

A Fine Line Between Carbon Source and Sink: Potential CO₂ Sequestration through Sustainable Grazing Management in the Nama-Karoo

Oksana Rybchak, Justin duToit, Amukelani Maluleke, Mari Bieri, Guy F. Midgley _D, Gregor Feig, and Christian Brümmer

Abstract

Semiarid South African ecosystems are managed for livestock production with different practices and intensities. Many studies have found grazing to be an important driver of vegetation change; however, its impacts on carbon fluxes remain poorly studied. Unsustainable management over the past 200 years has led to an increase of degraded areas and a reduction in species diversity, but destocking trends in the past three decades may be facilitating a recovery of net primary productivity and vegetation cover in some areas. This chapter provides a brief historical overview on livestock management practices and their likely impact on carbon exchange in the Nama-Karoo Biome. We present a case study based on five years of eddy covariance measurements, in which effects of past and current livestock grazing on CO_2 exchange were studied. Two sites with different livestock management but similar climatic conditions formed the basis

O. Rybchak (🖂) · M. Bieri · C. Brümmer

Thünen Institute of Climate-Smart Agriculture, Braunschweig, Germany e-mail: oksana.rybchak@thuenen.de; mari.bieri@thuenen.de; christian.bruemmer@thuenen.de

J. du Toit Grootfontein Agricultural Development Institute, Middelburg, South Africa

A. Maluleke · G. F. Midgley

School for Climate Studies and Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

e-mail: amukelani.maluleke@thuenen.de; gfmidgley@sun.ac.za

G. Feig

Department of Geography, Geoinformatics and Meteorology, University of Pretoria, Pretoria, South Africa

South African Environmental Observation Network, Colbyn, Pretoria, South Africa e-mail: gregor@saeon.ac.za

for this preliminary effort to improve the understanding of carbon exchange and its drivers under contrasting management regimes. The case study revealed that net CO_2 exchange is near-neutral over an annual scale, with precipitation distribution emerging as the main controlling factor of subannual variance. Although CO_2 release at the lenient grazing site was slightly higher than at the experimental grazing site, longer time series are likely needed in such variable ecosystems to make a pronouncement regarding long-term net fluxes. Given their vast extent, livestock rangelands may have an important effect on regional carbon balance.

17.1 Livestock Grazing Systems in the Nama-Karoo

The Nama-Karoo is the third largest biome in South Africa, characterized by vast, flat plains in the lower Karoo (~ 800 m.a.s.l.) and rugged reliefs in the upper Karoo $(\sim 1300 \text{ m.a.s.l.})$ with shallow, weakly developed lime-rich soils (Dean and Milton 1999; Mucina et al. 2006). It is dominated by shrubs, grasses, herbs and geophytes. The major disturbance to vegetation in the Nama-Karoo has been extensive livestock grazing (mainly sheep) restrained within paddock boundaries since the last decades of the nineteenth century (Skead 1982; Archer 2000). Approximately 60% of the Nama-Karoo Biome is characterized by moderately to severely degraded soil and vegetation cover (change in species assemblage) (Mucina et al. 2006). Many research efforts have been focused on understanding the causes of land and vegetation degradation in the Nama-Karoo Biome, and inappropriate grazing management is considered one of the major drivers (Hoffman and Ashwell 2001). Regardless of extensive theoretical background, a fully predictive understanding of the effects of livestock grazing on biodiversity and ecosystem processes in semiarid Nama-Karoo ecosystems remains elusive (Bekele 2001; Tilman et al. 2012; Rutherford and Powrie 2013).

17.1.1 Historical Overview

Springbok (*Antidorcas marsupialis*) was the most numerous native grazer in the Nama-Karoo prior to large-scale human livestock management (Dean and Milton 1999). Namaqua Afrikaner sheep grazing (transhumance¹ or nomadic² ranching) has been present in the Karoo for approximately 1800 years among the Khoekhoen people (Truter et al. 2015). In the eighteenth century, the abundance of ungulates in the Karoo was largely determined by surface water availability (Milton 1993;

¹ Transhumance livestock ranching is a mobile method of land management based on regular (generally predictable) seasonal movements of livestock along the same paths and rangelands.

² Nomadic ranging is characterised by a continuous, irregular and unpredictable movement pattern to find new rangelands in which to graze.



Fig. 17.1 Historical overview of livestock grazing in the Karoo (adapted from Milton 1993; Archer 2000; Truter et al. 2015; Du Toit and O'Connor 2020, Shaw 1873; Acocks 1966, 1979; Roux and Vorster 1983; McLeod 1997; Hoffman et al. 1999)

Owen-Smith and Danckwerts 1997; Archer 2000; Du Toit and O'Connor 2020). In the 1800s, with the advent of European settlers, the number of livestock increased to much higher stocking rates, which negatively affected the vegetation cover in the Nama-Karoo (Fig. 17.1) (Shaw 1873; Archer 2000).

In the 1880s, the concept of rangelands carrying capacity, which determines the number of livestock that can be sustainably kept per unit area, was being implemented as grazing systems in South Africa (Sayre 2008). Farmers used the carrying capacity concept to determine the sustainable stocking rates. The carrying capacity concept was seen as an imposition of foreign land management practices over essentially incompatible indigenous ecosystems (McLeod 1997). By the end of the nineteenth century, large herbivorous historical herds of Springbok had been substantially reduced due to the direct displacement by domestic livestock and reduced grass production (Fig. 17.1) (Hoffman et al. 1999, 2018). By the midnineteenth century, the number of sheep had reached about 5 million, and by the 1930s, it had reached 45 million (Van den Berg et al. 2019). By 1904, the density of livestock had increased to the highest recorded level (more than 5 large stock unit (LSU³) per 100 ha) and remained high until the late 1960s (Hoffman et al. 1999; Van den Berg et al. 2019). In the early 1920s, most of Nama-Karoo had been transformed into fenced rangelands for livestock grazing (mainly sheep and mohair goats, which favor higher-quality plant species) (Hoffman et al. 1999).

The historical trends in land use and alteration of the grazing regime have been responsible for changes in vegetation cover and species composition (Rutherford and Powrie 2013; Du Toit and O'Connor 2020), which are likely to translate into effects on ecosystem functioning (Susiluoto et al. 2008; Pérez-Hernández and Gavilán 2021). Many farms in the Nama-Karoo Biome have undergone a variety of historical land management practices, regimes and stocking at unsustainable rates

³ Large Stock Unit is a reference unit that facilitates the aggregation of livestock of different species and ages (1 LSU is equivalent to 450 kg beef steer).

(Teague and Dowhower 2003; O'Farrell et al. 2008). Grazing is thought to be a major factor responsible for the perceived vegetation degradation (change in species assemblages to species with lower grazing quality/palatability) in the area (Acocks 1966; Owen-Smith and Danckwerts 1997). Even when animals are stocked at low densities, continuous selective grazing benefits unpalatable species by depleting root stocks and decreasing the seed abundance, size and reproductive success of palatable plant species (Acocks 1979; Milton 1993).

Continued livestock grazing has also led to a reduction of palatable plant species and a transition to unpalatable plant species (Kraaij and Milton 2006; Anderson and Hoffman 2007), making Nama-Karoo less productive than before in terms of its grazing capacity (Tidmarsh 1951; Roux and Theron 1987), with effects amplified during times of below long-term average precipitation (du Toit and O'Connor 2014).

Following a drought period (1900-1915) with mean annual precipitation of 288 mm (significantly (20%) lower than the long-term average of 373 mm), a commission of inquiry disseminated recommendations for the management of livestock grazing, separating it into paddocks (du Toit et al. 1923; du Toit and O'Connor 2014). These recommendations helped to optimize livestock distribution on rangelands with rest periods for paddocks as needed. The final report of the Drought Investigation Commission indicated how livestock grazing could degrade Karoo ecosystems (du Toit et al. 1923). One of the main recommendations was to stop stockading animals at night in the same place and limit livestock to paddocks, where livestock remains for a period of a few weeks to months before moving to the next paddock. Equilibrium-based models of vegetation response to livestock grazing and precipitation provided guidance to landowners for best veld management practices (Roux and Vorster 1983; Moll and Gubb 1989). These models are based on recommendations on the control of livestock grazing regimes (paddocks division) (du Toit et al. 1923) and grazing trials near Middelburg in the eastern Karoo (Tidmarsh 1951). Discussions on the benefits of lenient, heavy, or intermediate grazing resulted in the development of rotational grazing systems.

17.1.2 Current Grazing Practices in the Nama-Karoo

Of the total land area of South Africa, 84% is currently used for extensive grazing, and the majority of the Nama-Karoo ($\sim 95\%$) is commercial rangeland under freehold tenure, mainly used for extensive livestock production (sheep and goats) (Roux et al. 1981; Hoffman et al. 1999). As discussed under the previous section, heavy historical grazing has led to widespread degradation of vegetation in the Nama-Karoo, often to the extent beyond which vegetation composition cannot be naturally restored despite livestock removal (Curtin 2002; Snyman 2003; Anderson and Hoffman 2007). However, this trend of heavy grazing has reversed in many regions in the last few decades (Timm Hoffman et al. 2018). It has recently been concluded that since the significant reduction in the numbers of domestic livestock, more than 95% of the greater Karoo region can be viewed as "natural."



Fig. 17.2 Main characteristics of commercial rangelands system in South Africa (adapted from Hoffman et al. 1999; Todd and Hoffman 1999)

There are two main land tenure systems in operation in South Africa, which differ in land management practices, namely: communal and commercial (more than 80% of land in South Africa) (Hoffman et al. 1999; Todd and Hoffman 1999); in the Nama-Karoo Biome almost the entire area is under commercial livestock production. Commercial rangelands have clear boundaries and exclusive property rights (Fig. 17.2) (Palmer and Ainslie 2005). Management systems can be divided into the following categories: continuous grazing, rotational grazing, short-duration grazing and nonselective grazing system (McCabe 1987). In the continuous grazing system, livestock are constantly kept on one rangeland which is not divided into paddocks, so the stock density should be low, but with selective livestock grazing (for example, small ruminants may be pickier and spend more time looking for high quality palatable plants, while unpalatable species are often discarded) (McCabe 1987; O'Connor et al. 2010). The rotational grazing system (multiple paddocks) was developed and recommended by the Commission of Inquiry to improve rangeland conditions and enhance wildlife habitat through appropriate resting periods (du Toit et al. 1923). The short duration grazing system was advocated based on the untested hypotheses of Acocks (1966) to improve sustained forage and livestock productivity and prevent land degradation (Acocks 1966; Savory 1978; Holechek et al. 2000). The main characteristic of this system is that livestock is rotated through many (≥ 8) paddocks for a relatively short period of time. Theoretically, it would reduce the competitive advantage of unpalatable species. While discussions regarding the benefits of the different grazing management practices are ongoing (Roberts 1969; Parsons et al. 1983; Westoby et al. 1989), most commercial farms in the Karoo practice some form of rotational grazing with rest periods from several months to more than a year (Hoffman 1988). Outside commercial farms, in, e.g., National Parks, where animals cannot be fenced and rotated, continuous grazing is practiced.

17.2 Components of the Carbon Cycle and Their Quantification

17.2.1 Carbon Cycling in the Semiarid Rangelands of South Africa

Box 17.1 Carbon in Terrestrial Ecosystems

Terrestrial ecosystems contain carbon in the form of plants, animals, soils and microorganisms (bacteria and fungi) (Schimel 1995). Of total carbon, plants and soils account for the largest share. Most of the carbon in terrestrial ecosystems is in organic forms (compounds formed by living organisms such as leaves, roots, dead plant and the organic residues from the decomposition of previous living tissues). The terrestrial carbon cycle includes photosynthesis (carbon sequestration), ecosystem respiration (carbon release) and storage (biomass and soil storage).

This section summarizes the current understanding of the terrestrial carbon cycle (Box 17.1) (with a focus on the factors (such as climatic variables, biodiversity change and livestock grazing) that affect the uptake or release of CO_2 in semiarid rangelands.

The carbon cycle is governed by net ecosystem exchange (NEE), which is the balance of gross primary production (GPP) (photosynthesis) and ecosystem respiration ($R_{eco} = R_a^4 + R_h^5$) (Box 17.2) (Ciais et al. 2011). Carbon exchange between the plants and the atmosphere occurs through photosynthesis and respiration (Fig. 17.3). During photosynthesis, plants use solar energy to absorb CO₂ from the atmosphere (by diffusion through the stomata) and water from the soil to produce carbohydrates. Most of the absorbed CO₂ is reemitted. The amount of CO₂ converted to carbohydrates during photosynthesis is called gross primary production (GPP). Plants also release CO₂ into the atmosphere through respiration (corresponding to the exhalation of plants); plant cells use carbohydrates produced during photosynthesis as energy. An ecosystem usually absorbs and releases carbon due to these processes taking place simultaneously.

Box 17.2 Ecosystem Respiration (Reco)

Ecosystem respiration is the sum of all respiration processes of living organisms in an ecosystem. Ecosystem respiration can be divided into autotrophic respiration (R_a), which comes from organisms with the sun as their main source of energy (i.e., plants), and heterotrophic respiration (R_h) from heterotrophic organisms (e.g., microbial decomposition of residues and soil organic matter), whose main source of energy are other organisms.

⁴ Autotrophic respiration.

⁵ Heterotrophic respiration.



Fig. 17.3 The schematic diagram describes the ecosystem–atmospheric carbon exchange in the semiarid grazing ecosystems (adapted from Schimel 1995; Asner and Archer 2010)

Some of the aboveground biomass is consumed by livestock, and carbon compounds are transferred through the food chain (Spangler et al. 2021). Most of the carbon they consume is exhaled in the form of CO_2 produced by aerobic respiration. Eventually, some of the carbon returns to the soil as manure, which can also increase rangeland yields, thereby improving soil carbon storage (Gross and Glaser 2021), or into the atmosphere through intestinal fermentation (Lee et al. 2017).

Most of the carbon is ultimately re-emitted to the atmospheric carbon pool via heterotrophic and autotrophic respiration. Most of the carbon in the soils comes in the form of dead plants, which is decayed by microorganisms (consumed by bacteria and fungi) during the decomposition process (Gougoulias et al. 2014). Over time, the metabolic processes of microorganisms decompose most of the organic matter into CO_2 . The decomposition process releases carbon into the atmosphere at a rate that depends on the chemical composition of the dead tissues and environmental conditions (dry conditions, flooding and low temperatures slow down decomposition) (Bardgett et al. 2008; Paz-Ferreiro et al. 2012). Plant material can take years to decades (large trees) to decompose, and carbon is temporarily stored in soil organic matter.

The effectiveness of the terrestrial absorption of CO_2 depends on the transition of carbon to long-lived forms (i.e., trees and woody shrubs). Management practices could increase the carbon sink potential due to the inertia of these "slow" carbon pools. The difference between R_{eco} and GPP determines how much carbon is released or absorbed by the ecosystem without interferences that removes carbon from the ecosystem, such as harvest or fire (Prentice et al. 2001). This carbon balance can be estimated from changes in carbon stocks or by measuring CO_2 fluxes between the ecosystem and the atmosphere (Sect. 17.2.2). In the absence of disturbance, R_{eco} should balance GPP, and NEE would be zero. Anthropogenic activities, natural disturbances and climate variability change GPP and R_{eco} causing temporary changes in the terrestrial carbon pool and, consequently, nonzero NEE (Williams et al. 2014; Hamidi et al. 2021). A steady increase in GPP is expected to result in a sustained larger net carbon uptake so that increased terrestrial carbon is not processed through the respiring carbon pools.

The African continent is playing an increasingly important role in the global carbon cycle (due to global warming and land cover change) and has a potentially significant impact on climate change (Epple et al. 2016; Simpkin et al. 2020). In general, it is estimated that the African continent is a small carbon sink (Valentini et al. 2014), but due to the lack of long-term CO_2 measurements in many critical ecosystems on the continent, the uncertainty of these estimates is high. South Africa is particularly vulnerable to the impacts of climate change (DEA and SANBI 2016). Large parts of the country are affected by droughts (Archibald et al. 2009; du Toit 2017), which can cause changes in the magnitude and pattern of the carbon cycle. The duration, frequency and strength of droughts have increased substantially in recent decades, particularly in semiarid ecosystems. Droughts could interact with other biotic and abiotic changes (global warming, grazing intensities) and thus could fundamentally alter the function, structure and vegetation composition of ecosystems (Abdulai et al. 2020; Malik et al. 2020). Moreover, droughts are the main cause of interannual variability in the carbon balance of semiarid ecosystems and are closely linked to terrestrial carbon cycling at various scales (Archibald et al. 2009; Merbold et al. 2009). The distribution of sequestered carbon in the semiarid ecosystems of South Africa, as well as their potential capacity to store and sequester carbon in soils, is still uncertain (Brent et al. 2011; Von Maltitz et al. 2020). Compared to other ecosystems, semiarid shrub/grassland ecosystems are more susceptible to subtle environmental and land management changes in terms of function and structure (Milton and Dean 2021). Semiarid grassland ecosystems with high root productivity store most of their carbon in soils, the turnover of which is relatively slow (Leifeld et al. 2015; Mureva et al. 2018). Viewed together, these traits of semiarid shrub/grasslands would emphasize their importance for sustainable land management.

17.2.2 Methods for Quantifying Carbon Uptake and Release

The scarce observation networks in and around the African continent mean that Africa is one of the weakest links in our understanding of the global carbon cycle. CO_2 can be measured over a range of scales, from a small landscape to a global extent (Fig. 17.4). There are several sites that monitor terrestrial CO_2 in South Africa (Feig et al. 2017 and the references therein):

 Stations equipped with high-precision spectroscopic analyzers for atmospheric concentration: the Cape Point Global Atmosphere Watch station; the Eskom Ambient Air Quality Monitoring network of stations mainly Elandsfontein and



Fig. 17.4 The schematic representation of the methods for quantifying carbon uptake and release integrated across time and space scales (adapted from Ciais et al. 2010)

Medupi located stations in the vicinity of major coal power stations in the country.

• The network of eddy covariance (EC) flux towers: Skukuza, Malopeni, Agincourt, Vuwani; Middelburg Karoo (study sites in this chapter), Cathedral Peak, Welgegund.

Eddy covariance (EC) has been proven to be the most effective method of measuring carbon exchange between the ecosystem and atmosphere on a landscape scale (Swinbank 1951; Verma 1990; Moncrieff et al. 1996; Twine et al. 2000; Burba 2013). In the last two decades, the technology has become reliable enough (due to the continuous development of computer acquisition, sensors such as highperformance CO_2 analyzers, ultrasonic anemometers and data processing capacity) to continuously measure fluxes over several years, allowing the study of seasonal and annual variability of CO₂. EC has the advantages of a strong theoretical basis, few theoretical assumptions and wide application range, but also imposes high hardware requirements, such as fast response sensors and rapid data acquisition. It is widely used to study the ecosystem-atmosphere carbon exchange over crops, forests and grassland sites, but is difficult to apply over sloping areas and heterogeneous canopies. To understand the responses of NEE to climatic and anthropogenic changes, it is important to separate and analyze GPP and R_{eco} flux components, which can be derived using two common partitioning methods: (1) the night-timebased flux partitioning method is based on the modeling of the night ecosystem

respiration (GPP = 0) extrapolated to daytime as a temperature function (Reichstein et al. 2005); (2) the day-time-based flux partitioning method is based on light-response curves that are fitted to the measurements of daytime NEE (Lasslop et al. 2010).

Chamber measurements were the dominant technique for monitoring field-scale soil CO_2 flux for almost a century (Lundegårdh 1927; Acosta et al. 2013) until the EC technique became the standard method (Aubinet et al. 2012). There are several methods available to implement an automated technique for the measurement of CO_2 : an open dynamic chamber (CO_2 exchange is measured using the increase in concentration inside the chamber) (Livingston and Hutchinson 1995; Liang et al. 2003) and a closed dynamic chamber (air is directed from the chamber headspace to a portable CO_2 analyzer and returned to the chamber) methods (Rochette et al. 1997). Chamber measurements are relatively easy to use and adaptable to a variety of studies, especially important in situations where the EC method cannot be implemented such as on smaller plots under different treatment.

Leaf gas exchange occupies a central position in the analysis of photosynthetic processes. This has resulted in rapid development of techniques used for commercial and research purposes to directly measure the net rate of photosynthetic carbon assimilation of individual leaves or plant canopies, combining infrared gas analysis and chlorophyll fluorescence capabilities (Farquhar et al. 1980; Von Caemmerer and von Farquhar 1981; Field and Mooney 1990). Systems use a closed transparent chamber that measures the change in the concentration of CO_2 of the air flowing across the chamber.

Measurements of greenhouse gas concentrations, typically from tall towers (at elevations high enough to be representative of greenhouse gas concentrations in the planetary boundary layer), are used to refine preliminary estimates of greenhouse gas release and uptake (Tans 1993; Haszpra et al. 2015). Measurements of atmospheric CO_2 concentrations and transport model simulations are used to constrain surface fluxes using inverse modeling (the atmospheric transport model is linearized and the transport operator is inverted to relate emissions to a measured concentration at low and medium resolutions) (Enting and Mansbridge 1989; Masarie et al. 2011).

Stable isotopes have been shown to be a conversion tool for distinguishing between two different sources of an element (e.g., soil vs. plant C) (Peterson and Fry 1987; Whitman and Lehmann 2015). This is an important method for high-precision, small-volume, automated and relatively rapid measurements for multiscale geochemical cycle studies using the traditional dual inlet Isotope Ratio Mass Spectrometry (IRMS) with cryogenic extraction (large air samples) or Gas Chromatography-Isotope Ratio Mass Spectrometry (GC-IRMS) (smaller air samples, less accurate) (Reinnicke et al. 2012).

Traditional field measurements of CO_2 using the above-mentioned methods are the most accurate approach for obtaining reliable data, but they are difficult to carry out over large areas. Remote sensing methods can measure the spectral reflectance of vegetation and analyze carbon-stock dynamics using spectral band imaging (Situmorang et al. 2016). Satellite data can be easily collected and used to estimate the aboveground carbon stocks by generating regression models that focus on the relationship between observations and satellite image vegetation indices. Remote sensing, however, is sensitive to the vegetation structure, texture, shadow and does not provide a direct estimate of the above-ground biomass (Gerber 2000; Ramankutty et al. 2007).

Physical models of Soil-Vegetation-Atmosphere Transfer (SVAT) are fundamental mathematical representation of the ecosystem–atmosphere interactions and prediction of the surface fluxes (energy fluxes, carbon flux, evapotranspiration) (Breil et al. 2017; Bigeard et al. 2019). In general, SVAT models are considered overly parameterized due to the limited data availability for calibration, which affects the robustness of the parameters. Local SVAT models are based on accurate descriptions of the energy balance of the ecosystem canopy, while larger-scale models use simplified assumptions that are based on typical deposition rates instead of site-specific parameters.

Earth system models (ESMs) differ in their representation of many key processes (e.g., vegetation dynamics, carbon–nitrogen interactions, physiological effects of CO_2 increase, climate sensitivity, etc.) (Friedlingstein et al. 1999; Kolby Smith et al. 2016). The modern fully coupled carbon-climate ESMs have been triggered by studies on the feedback between climate change and the carbon cycle, which can be classified into three categories depending on their complexity (Hajima et al. 2014): conceptual models, intermediate complexity ESMs (EMICs) and ESMs based on general circulation models (GCMs).

17.3 Multiyear CO₂ Budgets Under Different Grazing Intensities: A Case Study from the Nama-Karoo

17.3.1 Site Description and Measurement Setup

In October 2015, two (EC) towers were installed 1.5 km apart at Middelburg, Eastern Cape, to measure the ecosystem–atmosphere exchange of carbon, water and heat flux (Fig. 17.5). To be able to study the impacts of grazing, the towers were placed at lenient grazing (LG) and experimental grazing (EG) sites. A three-dimensional sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, UT, USA), mounted 3 m above the ground, was used to measure three orthogonal wind components in conjunction with an enclosed path fast-response Infra-Red Gas Analyzer (IRGA) Li-7200 (IRGA, Li-Cor, Lincoln, NE, USA) for CO₂ and H₂O measurements and the extended weather station (temperature/humidity probe to record relative humidity and air temperature, tipping bucket rain gauge for precipitation, net radiometer for radiation components, two heat flux plates, soil moisture and soil temperature probes).

The studied ecosystems are located in the Nama-Karoo Biome at an altitude of 1310 m.a.s.l. (Mucina et al. 2006) (Fig. 17.5). The vegetation is codominated by dwarf shrubs (perennial, both succulent and nonsucculent) and grasses (short-lived and perennial), including shrubs, sedges, geophytes and herbs (O'Connor and Roux 1995; du Toit et al. 2018). The warm season benefits the growth of grasses, while



Fig. 17.5 South African biomes with location of the study sites marked as a red circle and location of paddocks on the top right side, and pictures in the dry and growing seasons for the lenient grazing (LG) (bottom left) and the experimental grazing (EG) sites (bottom right) (South African Environmental GIS Data 2013) (Base map: Satellite, Map data ©2015 Google)

the growth of dwarf shrubs is promoted in the cool season (du Toit and O'Connor 2014). The soils are loamy at both research sites (Roux, 1993). Four main seasons can be identified: cold and dry winter (June-August), warm and relatively dry spring (September-November), hot and wet summer (December-February) and warm and relatively wet autumn (March-May). In summer, it is usually hot during the day (30- 40° C) and moderately warm at night (10–16°C), while in winter, days are moderate to warm $(14-25^{\circ}C)$ and nights are cold $(-4-4^{\circ}C)$. The long-term mean annual temperature is 15°C. Precipitation and droughts are unpredictable (Booysen and Rowswell 1983). Annual precipitation in the years 1889–2013 ranged from 163 mm to 749 mm, with a mean annual precipitation of 374 mm (du Toit and O'Connor 2014). Precipitation mainly occurs in the summer and autumn, with March being the rainiest month. Seasonality and amount of precipitation, including long-term droughts and wet periods, are important drivers of ecosystem processes in the area, especially for the vegetation dynamics, composition, structure and functioning (Anderson and Hoffman 2007; Du Toit and O'Connor 2020). Droughts are common in the Nama-Karoo region with severe droughts occurring approximately every 20 years (du Toit 2017).

The LG site $(31^{\circ}25'20.97" \text{ S}, 25^{\circ}1'46.38'' \text{ E})$ has been grazed by sheep and cattle (Fig. 17.5) using a rotational grazing system (about 2 weeks of grazing followed by 24–26 weeks of rest) at recommended stocking rates of 1/16 animal

units per hectare (AU ha⁻¹) since the 1970s. In terms of botanical composition, the site is considered an excellent "reference" site, with high species diversity and codominance of grasses (Digitaria eriantha (palatable perennial grass), Sporobolus fimbriatus (palatable perennial grass) and dwarf shrubs (Pentzia globosa (palatable nonsucculent dwarf-shrub) and Eriocephalus ericoides (palatable shrub)) (Fig. 17.5) (du Toit and Nengwenani 2019). The EG site $(31^{\circ}25'48.69'' \text{ S}, 25^{\circ}0'57.70'' \text{ E})$ was grazed by Dorper sheep using a two-paddock rotational system (120 days grazing followed by 120 days rest) at stocking rates approximately double the recommended rate $(2/16 \text{ AU ha}^{-1})$ as part of an experimental trial from 1988 to 2007 (Fig. 17.5). The Dorper breed is described as a hardy sheep that prefers shrubs to grasses (Brand 2000). This intensive grazing treatment has eradicated almost all palatable species and nearly all dwarf shrubs. Therefore, the site is dominated by Aristida diffusa (unpalatable perennial grass), Aristida congesta (short-lived unpalatable grass) and Tragus koelerioides (creeping unproductive grass) (van Lingen 2018). As a result, the EG site is degraded from an agricultural perspective, having transformed from a diverse grassy shrubland to unpalatable semiarid grassland. The site was ungrazed from 2008 to 2017, but did not recover in terms of species composition, where the bulk of fodder available to animals comprised grasses of relatively low palatability. In July 2017, Dorpers were reintroduced at a slightly higher stocking rate $(1/5 \text{ AU ha}^{-1})$ (Fig. 17.5), and the paddock was continuously grazed unless food capacity was too low (for short periods). Vegetation biomass has never been completely removed by grazers (Du Toit and O'Connor 2020). In addition, nongrowing plants retain their quality well (almost like standing hay) and remain palatable to animals. Compared with the 10 plant species at the EG site, the LG site shows a clearly higher species richness, with 32 species. Climatic conditions of the two sites are similar.

We analyzed and defined the following periods as hydrological years: Year I (Nov 2015–Oct 2016), Year II (Nov 2016–Oct 2017), Year III (Nov 2017–Oct 2018), Year IV (Nov 2018–Oct 2019) and Year V (Nov 2019–Oct 2020).

17.3.2 Ecosystem–Atmosphere CO₂ Exchange

17.3.2.1 Diurnal Variations of Carbon Fluxes

The mean diurnal variations of carbon fluxes were compared between the EG and LG sites and past (years I–II) and current (years III–V) livestock grazing due to the reintroduced livestock grazing at the EG site in the end of the year II (Fig. 17.6). The patterns of carbon fluxes were grouped by dry (June–December) and growing (January–May) seasons. In our study, positive numbers indicate net CO_2 release to the atmosphere and negative numbers net CO_2 sequestration by the ecosystem through higher photosynthetic uptake by plants than respiratory losses. The positive nighttime values of CO_2 indicate that CO_2 is released into the atmosphere by ecosystem respiration processes (Sect. 17.2.1). During the daytime (between 6:00 and 18:00 LT), however, CO_2 uptake by photosynthesis is higher than CO_2 release by ecosystem respiratory processes, and thus, the CO_2 values are negative. As shown



Fig. 17.6 Mean diurnal carbon fluxes in the dry (June–December) (**a**, **c**) and growing (January–May) (**b**, **d**) seasons for years I–II (top) and III–V (bottom) in the (blue) lenient grazing (LG) and (red) experimental grazing (EG) sites. Shaded area indicates ± 1 standard deviation. Positive numbers refer to net CO₂ release to the atmosphere, while negative numbers indicate net CO₂ sequestration by the ecosystem

in Fig. 17.6, diurnal CO $_2$ fluctuations at the study sites show stable positive CO $_2$ release during the night and negative CO $_2$ fluxes during daytime, peaking around noon.

Averaging all dry seasons, the mean daily CO_2 fluxes were 14 mg C m⁻² h⁻¹ and 13 mg C m⁻² h⁻¹ for the LG and EG sites, respectively. These values are quite low, implying that net carbon uptake was limited due to the lack of water availability and the inactivity of vegetation.

During the growing seasons, diurnal cycles of carbon fluxes for both sites showed predominance of carbon uptake during the day and only respiration at night (Fig. 17.6b, d). However, there were small differences between the CO₂ fluxes of the study ecosystems. Peak of the mean diurnal CO₂ uptake (higher negative NEE) was higher in years I–II at the EG site with unpalatable grass species as dominant vegetation cover (124 mg C m⁻² h⁻¹) than at the LG site (94 mg C m⁻² h⁻¹) (Fig. 17.6a, c). However, the situation changed when heavy livestock grazing was reintroduced at the EG site (July 2017) and the sites showed similar peak of the mean diurnal CO₂ uptake in years III–V (160 mg C m⁻² h⁻¹) for both sites).

In general, during the measurement period, the highest hourly carbon uptake rates were observed in year V with the highest amount of precipitation during the growing season. This was also the year when the highest carbon release was measured after the longest dry period in the previous year.

17.3.2.2 Seasonal NEE, GPP and Reco Variations

The daily sums of NEE, R_{eco} and GPP showed clear seasonal variability (Fig. 17.7) that followed the patterns of precipitation. The length of the wet season (NEE < 0 on a daily basis) varied from year to year depending on the distribution of precipitation throughout the year (from 60 (year I) to 150 wet days (year III)) (Fig. 17.8).

At the study sites, the magnitude of daily NEE ranged from $-4.2 \text{ g C m}^{-2} \text{ d}^{-1}$ to 5.4 g C m⁻² d⁻¹ during the measurement period. At both sites, carbon sequestration was always highest during the growing season and decreased during the dry season, with the lowest values observed in June–October (Fig. 17.8). The occurrence of the maximum daily NEE uptake during the growing seasons over the five years measurement period demonstrated the important role that precipitation and soil moisture play in the CO₂ uptake and release rates in the semiarid water-limited ecosystems (Fig. 17.7).

The dry periods were mainly characterized by low precipitation (<10 mm month⁻¹), low soil water content (<15%), and almost inactive (low NEE, GPP and R_{eco}) carbon cycling between the ecosystem and the atmosphere (Fig. 17.7). Mean daily CO₂ rates during the dry seasons of the measurement period were similar (~130 mg C m⁻² d⁻¹) with maximum R_{eco} and GPP of 2.1 g C m⁻² d⁻¹ and 1.9 g C m⁻² d⁻¹ for both sites.



Fig. 17.7 Daily cumulative measured net ecosystem exchange (NEE) and partitioned component fluxes (i.e., gross primary production (GPP), ecosystem respiration (R_{eco})) across different grazing intensities for (**a**) lenient grazing (LG) and (**b**) experimental grazing (EG) sites, (**c**) daily means of soil water content (SWC, left) and cumulative precipitation (P, right). The blue and red patterns represent livestock periods in the LG and EG sites, respectively



Fig. 17.8 Temporal dynamics of the hourly carbon fluxes for the entire measurement period in the (a) lenient grazing (LG) and (b) experimental grazing (EG) sites

During the November–December transition period from the dry to the growing season, there was an increased release of CO₂ (Fig. 17.8). R_{eco} responded immediately to the first major precipitation events turning the ecosystem into a carbon source, while GPP showed a delayed response (\sim 1–4 weeks, during which carbon uptake begins to rise as assimilation by grasses and herbs increases).

The growing season was characterized by high precipitation (>65% of annual precipitation) and high soil water content (15%–35%) compared to the dry season, which resulted in a higher water content available for plants and enhanced CO₂ uptake (Fig. 17.7). The mean daily values of NEE during the growing seasons (January–May) of the measurement period ($-74 \text{ mg C} \text{ m}^{-2} \text{ d}^{-1}$ for the LG site and $-152 \text{ mg C} \text{ m}^{-2} \text{ d}^{-1}$ for the EG site) showed high CO₂ uptake compared to the dry seasons with maximum values of GPP and R_{eco} of 7.6 g C m⁻² d⁻¹ and 7.7 g C m⁻² d⁻¹, respectively, in the peak of the growing season (February–March) for both sites.

17.3.2.3 Seasonal and Annual Carbon Balances

Seasonal and annual carbon balances were estimated to illustrate the carbon source/sink potential of the studied ecosystems (Fig. 17.9). The seasonal and annual ecosystem–atmosphere CO_2 fluxes show how climatic (water availability and its distribution) and land management (grazing intensity) factors affect carbon budgets.



Fig. 17.9 Annual cumulative net ecosystem exchange (NEE) (**a–e**), annual cumulative precipitation (P) (**f–j**) for the years I–V, (**k**) cumulative delta NEE (EG NEE–LG NEE) with shaded areas that represent livestock grazing periods at the LG (green) and EG (gray) sites and (I) Standardized Precipitation Evapotranspiration Index (SPEI) (Beguería et al. 2014) monthly basis

Similar mean seasonal carbon releases were observed (50 g with a seasonal mean uncertainty ⁶ of 24 g C m⁻² for the LG site and 45 g with a seasonal mean uncertainty of 24 g C m⁻² for the EG site) during the dry seasons (June–December), with the highest carbon release in the dry season of year V (Fig. 17.8). Although the studied ecosystems temporarily acted as carbon sinks during high precipitation events (e.g., July–August 2016), this was not reflected in seasonal budgets.

While only minor differences in NEE occurred during the dry seasons at the study sites between years I–V, significant variations were observed during the growing seasons (January–May). The length of the wet season and strength of carbon uptake varied significantly from 2 to 6 months during the measurement period. Net carbon release was observed on a seasonal basis during the growing seasons of years I and IV, while those of years II, III and V showed enhanced carbon sequestration. Mean seasonal carbon uptake during the growing seasons of the measurement periods was

⁶ Uncertainty was estimated as random uncertainty after (Finkelstein and Sims 2001) plus uncertainty that originates from gap filling after (Lucas-Moffat et al. 2018).

 -24 ± 15 g C m⁻² for the LG site and -49 ± 19 g C m⁻² for the EG site with the highest carbon uptake in the year III for both sites ($\sim -120 \pm 26$ g C m⁻²) (Fig. 17.7).

Over the five-year measurement period, the studied ecosystems varied from carbon sink to source with a mean annual NEE of 26 ± 39 g m⁻² for the LG site compared to -5 ± 42 g m⁻² for the EG site (Fig. 17.9). Compared to the EG site, which acted as a carbon sink during years II–III, the LG site acted as a net carbon sink (-NEE) only in year III (Fig. 17.9b, c). Carbon releases were observed annually at both sites in years I, IV and V, with higher carbon release at the LG site (Fig. 17.9a, d, e). In the year II, a net carbon release was observed at the LG site (24 ± 36 g m⁻²), while the EG site acted as a carbon sink ecosystem (-31 ± 38 g m⁻²) (Fig. 17.9b). Similar NEE was found in year III (92 ± 49 g m⁻²) (Fig. 17.9c). Meanwhile, a lack of water contributed to the highest carbon release rates during the year IV (84 ± 35 g C m⁻² for the LG site and 60 ± 38 g C m⁻² for the EG site) (Fig. 17.9d).

The difference in NEE between sites was statistically significant in years I-II and showed negative delta NEE trends during the growing season (Fig. 17.9k). Following the reintroduction of continuous livestock grazing to the EG site, the differences decreased, showing positive delta NEE trends at the beginning of the growing season in years III–V (temporarily higher uptake at LG) (Fig. 17.9k). As a result of the five years of measurement period, the cumulative NEE indicates that the LG site acted as a carbon source ecosystem and released 131 ± 39 g C m⁻² of carbon, while the EG site was a small carbon sink with a sequestration rate of -22 ± 42 g C m⁻².

17.3.3 Carbon Flux Drivers

17.3.3.1 Historical and Current Grazing

Understanding the effects of livestock grazing on carbon exchange is indispensable for predicting and assessing the feedbacks between global change and carbon cycles (Okach et al. 2019; Ondier et al. 2021). Many studies suggest that livestock grazing reduces productivity and CO_2 exchange by decreasing photosynthetic biomass and altering soil water capacity, increasing soil compaction, often resulting in losses of soil organic matter necessary for biomass development. A wide range of factors contribute to the recovery of the grazing area, such as the intensity and duration of grazing and the availability of soil moisture and nutrients (Leriche et al. 2003; Seymour et al. 2010).

In the Karoo study, a comparison of the carbon exchange during years I and II allowed us to compare a site showing the impacts of past overgrazing (EG) to a leniently grazed site with near-natural species composition (LG). After grazing was reintroduced to the EG site, we further observed the impacts of current heavy grazing at the EG site, compared to parallel lenient grazing at the LG site (years III–V).

Based on the results of the first two years of measurements, we found the LG site to act as a net carbon source (84 g C m⁻² with an annual mean uncertainty of 42 g C m⁻²), while the EG site was carbon neutral (-4 g C m⁻² with an annual mean uncertainty of 41 g C m^{-2}) with temporarily higher carbon sequestration rates (Fig. 17.7). This indicates that the change in species composition (due to past overgrazing) and the recovery period (2007-2017) from long-term disturbance (regrowth of biomass) resulted in an increase of the carbon sink strength at the EG site. Differences in grasses and shrubs and their response to pulse rain and drought events in the studied ecosystems, in turn, may explain the differences in carbon sink strength between the sites. For example, Aristida diffusa is a droughttolerant dominant grass at the EG site (Du Toit and O'Connor 2020). In a study conducted by Zhou et al. (2012), the fine root biomass of perennial grasses was more abundant in the top layer of the soil than those of shrubs. This implies that the grass cover in the EG ecosystem can respond more quickly to precipitation events by using discontinuous and erratic water sources in the upper soil layers, unlike shrubs (with deep-root systems) that use water in deeper soil layers (Canadell et al. 1996; Hipondoka et al. 2003; Zhou et al. 2012). Furthermore, the higher soil organic carbon inputs of perennial grasses and their slower decomposition allow them to store more soil organic carbon than shrubs. After continuous heavy grazing was reintroduced at the EG site in July 2017, the difference in NEE between sites was reduced in years III–V (Fig. 17.9). Despite this, differences in grazing intensity were not reflected as differences in carbon fluxes, and the EG site still indicated slightly higher carbon sink strength than the LG site. Furthermore, our results support the assumption that in highly seasonal systems, grazing pressure may be enhanced when coupled with drought stress. After a long drought in year IV (with just 5 mm of precipitation in June–November), the highest respiration peak was observed at the beginning of the growing season in year V. Despite the fact that continuous heavy grazing (with stocking rate and duration many times higher than recommended) was reintroduced at the EG site, we found great NEE resilience of the EG site that was dominated by grasses and which had a low species richness. Similar annual NEE ranging from $-98 \text{ g C m}^{-2} \text{ yr}^{-1}$ to 21 g C m⁻² yr⁻¹ have been observed in the semiarid Kendall grassland, USA with precipitation of 345 mm (63% in summer) (Scott et al. 2010). During 2011–2013, Räsänen et al. (2017) reported annual carbon budgets of $-85 \text{ Cm}^{-2} \text{ yr}^{-1}$, 67 Cm⁻² yr⁻¹ and 139 Cm⁻² yr⁻¹ in the Welgegund atmospheric measurement station grassland ecosystem, South Africa (540 mm). On a broader perspective, Valentini et al. (2014) reported a small carbon sink of 0.61 ± 0.58 Pg C yr⁻¹ (-20 g C m⁻² yr⁻¹) for the entire African continent. In our study, we found an annual mean of 20 g C m⁻² yr⁻¹ for the LG site and -9 g C $m^{-2} yr^{-1}$ for the EG site, illustrating the fine line between net carbon releases and sequestration due to differing land use and management.

17.3.3.2 Water Availability

Semiarid ecosystems, which are also referred to as water-limited ecosystems, usually receive between 200 and 700 mm precipitation annually (Gallart et al. 2002). For periods within this range, the mean annual precipitation was 319 mm

in 1899-1937, 401 mm in 1938-1952, 353 mm in 1953-1984, 426 mm in 1985-2010, 481 mm in 2011–2015 and 384 mm in 2016–2020 (du Toit and O'Connor 2014). In these environments, it is typically warm enough for physiological activity, and thus, temperature is not considered a limiting factor to ecosystem production (Archibald et al. 2009). The pulsed input of water in semiarid ecosystems is understood to drive ecosystem responses such as ecosystem water use, productivity and respiration (Archibald et al. 2009; Williams et al. 2009) with water availability in these environments characterized by a strong seasonality component (Merbold et al. 2009). In the Karoo ecosystems, as the growing seasons progressed, negative carbon fluxes (correlated with daytime light intensity) occurred during the daytime, whereas positive fluxes (carbon release) were observed at night. Plant germination and small increase in GPP was observed at the onset of summer precipitation events (beginning of the growing season), while Reco responded rapidly to precipitation, so ecosystems acted as a small source of carbon. In contrast, the ecosystems turned into a carbon sink when GPP exceeded Reco at the peak of the growing season. Limited water availability slowed ecosystem activity during dry seasons, mainly indicating an inactive (carbon-neutral) ecosystem. This seasonality is described by the widely applied pulse-reserve paradigm to explain ecosystem functional responses to inputs of rain or soil water (Kutsch et al. 2008; Yepez and Williams 2009). This paradigm brings to attention the thresholds and lags in ecosystem responses to water availability. The timing, degree and duration to which these responses are controlled and sustained however remains poorly understood.

While the pulse-paradigm attempts to describe ecosystem responses to water inputs, it has rarely been tested with high frequency medium term observation approaches. In addition, the nonlinearity of ecosystem responses to water inputs highlights the observed rapid responses (respiration pulses) to even small wetting events in these ecosystems (i.e., R_{eco} began to increase rapidly with precipitation of 9 mm during the transition months from the dry to the growing season in the water-limited Karoo ecosystems). To further complicate matters, these responses are seemingly not only dependent on water inputs and availability but also on the physiological recovery of the ecosystem from preceding dry periods which may modify the sensitivity of responses. In the Karoo ecosystems, for example, high carbon releases were observed after a long drought period (June–November 2019) with only 5 mm of precipitation at the beginning of the growing season in year V. Therefore, it appears that the status of antecedent vegetation state, soil condition and the timing of rainfall significantly influence ecosystem responses.

17.4 Potential Adjustments and Recommendations for C Sequestration

Considering the wide coverage of rangelands in southern Africa and their likely ongoing recovery from previously unsustainable stocking rates, they may play an important role in carbon sequestration (Dean et al. 2015; Wigley et al. 2020). In semiarid ecosystems, the rate of carbon sequestration may be relatively slow,

but appears to be substantial when scaled up under optimal management regimes. Sustainable livestock farming should take into account the needs and aims of both public (carbon sequestration and food security) and private stakeholders (income and sustainability of production) (Eisler et al. 2014; Hasselerharm et al. 2021). While climate-smart management practices appear to offer multiple benefits, it will be critical to support their development based on good evidence to better inform policies that could enhance such multiple benefits.

As shown by O'Reagain and Turner (1992), key decisions determining long-term influence in vegetation dynamics in southern African rangelands systems include stocking rate, management system and livestock type. The majority of Nama-Karoo is commercial rangeland, and the adoption of climate-smart management practices in these systems could therefore have a large potential impact on climate mitigation. A wide range of management proposals has been made, from destocking to intensive "nonselective grazing" as extreme ends of a management continuum. Some practitioners have made remarkable claims of large sequestration potential from intensive grazing that is applied with some temporal precision (Frith 2020). The results that we present here suggest that a site that is subjected to intensive grazing and then rested has a higher carbon sequestration potential than a leniently grazed site, based on results for 2016 and 2017, and that this sequestration appears somehow resilient to the reintroduction of grazing even at higher than recommended rates. Whether this resilience would persist over time is unknown, as is the influence of other factors such as drought. It is anticipated that species diversity would remain low as the continued presence of grazers would prevent ingress of palatable shrubs and grasses. In the case of a drought, it would be predicted that grasses may die out (Du Toit and O'Connor 2020), and the agricultural potential would collapse in the absence of drought-tolerant dwarf shrubs. There is also a strong interaction with rainfall amount, showing a greater sequestration capacity in leniently grazed vegetation when water availability is higher and well distributed throughout the growing season. Taken together, this suggests that the ecosystem composition change may have facilitated a greater resilience of carbon sequestration to grazing and drought, perhaps due to greater dominance of unpalatable species that continue to sequester carbon irrespective of grazing intensity or drought stress. Such a result requires confirmation in a wider range of sites, as this would be important in designing optimal management strategies based on composition and rainfall variability. In highly seasonal systems with large interannual variability, such as the Nama-Karoo, long time series are particularly important in understanding the patterns of land-atmosphere carbon exchange and ecosystem carbon balance. Furthermore, an important axis of future investigation would be to explore different rates of grazing in "good quality" vegetation. Scientifically based evidence derived from techniques such as described here could be pivotal in supporting policy application and cost-benefit analysis (Snyman 1998; Schurch et al. 2021).

17.5 Conclusions

Large uncertainties remain in the understanding of carbon dynamics of southern African semiarid rangelands. In this chapter, we presented a case study on the impacts of livestock grazing on carbon exchange in the Nama-Karoo biome in South Africa. Historically, the Nama-Karoo biome was over-stocked with livestock; however, a recent reduction in stocking rates has facilitated recovery of primary productivity and vegetation cover in many areas. We found that a leniently grazed study site was a slight net source of carbon during the five-year measurement period (wet year III and extremely dry year IV compared to the long-term mean annual precipitation (373 mm), while a previously overgrazed, recovering site, characterized by unpalatable species, had higher carbon sequestration potential and was nearly carbon neutral. Furthermore, the previously overgrazed site seemed to show better resilience to drought. Taking the vast areal importance of livestock rangelands in South Africa, we recommend exploring the impact of different intensities of livestock grazing on carbon balance on natural ecosystems.

References

- Abdulai I, Hoffmann MP, Jassogne L et al (2020) Variations in yield gaps of smallholder cocoa systems and the main determining factors along a climate gradient in Ghana. Agric Syst 181:102812. https://doi.org/10.1016/j.agsy.2020.102812
- Acocks JPH (1966) Non-selective grazing as a means of veld reclamation. Proc Annu Congr Grassl Soc South Africa 1:33–39. https://doi.org/10.1080/00725560.1966.9648517
- Acocks JPH (1979) The flora that matched the fauna. Bothalia 12:673–709. https://doi.org/ 10.4102/abc.v12i4.1442
- Acosta M, Pavelka M, Montagnani L et al (2013) Soil surface CO2 efflux measurements in Norway spruce forests: comparison between four different sites across Europe—from boreal to alpine forest. Geoderma 192:295–303
- Anderson PML, Hoffman MT (2007) The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. J Arid Environ 70:686–700. https://doi.org/10.1016/ j.jaridenv.2006.05.017
- Archer S (2000) Technology and ecology in the Karoo: a century of windmills, wire and changing farming practice. J South Afr Stud 26:675–696. https://doi.org/10.1080/03057070020008224
- Archibald SA, Kirton A, Van Der Merwe MR et al (2009) Drivers of inter-annual variability in net ecosystem exchange in a semi-arid savanna ecosystem, South Africa. Biogeosciences 6:251–266. https://doi.org/10.5194/bg-6-251-2009
- Asner GP, Archer SR (2010) Livestock and the global carbon cycle. In: Steinfeld, H., Mooney, HA, Schneider, F., Neville, LE (ed) Livestock in a changing landscape: drivers, consequences and responses. pp. 69–82, Island Press, Washington, DC
- Aubinet M, Vesala T, Papale D (2012) Eddy covariance: a practical guide to measurement and data analysis. Springer Science & Business Media, Dordrecht
- Bardgett RD, Freeman C, Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. ISME J 2:805–814. https://doi.org/10.1038/ismej.2008.58
- Beguería S, Vicente-Serrano SM, Reig F, Latorre B (2014) Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Int J Climatol 34:3001–3023. https://doi.org/10.1002/joc.3887
- Bekele SG (2001) Grasshopper ecology and conservation in the Nama-Karoo. 1-226

- Bigeard G, Coudert B, Chirouze J et al (2019) Ability of a soil–vegetation–atmosphere transfer model and a two-source energy balance model to predict evapotranspiration for several crops and climate conditions. Hydrol Earth Syst Sci 23:5033–5058. https://doi.org/10.5194/hess-23-5033-2019
- Booysen J, Rowswell DI (1983) The drought problem in the Karoo areas. Proc Annu Congr Grassl Soc South Africa 18:40–45. https://doi.org/10.1080/00725560.1983.9648979
- Brand TS (2000) Grazing behaviour and diet selection by Dorper sheep. Small Rumin Res 36:147– 158. https://doi.org/10.1016/S0921-4488(99)00158-3
- Breil M, Panitz H-J, Schädler G (2017) Impact of soil-vegetation-atmosphere interactions on the spatial rainfall distribution in the Central Sahel. Meteorol Zeitschrift 26:379–389. https:// doi.org/10.1127/metz/2017/0819
- Brent A, Hietkamp S, Wise R, O'Kennedy K (2011) Estimating the carbon emissions balance for South Africa. South African J Econ Manag Sci 12:263–279. https://doi.org/10.4102/ sajems.v12i3.216
- Burba G (2013) Eddy covariance method-for scientific, industrial, agricultural, and regulatory applications. LI-COR Biosciences, Lincoln, Nebraska Copyright
- Canadell J, Jackson RB, Ehleringer JR et al (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:538–595
- Ciais P, Dolman H, Dargaville R, et al (2010) GEO carbon strategy
- Ciais P, Bombelli A, Williams M et al (2011) The carbon balance of Africa: synthesis of recent research studies. Philos Trans R Soc A 369:1–20. https://doi.org/10.1098/rsta.2010.0328
- Curtin CG (2002) Livestock grazing, rest, and restoration in arid landscapes. Conserv Biol 16:840– 842
- DEA, SANBI (2016) Strategic framework and overarching implementation plan for ecosystem based adaptation (EbA) in South Africa: 2016–2021. DEA/SANBI, Pretoria
- Dean WRJ, Milton SJ (1999) The Karoo, ecological patterns and processes, (eds). Cambridge University Press, Cambridge
- Dean C, Kirkpatrick JB, Harper RJ, Eldridge DJ (2015) Optimising carbon sequestration in arid and semiarid rangelands. Ecol Eng 74:148–163
- du Toit JCO (2017) Droughts and the quasi-20-year rainfall cycle at Grootfontein in the eastern Karoo, South Africa. Grootfontein Agric 17:36–42
- du Toit JCO, Nengwenani TP (2019) Boesmanskop compositional data 2007–2019. Unpublished data
- du Toit JCO, O'Connor TG (2014) Changes in rainfall pattern in the eastern Karoo, South Africa, over the past 123 years. Water SA 40:453–460. https://doi.org/10.4314/wsa.v40i3.8
- Du Toit JCO, O'Connor TG (2020) Long-term influence of season of grazing and rainfall on vegetation in the eastern Karoo, South Africa. African J Range Forage Sci 37:159–171. https:// doi.org/10.2989/10220119.2020.1725122
- du Toit HSD, Gadd SM, Kolbe GA et al (1923) Final report of the drought investigation commission. Cape Times Limited. Gov Printers, Cape Town
- du Toit JCO, Ramaswiela T, Pauw MJ, O'Connor TG (2018) Interactions of grazing and rainfall on vegetation at Grootfontein in the eastern Karoo. African J Range Forage Sci 35:267–276. https://doi.org/10.2989/10220119.2018.1508072
- Eisler MC, Lee MRF, Tarlton JF et al (2014) Agriculture: steps to sustainable livestock. Nat News 507:32
- Enting IG, Mansbridge JV (1989) Seasonal sources and sinks of atmospheric CO2 direct inversion of filtered data. Tellus Ser B Chem Phys Meteorol 41:111–126
- Epple C, García Rangel S, Jenkins M, Guth M (2016) Managing ecosystems in the context of climate change mitigation: a review of current knowledge and recommendations to support ecosystem-based mitigation actions that look beyond terrestrial forests. Montreal
- Farquhar GD, von Caemmerer S, von Berry JA (1980) A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. Planta 149:78–90

- Feig GT, Joubert WR, Mudau AE, Monteiro PMS (2017) South African carbon observations: CO₂ measurements for land, atmosphere and ocean. S Afr J Sci 113:2–5. https://doi.org/10.17159/ sajs.2017/a0237
- Field CB, Mooney HA (1990) Leaf chamber methods for measuring photosynthesis under field conditions. Remote Sens Rev 5:117–139. https://doi.org/10.1080/02757259009532125
- Finkelstein PL, Sims PF (2001) Sampling error in eddy correlation flux measurements. J Geophys Res Atmos 106:3503–3509. https://doi.org/10.1029/2000JD900731
- Friedlingstein P, Joel G, Field CB, Fung IY (1999) Toward an allocation scheme for global terrestrial carbon models. Glob Chang Biol 5:755–770. https://doi.org/10.1046/j.1365-2486.1999.00269.x
- Frith S (2020) The evidence for holistic planned grazing. In: Green meat. pp 89-106
- Gallart F, Sole A, Puigdefabregas J, Lazaro R (2002) Badland systems in the mediterranean. In: Bull LJ, Kirkby MJ (eds) Dryland rivers: hydrology and geomorphology of semi-arid channels. Wiley, Chichester, pp 299–326
- Gerber L (2000) Development of a ground truthing method for determination of rangeland biomass using canopy reflectance properties. Afr J Range Forage Sci 17:93–100. https://doi.org/10.2989/ 10220110009485744
- Gougoulias C, Clark JM, Shaw LJ (2014) The role of soil microbes in the global carbon cycle: tracking the below-ground microbial processing of plant-derived carbon for manipulating carbon dynamics in agricultural systems. J Sci Food Agric 94:2362–2371
- Gross A, Glaser B (2021) Meta-analysis on how manure application changes soil organic carbon storage. Sci Rep 11:5516. https://doi.org/10.1038/s41598-021-82739-7
- Hajima T, Kawamiya M, Watanabe M et al (2014) Modeling in Earth system science up to and beyond IPCC AR5. Prog Earth Planet Sci 1:29. https://doi.org/10.1186/s40645-014-0029-y
- Hamidi D, Komainda M, Tonn B et al (2021) The effect of grazing intensity and sward heterogeneity on the movement behavior of Suckler cows on semi-natural grassland. Front Vet Sci 8:639096. https://doi.org/10.3389/fvets.2021.639096
- Hasselerharm CD, Yanco E, McManus JS et al (2021) Wildlife-friendly farming recouples grazing regimes to stimulate recovery in semi-arid rangelands. Sci Total Environ 788:147602
- Haszpra L, Barcza Z, Haszpra T et al (2015) How well do tall-tower measurements characterize the CO2 mole fraction distribution in the planetary boundary layer? Atmos Meas Tech 8:1657– 1671. https://doi.org/10.5194/amt-8-1657-2015
- Hipondoka MHT, Aranibar JN, Chirara C et al (2003) Vertical distribution of grass and tree roots in arid ecosystems of Southern Africa: niche differentiation or competition? J Arid Environ 54:319–325. https://doi.org/10.1006/jare.2002.1093
- Hoffman M (1988) The rationale for karoo grazing systems: criticisms and research implications. S Afr J Sci/S-Afr TYDSKR Wet 84:556–559
- Hoffman T, Ashwell A (2001) Nature divided: land degradation in South Africa. University of Cape Town Press, Cape Town
- Hoffman M, Cousins B, Meyer T, et al (1999) The karoo: Historical and contemporary land use and the desertification of the Karoo. In The Karoo: Ecological patterns and processes. Cambridge University Press, Cambridge, pp. 257–273
- Hoffman M, Skowno A, Bell W, Mashele S (2018) Long-term changes in land use, land cover and vegetation in the Karoo drylands of South Africa: implications for degradation monitoring§. Afr J Range Forage Sci 35:209–221. https://doi.org/10.2989/10220119.2018.1516237
- Holechek JL, de Souza Gomes H, Molinar F, Society for Range Management (2000) Short-duration grazing: the facts in 1999. Rangelands 22. https://doi.org/10.2458/ azu_rangelands_v22i1_holechek
- Kolby Smith W, Reed SC, Cleveland CC et al (2016) Large divergence of satellite and Earth system model estimates of global terrestrial CO2 fertilization. Nat Clim Chang 6:306–310. https:// doi.org/10.1038/nclimate2879
- Kraaij T, Milton SJ (2006) Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: effects of rainfall, wild herbivores and change in land use. J Arid Environ 64:174–192. https://doi.org/10.1016/j.jaridenv.2005.04.009

- Kutsch WL, Hanan N, Scholes B, et al (2008) Response of carbon fluxes to water relations in a savanna ecosystem in South Africa. Biogeosciences 5(6):1797–1808
- Lasslop G, Reichstein M, Papale D et al (2010) Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. Glob Chang Biol 16:187–208. https://doi.org/10.1111/j.1365-2486.2009.02041.x
- Lee MA, Todd A, Sutton MA et al (2017) A time-series of methane and carbon dioxide production from dairy cows during a period of dietary transition. Cogent Environ Sci 3:1385693. https://doi.org/10.1080/23311843.2017.1385693
- Leifeld J, Meyer S, Budge K et al (2015) Turnover of grassland roots in mountain ecosystems revealed by their radiocarbon signature: role of temperature and management. PLoS One 10:e0119184. https://doi.org/10.1371/journal.pone.0119184
- Leriche H, Le Roux X, Desnoyers F et al (2003) Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. Ecol Appl 13:1346–1354. https://doi.org/10.1890/02-5199
- Liang N, Inoue G, Fujinuma Y (2003) A multichannel automated chamber system for continuous measurement of forest soil CO₂ efflux. Tree Physiol 23:825–832. https://doi.org/10.1093/ treephys/23.12.825
- Livingston GP, Hutchinson GL (1995) Enclosure-based measurement of trace gas exchange: applications and sources of error. In: Matson PA, Harriss RC (eds) Biogenic trace gases : measuring emissions from soil and water, vol 51. Blackwell Science, Oxford, pp 14–51
- Lucas-Moffat AM, Huth V, Augustin J et al (2018) Towards pairing plot and field scale measurements in managed ecosystems: using eddy covariance to cross-validate CO₂ fluxes modeled from manual chamber campaigns. Agric For Meteorol 256–257:362–378. https:// doi.org/10.1016/j.agrformet.2018.01.023
- Lundegårdh H (1927) Carbon dioxide evolution of soil and crop growth. Soil Sci 23:417-453
- Malik AA, Swenson T, Weihe C et al (2020) Drought and plant litter chemistry alter microbial gene expression and metabolite production. ISME J 14:2236–2247. https://doi.org/10.1038/s41396-020-0683-6
- Masarie KA, Pétron G, Andrews A et al (2011) Impact of CO2 measurement bias on carbon tracker surface flux estimates. J Geophys Res 116:D17305. https://doi.org/10.1029/2011JD016270
- McCabe K (1987) Veld management in the Karoo. The Naturalist 31:8-15
- McLeod SR (1997) Is the concept of carrying capacity useful in variable environments? Oikos 79:529. https://doi.org/10.2307/3546897
- Merbold L, Ardö J, Arneth A et al (2009) Precipitation as driver of carbon fluxes in 11 African ecosystems. Biogeosciences 6:1027–1041. https://doi.org/10.5194/bg-6-1027-2009
- Milton SJ (1993) Studies of herbivory and vegetation change in Karoo shrublands
- Milton SJ, Dean WRJ (2021) Anthropogenic impacts and implications for ecological restoration in the Karoo, South Africa. Anthropocene 36:100307
- Moll EJ, Gubb AA (1989) Southern African shrublands. Academic Press, New York, pp. 145-175
- Moncrieff JB, Malhi Y, Leuning R (1996) The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. Glob Chang Biol 2:231–240
- Mucina L, Rutherford MC, Palmer AR et al (2006) Nama-Karoo Biome. In: Mucina L, Rutherford MC (eds) The vegetation of South Africa, Lesotho and Swaziland. SANBI, Pretoria, pp 324–347
- Mureva A, Ward D, Pillay T et al (2018) Soil organic carbon increases in semi-arid regions while it decreases in humid regions due to Woody-Plant encroachment of grasslands in South Africa. Sci Rep 8:15506. https://doi.org/10.1038/s41598-018-33701-7
- O'Connor TG, Roux PW (1995) Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. J Appl Ecol 32:612–626
- O'Connor TG, Kuyler P, Kirkman KP, Corcoran B (2010) Which grazing management practices are most appropriate for maintaining biodiversity in South African grassland? Afr J Range Forage Sci 27:67–76. https://doi.org/10.2989/10220119.2010.502646

- O'Farrell PJ, Le Maitre DC, Gelderblom C et al (2008) Applying a resilience framework in pursuit of sustainable land-use development in the Little Karoo, South Africa. In: Burns M, Weaver A (eds) Advancing sustainability science in South Africa. SUN, Stellenbosch, pp 383–432
- O'Reagain PJ, Turner JR (1992) An evaluation of the empirical basis for grazing management recommendations for rangeland in southern Africa. J Grassl Soc South Africa 9:38–49
- Okach DO, Ondier JO, Kumar A et al (2019) Livestock grazing and rainfall manipulation alter the patterning of CO2 fluxes and biomass development of the herbaceous community in a humid savanna. Plant Ecol 220:1085–1100. https://doi.org/10.1007/s11258-019-00977-2
- Ondier JO, Okach DO, Onyango JC, Otieno DO (2021) Ecosystem productivity and CO2 exchange response to the interaction of livestock grazing and rainfall manipulation in a Kenyan savanna. Environ Sustain Indic 9:100095. https://doi.org/10.1016/j.indic.2020.100095
- Owen-Smith N, Danckwerts JE (1997) Herbivory. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 397–420
- Palmer AR, Ainslie AM (2005) Grasslands of South Africa. In: Grasslands of the world. p 77
- Parsons AJ, Leafe EL, Collett B et al (1983) The physiology of grass production under grazing. II. Photosynthesis, crop growth and animal intake of continuously-grazed swards. J Appl Ecol 20:127–139
- Paz-Ferreiro J, Medina-Roldán E, Ostle NJ et al (2012) Grazing increases the temperature sensitivity of soil organic matter decomposition in a temperate grassland. Environ Res Lett 7:14027. https://doi.org/10.1088/1748-9326/7/1/014027
- Pérez-Hernández J, Gavilán RG (2021) Impacts of land use changes on vegetation and ecosystem functioning : old Field secondary succession. Plan Theory 10:990. https://doi.org/10.3390/ plants10050990
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293-320
- Prentice IC, Farquhar GD, Fasham MJR, et al (2001) The carbon cycle and atmospheric carbon dioxide
- Ramankutty N, Gibbs HK, Achard F et al (2007) Challenges to estimating carbon emissions from tropical deforestation. Glob Chang Biol 13:51–66
- Räsänen M, Aurela M, Vakkari V et al (2017) Carbon balance of a grazed savanna grassland ecosystem in South Africa. Biogeosciences 14:1039–1054. https://doi.org/10.5194/bg-14-1039-2017
- Reichstein M, Falge E, Baldocchi D et al (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob Chang Biol 11:1424–1439. https://doi.org/10.1111/j.1365-2486.2005.001002.x
- Reinnicke S, Juchelka D, Steinbeiss S et al (2012) Gas chromatography/isotope ratio mass spectrometry of recalcitrant target compounds: performance of different combustion reactors and strategies for standardization: GC/IRMS of recalcitrant target compounds. Rapid Commun Mass Spectrom 26:1053–1060. https://doi.org/10.1002/rcm.6199
- Roberts BR (1969) The multicamp controversy: a search for evidence. In: Proceedings of the veld management conference, Bulawayo, Rhodesie Management Conference. pp. 41–57
- Rochette P, Ellert B, Gregorich EG et al (1997) Description of a dynamic closed chamber for measuring soil respiration and its comparison with other techniques. Can J Soil Sci 77:195–203
- Roux PW, Theron GK (1987) Vegetation change in the Karoo biome. Karoo biome a Prelim Synth Part:50–69
- Roux PW, Vorster M (1983) Vegetation change in the Karoo. Proc Annu Congr Grassl Soc South Africa 18:25–29. https://doi.org/10.1080/00725560.1983.9648976
- Roux PW, Vorster M, Zeeman PJL, Wentzel D (1981) Stock production in the Karoo region. Proc Annu Congr Grassl Soc South Africa 16:29–35
- Rutherford MC, Powrie LW (2013) Impacts of heavy grazing on plant species richness: a comparison across rangeland biomes of South Africa. South African J Bot 87:146–156. https:// doi.org/10.1016/j.sajb.2013.03.020
- Savory A (1978) A holistic approach to ranch management using short duration grazing. In: Proceedings of the first international rangeland congress. Denver, Colorado, pp 555–557

- Sayre NF (2008) The genesis, history, and limits of carrying capacity. Ann Assoc Am Geogr 98:120–134. https://doi.org/10.1080/00045600701734356
- Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. Glob Chang Biol 1:77–91. https://doi.org/10.1111/j.1365-2486.1995.tb00008.x
- Schurch MPE, McManus J, Goets S et al (2021) Wildlife-friendly livestock management promotes mammalian biodiversity recovery on a semi-arid Karoo farm in South Africa. Front Conserv Sci 2:6
- Scott RL, Hamerlynck EP, Jenerette GD et al (2010) Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. J Geophys Res 115:G03026. https:// doi.org/10.1029/2010JG001348
- Seymour CL, Milton SJ, Joseph GS et al (2010) Twenty years of rest returns grazing potential, but not palatable plant diversity, to Karoo rangeland, South Africa. J Appl Ecol 47:859–867. https:// /doi.org/10.1111/j.1365-2664.2010.01833.x
- Shaw J (1873) On the changes going on in the vegetation of South Africa through the introduction of the merino sheep. J Linn Soc London Bot 14:202–208
- Simpkin P, Cramer L, Ericksen PJ, Thornton PK (2020) Current situation and plausible future scenarios for livestock management systems under climate change in Africa. CCAFS Work Pap
- Situmorang JP, Sugianto S, Darusman D (2016) Estimation of carbon stock stands using EVI and NDVI vegetation index in production forest of lembah Seulawah sub-district, Aceh Indonesia. Aceh Int J Sci Technol 5:126–139
- Skead C (1982) Historical mammal incidence in the Cape Province. Department of Nature and Environmental Conservation, Cape Town
- Snyman HA (1998) Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. J Arid Environ 39:645–666
- Snyman HA (2003) Revegetation of bare patches in a semi-arid rangeland of South Africa: an evaluation of various techniques. J Arid Environ 55:417–432. https://doi.org/10.1016/S0140-1963(02)00286-0
- South African Environmental GIS Data (2013) South Africa Biomes. In: OpenAfrica. https://africaopendata.org/dataset/e2ef64dd-6577-4a73-9eff-87f677b2dd92/resource/ 620721d9-2605-44dc-81f8-efb5af9169da/download/rsabiome4xkhi.zip%0A%0A
- Spangler D, Tyler A, McCalley C (2021) Effects of grazer exclusion on carbon cycling in created freshwater wetlands. Land 10:805. https://doi.org/10.3390/land10080805
- Susiluoto S, Rasilo T, Pumpanen J, Berninger F (2008) Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. Arctic, Antarct Alp Res 40:422–431. https://doi.org/10.1657/1523-0430(07-035)[SUSILUOTO]2.0.CO;2
- Swinbank WC (1951) The measurement of vertical transfer of heat and water vapor by eddies in the lower atmosphere. J Atmos Sci 8:135–145
- Tans PP (1993) Observational strategy for assessing the role of terrestrial ecosystems in the global carbon cycle: scaling down to regional levels. In: Scaling physiological processes. Elsevier, pp 179–190
- Teague WR, Dowhower SL (2003) Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. J Arid Environ 53:211–229
- Tidmarsh C (1951) Pasture research in South Africa. Progress report No. 3. Veld management studies: 1934–1950. Middelburg, Cape Province
- Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc Natl Acad Sci U S A 109:10394–10397. https://doi.org/10.1073/pnas.1208240109
- Todd S, Hoffman MT (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecol 142:169–178. https://doi.org/10.1023/A:1009810008982
- Truter WF, Botha PR, Dannhauser CS et al (2015) Southern African pasture and forage science entering the 21st century: past to present. Afr J Range Forage Sci 32:73–89. https://doi.org/ 10.2989/10220119.2015.1054429

- Twine TE, Kustas WP, Norman JM et al (2000) Correcting eddy-covariance flux underestimates over a grassland. Agric For Meteorol 103:279–300. https://doi.org/10.1016/S0168-1923(00)00123-4
- Valentini R, Arneth A, Bombelli A et al (2014) A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities. Biogeosciences 11:381–407. https://doi.org/10.5194/bg-11-381-2014
- Van den Berg L, Du Toit JCO, Van Lingen M, Van der Merwe H (2019) The effect of sheep farming on the long-term diversity of the vegetation of the Karoo – a review. Grootfontein Agric 19:66– 72
- van Lingen M (2018) Afrikaner/Hereford compositional data 2018. Unpublished data
- Verma SB (1990) Micrometeorological methods for measuring surface fluxes of mass and energy. Remote Sens Rev 5:99–115
- Von Caemmerer S, von Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387
- Von Maltitz G, Scholes B, Pienaar M, et al (2020) National terrestrial carbon sinks assessment 2020. Technical Report. Pretoria, South Africa
- Westoby M, Walker B, Noy-Meir I (1989) Opportunistic management for rangelands not at equilibrium. J Range Manag 42:266. https://doi.org/10.2307/3899492
- Whitman T, Lehmann J (2015) A dual-isotope approach to allow conclusive partitioning between three sources. Nat Commun 6:8708. https://doi.org/10.1038/ncomms9708
- Wigley BJ, Augustine DJ, Coetsee C et al (2020) Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. Ecology 101:e03008
- Williams CA, Hanan N, Scholes RJ, Kutsch W (2009) Complexity in water and carbon dioxide fluxes following rain pulses in an African savanna. Oecologia 161:469–480. https://doi.org/ 10.1007/s00442-009-1405-y
- Williams IN, Torn MS, Riley WJ, Wehner MF (2014) Impacts of climate extremes on gross primary production under global warming. Environ Res Lett 9:94011. https://doi.org/10.1088/ 1748-9326/9/9/094011
- Yepez EA, Williams DG (2009) Precipitation pulses and ecosystem carbon and water exchange in arid and semi-arid environments. In: De la Barrera E, Smith WK (eds) Perspectives in biophysical plant ecophysiology: a tribute to park S. Nobel. Universidad Nacional Autónoma de México, México, p 27
- Zhou Y, Pei Z, Su J et al (2012) Comparing soil organic carbon dynamics in perennial grasses and shrubs in a saline-alkaline arid region, northwestern China. PLoS One 7. https://doi.org/ 10.1371/journal.pone.0042927

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

