD	mm	Water depth equivalent when air dry ($\psi = -9$ MPa)
KSat	mm/d	Saturated hydraulic conductivity
R	ND	Fraction of roots in layer (e.g., derived from the Jackson et al. 1996 equation)
H2Oinit	mm	Water depth equivalent

The input file for the model (SiteName.lay) contains variables listed sequentially by plate (Table 1). This file is automatically generated by the programme PlateGen.pas, from a file (siteName.sol) which is based on a standard soil profile description (Table 2).

Table 2. Soil profile description variables in siteName.sol.

Variable	Units	Description
HorTop	mm	Top depth of horizon
HorBot	mm	Bottom depth of horizon
Gravel	g/g	Mass fraction of particles >2 mm
BulkDen	Mg/m ³	Whole soil (i.e., including gravel fraction) bulk density
Texture	class	Sand, Loam, Clay, ClLo, LoSa, SaCl, SCLo, SaLo, Silt, SiCL, iCLo, SiLo

PlateGen uses the gravel content, texture and bulk density for the given horizons to access a lookup table of van Genuchten equation parameters, which then allows the various soil water threshold parameters (saturation, field capacity, wilting point and airdry volumetric water contents) as well as the saturated hydraulic conductivity to be calculated and assigned to layers. A plate one deeper than the profile (l+1) is assigned values which reflect the nature of the bottom boundary of the profile.

Table 3. PlateGen parameters.

Boundary condition	Thetasat	ThetaFC	ThetaWP	ThetaAD	K	R
Impermeable	0	0	0	0	0	0
Impeded drainage	0	0	0	0	$K=0.1 \cdot K_i$	0
Unimpeded drainage, no roots	>MAP	>MAP	>MAP	>MAP	$K=K_i$	0
Aquifer with roots	=MAP	=Thetasat	=0.1Thetasat	=0.05Thetasat	$K=K_i$	0.2

The second input to the plate model is the daily weather driver file (Table 4). It consists of daily records, with each element separated by a space.

Table 4. Daily weather inputs to the plate model.

Variable	Units	Description
Year	yyyy	
Month	mm	
Day	dd	
Rain	mm	Rainfall+snow+occult
EO	mm	Reference evaporation (hypothetical large open water body)
FAPAR		Fraction of absorbed photosynthetically active radiation, derived from remotely sensed data or from measurements <i>in situ</i>

The root depth probability distribution is assumed to follow an exponential decreasing function of depth $y=1-\beta^d$ (Jackson et al. 1996) where d is depth in cm. β varies between ecosystems (shallow roots 0.91, deep roots 0.975). You can edit the root fractions in SiteName.lay if you want an actual measured distribution.

A programme `budyko.pas` runs on the daily weather file (SiteName.wth, Table 4), before running the plate model, to calculate the P:E ratio, which then drives the runoff fraction used in the plate model. The runoff fraction is calculated with the Fu (2007) equation, which has one variable α . A value of 0.28 closely represents the Budyko equation, and works for most semi-arid regions.

Adjustable parameters in the plate model

These are all contained in the `const` part of the programme:

`MaxHorizons=55; {set to enough to get to the bottom of the zone of interest}`

`Runofffrac=0.03; {pre-calculated in Budyko.pas}`

`InterceptPerFAPAR=3.0; {mm of interception for FAPAR=1}`

`Ksat=10.0; {80 mm/d for clay loam x 0.13 for rock porosity}`

`Evaphor=5; {layers to which soil evaporation occurs}`

cropfactor=2.15; {adjusts transpiration, in this case to 0.43*E_o when FAPAR=0.2}

PAWcrit=0.3; {fraction of H₂O-Weighted Root Fraction for transpiration to be reduced}

Interception subroutine

Based on Gash (1979).

Algorithms

Plate.pas reads the year, month day and daily rainfall (P) and reference evaporation (E_o) from the file SiteName.wth. If rain>0 then two amounts are first subtracted: An interception loss which is equal to the smaller of E_o or 3*FAPAR; and a fraction of the rainfall is directly allocated to runoff following a Budyko logic (as implemented by (Fu, Charles, & Chiew, 2007)) based on the annual P:E ratio:

$$\text{Runoff fraction} = 1 - [1 + \phi - (1 + \phi^{2.8})^{1/2.8}] \quad (\text{Equation 1})$$

Where: $\phi = E_{o, \text{mean Annual}} / \text{MAP}$

The plate programme then uses the remaining rainfall to fill the plates to field capacity sequentially from the top. If it reaches the bottom of the profile and still has not used up all the rain, it fills each plate to saturation, from the bottom upward. If it reaches the top plate and still has unallocated rainfall, that rainfall gets added to the runoff already subtracted from the initial rainfall.

Water drains out of the bottom plate through a 'leak' equal to the hydraulic conductivity, which is reduced from the saturated hydraulic conductivity by a the relative water content of the horizon squared. In other words, the unsaturated hydraulic conductivity decreases very steeply as the water in the profile dries out.

The root weighted available soil water in each plate (i) is then calculated:

$$\text{RWW}[i] = (\text{H2O}[i] - \text{ThetaWP}[i]) * R[i] \quad (\text{Equation 2})$$

and summed over the plates, yielding a result in mm. The sum is ratio (Profile Available Water, PAW) to what the sum would have been if every plate was in fact saturated with water

The E_t is then calculated from a simple ramp-to-plateau function:

$$\text{If: PAW} \geq \text{critPAW} \text{ then: } E_t = E_{\text{potential}} \text{ else } E_t = E_{\text{potential}} * \text{PAW} / \text{CritPAW} \quad (\text{Equation 3})$$

This E_t is removed from the soil layers in proportion to their contribution to PAW.

Next, evaporation from the soil surface is removed from each plate. The maximum value of Esoil is:

$$\text{Esoilmax} = E0 * (1 - \text{FAPAR}) \quad (\text{Equation 4})$$

This quantity is extracted successively from surface plates (down to a depth you set), reducing them to ThetaAD until the maximum is satisfied, or until a depth greater than the vadose zone is reached (evap limit depth). The thickness of the vadose zone in mm is estimated as:

$$\text{Zvadose} = 50 + \text{clay\%} \quad (\text{Equation 5})$$

If this depth is reached without satisfying Esoil max, the Esoil continues at a much reduced rate, equal to:

$$\text{Esoil} = E0 * (1 - \text{FAPAR}) * (\text{evap limit depth} / \text{depth of horizon}) \quad (\text{Equation 6})$$

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See Combined Reference List

Appendix 2

Table 1. Values used for WUE calculations. Source: http://cdiac.ornl.gov/ftp/trends/co2/iso-sio/SIO_Mauna_Loa_13CO2.txt

Variable		Input value	Notes
Atmospheric CO ₂ (‰)	Leaf: October 2009	-8.11	
	Leaf: July 2010	-8.38	
	Stem: 2005	-8.216	
	2005	-8.238	
	2007	-8.246	
	2008	-8.243	
	2009	-8.243	
	Soil: Top	-8.243	1 mo. turnover (2008 value)
	Upper	-8.243	1 year turn over (2008 value)
	Mid	-8.236	5 year turn over (2005-2008 ave)
Atmospheric CO ₂ concentration (ppm/ $\mu\text{mol.mol}^{-1}$)	Lower	-8.048	10 year turnover (1998 value)
	Deep	-7.59	Passive – 1981 value/
	Leaf: October 2009	384.34	
	Leaf: July 2010	390.33	
	Stem: 2005	379.63	
	2005	381.81	
	2007	383.59	
	2008	385.46	
	2009	387.36	
	Soil: Top	387.36	1 mo. turnover (2009 value)
	Upper	385.46	1 year turn over (2008 value)
	Mid	382.62	5 year turn over (2005-2008 ave)
	Lower	366.63	10 year turnover (1998 value)
	Deep	339.94	Passive – 1981 ave monthly value

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