

# **JGR** Biogeosciences

# <del>-</del>

## RESEARCH ARTICLE

10.1029/2024JG008623

#### **Key Points:**

- Accounting for lateral carbon export from chickpea harvest adjusted the net carbon balance of cropland to near
  poutral
- Respiration in the rangeland was decoupled from increasing GPP likely due to nutrient limitations and waterconserving plant adaptations
- Rangelands conserve water at the expense of biomass, reducing water use efficiency during water-abundant periods like the growing season

#### **Supporting Information:**

Supporting Information may be found in the online version of this article.

#### Correspondence to:

V. Odongo, v.odongo@cgiar.org

#### Citation:

Odongo, V., Leitner, S. M., Dowling, T. P. F., Gluecks, I., Jackowicz-Korczynski, M., Rinne, J., et al. (2025). Contrasting carbon and water flux dynamics in an East African rangeland and cropland. *Journal of Geophysical Research: Biogeosciences*, 130, e2024IG008623. https://doi.org/10.1029/2024JG008623

Received 21 NOV 2024 Accepted 9 SEP 2025

#### **Author Contributions:**

Conceptualization: Vincent Odongo, Sonja M. Leitner, Lutz Merbold Data curation: Vincent Odongo, Marcin Jackowicz-Korczynski Formal analysis: Vincent Odongo Funding acquisition: Sonja M. Leitner, Thomas P. F. Dowling, Martin J. Wooster, Lutz Merbold

Investigation: Thomas P. F. Dowling, Janne Rinne, Martin J. Wooster Methodology: Vincent Odongo, Janne Rinne

Resources: Sonja M. Leitner, Thomas P. F. Dowling, Ilona Gluecks, Marcin Jackowicz-Korczynski,

© 2025 The Author(s).

This is an open access article under the terms of the Creative Commons

Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

# **Contrasting Carbon and Water Flux Dynamics in an East African Rangeland and Cropland**

Vincent Odongo<sup>1</sup>, Sonja M. Leitner<sup>1</sup>, Thomas P. F. Dowling<sup>2,3</sup>, Ilona Gluecks<sup>4</sup>, Marcin Jackowicz-Korczynski<sup>5</sup>, Janne Rinne<sup>5,6</sup>, Martin J. Wooster<sup>2</sup>, and Lutz Merbold<sup>1,7</sup>

<sup>1</sup>Mazingira Centre for Environmental Research and Education, International Livestock Research Institute (ILRI), Nairobi, Kenya, <sup>2</sup>Department of Geography, NERC National Centre for Earth Observation, Kings College London, London, UK, <sup>3</sup>Now at: University of Auckland, School of Environment, Science Centre, Auckland, New Zealand, <sup>4</sup>Clinical Research Facilities, International Livestock Research Institute (ILRI), Nairobi, Kenya, <sup>5</sup>Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden, <sup>6</sup>Now at: Bioeconomy and Environment, Natural Resources Institute Finland (Luke), Helsinki, Finland, <sup>7</sup>Department Agroecology and Environment, Integrative Agroecology Group, Zurich, Switzerland

**Abstract** This study examines carbon (C) and water dynamics in two East African dryland ecosystems: a savanna rangeland grazed by livestock and wildlife, and a rainfed cropland under minimal tillage. Over 185 days, both systems were showed a similar magnitude of C emissions with differing temporal patterns. The rangeland showed fluctuating C exchange, with losses followed by increased C uptake after rainfall events. The cropland initially acted as a C sink, and when lateral C export from chickpea harvest were accounted for, the overall C balance shifted to a net source. Cropland demonstrated higher carbon use efficiency (CUE), driven by efficient C allocation for crop growth, supported by fertilizers, pesticides, and minimum tillage practices. During the peak growing period, cropland also had greater water use efficiency (WUE) likely reflecting optimized agricultural management under favorable moisture conditions. However, over the entire period, WUE was significantly higher in the rangeland than in the cropland (p > 0.05) possibly due to more consistent vegetation cover and adaptive traits that minimize water loss. The cropland showed a complex relationship between WUE and CUE, where increased productivity also simultaneously drove higher respiration rates. Our findings, particularly the shift in cropland carbon balance following harvest emphasize the importance of including lateral C fluxes and intra-annual variations in C balance assessments for accurate budgeting. Both ecosystems were co-limited by water and nitrogen, with plant adaptations to drought and dry spells, including efficient water use and sustained photosynthesis under moisture stress playing a critical role in maintaining ecosystem CUE. Sustainable land management strategies that account for the interactions between C and water dynamics, biodiversity, and ecosystem functioning are vital to enhancing C storage, mitigating climate change, and improving resilience in rangelands and croplands.

Plain Language Summary East Africa's drylands are vital ecosystems, but how do they balance carbon and water under the dry environmental conditions? Our study sheds light on two such ecosystems: a savanna rangeland grazed by livestock and wildlife, and a cropland managed with minimal soil disturbance. Over 6 months, we discovered that both ecosystems gained and lost about the same amount of carbon overall. However, they did so in different ways: The rangeland's carbon levels fluctuated, with losses during dry spells and gains after rain, reflecting its long-term adaptation to semi-arid conditions. Meanwhile, the cropland initially acted as a carbon sink, but when we factored in the carbon removed during harvest, it balanced out. The cropland was also better at using carbon and water efficiently during the growing season, thanks to farming practices like fertilizer use and pest control. Our findings highlight the delicate balance between carbon and water in these ecosystems, shaped by rainfall, nutrients, and management practices. Understanding these dynamics is crucial for improving land management strategies that protect biodiversity, enhance carbon storage, and build resilience against climate change.

#### 1. Introduction

Rangelands cover about 43% of the African land mass, with grasses, shrubs and scattered trees comprising the dominant vegetation (Mgalula et al., 2021; UNCCD et al., 2009). These systems offer a wide range of ecosystem services from providing habitat for wildlife to supporting dryland agriculture and livestock grazing. While

ODONGO ET AL. 1 of 21



# Journal of Geophysical Research: Biogeosciences

10.1029/2024JG008623

Janne Rinne, Martin J. Wooster,
Lutz Merbold
Software: Marcin Jackowicz-Korczynski
Supervision: Sonja M. Leitner,
Lutz Merbold
Visualization: Vincent Odongo
Writing – original draft: Vincent Odongo
Writing – review & editing:
Vincent Odongo, Sonja M. Leitner,
Thomas P. F. Dowling, Ilona Gluecks,
Marcin Jackowicz-Korczynski,
Janne Rinne, Martin J. Wooster,
Lutz Merbold

grazing is a common land use type, large animal densities and high stocking rates can disrupt these ecosystems (Berardi, 2006In Berardi, 2006), whereas moderate grazing can stimulate vegetation regrowth and positively influence carbon (C) dynamics (Alkemade et al., 2013; Dobson et al., 2022; Gao & Carmel, 2020; McNaughton, 1985; Ritchie & Penner, 2020; Tadey & Souto, 2016). A key uncertainty remains in understanding how these dynamics affect the ecosystem carbon balance, particularly in terms of net ecosystem production (NEP), which reflects the balance between photosynthesis and respiration across ecosystems over seasonal to decadal scales (Fernández-Martínez, Vicca, Janssens, Luyssaert, et al., 2014). While water availability is a critical factor that profoundly affects ecosystem C cycling and thus NEP, especially in dryland regions (Biederman et al., 2017), the combined roles of nutrient availability, land management practices, and disturbance regimes remain less understood (Fernández-Martínez, Vicca, Janssens, Sardans, et al., 2014; Luyssaert et al., 2007; Valentini et al., 2000). These uncertainties are particularly acute in semi-arid African rangelands, where data scarcity limits our ability to predict ecosystem responses to changing environmental conditions and inform sustainable land management strategies (López-Ballesteros et al., 2018; Merbold et al., 2021).

Given these uncertainties in ecosystem carbon dynamics, grazing management becomes an especially relevant factor to consider. Evidence suggests that controlled grazing of rangelands can enhance soil C storage and improve ecosystem CO<sub>2</sub> exchange (Allard et al., 2007; Chen et al., 2015; Leu et al., 2021; Rybchak et al., 2024; Wilsey et al., 2002). However, some studies offer contrasting views, suggesting that grazing, regardless of its management intensity, may not contribute significantly to enhanced C sequestration (Graversen et al., 2022; Lajtha & Silva, 2022; Medina-Roldán et al., 2012). In this context, understanding the carbon use efficiency (CUE) of these systems, which indicates the efficiency by which plants convert absorbed CO2 into C stored in their biomass, can be helpful. Here, CUE is expressed as the ratio of net ecosystem production (NEP = GPP  $-R_{\rm eco}$ ) to gross primary production (GPP), that is,  $CUE = (GPP - R_{eco})/GPP$ . NEP is the difference between GPP and ecosystem respiration ( $R_{\text{eco}}$ ), and by sign convention NEP = -NEE, where positive NEP indicates a net C sink. GPP represents the total photosynthetic  $CO_2$  uptake, while  $R_{eco}$  denotes the sum of autotrophic and heterotrophic respiratory CO<sub>2</sub> release. Grazing can simultaneously stimulate GPP through compensatory plant growth while also increasing ecosystem respiration through litter turnover, soil disturbance, and manure input (Gourlez de la Motte et al., 2016; Jérôme et al., 2014; Zhou et al., 2024; Zhu et al., 2020). CUE is a useful metric that integrates over both C uptake and release, which helps to assess the overall C footprint of grazed ecosystems (Feng et al., 2024).

In contrast to rangelands, semi-arid croplands exhibit strong seasonal flux dynamics since vegetation is only present during the crop cycle, leaving bare soil to dominate water and carbon exchange outside of these periods (Béziat et al., 2009; Han et al., 2024). Evaporation from exposed soil can drive large water losses when crops are absent (Liu et al., 2017), while fertilizer and tillage inputs can enhance nutrient availability and temporarily increase photosynthetic efficiency during active growth (Ghimire et al., 2024). Consequently, cropland WUE and CUE are highly dependent on rainfall timing, crop phenology, and management practices, making them more variable across years than rangelands (Béziat et al., 2009; Xia et al., 2015; Zhang et al., 2020). Understanding these seasonal contrasts is critical to assess how land-use change from rangeland to cropland alters coupled carbon-water dynamics in drylands.

Beyond contrasting seasonal flux dynamics between rangelands and croplands, climatic factors such as water stress further complicate carbon dynamics by potentially uncoupling productivity and respiration. The potential asynchrony between the water-sensitivity of productivity and respiration plays a crucial role in an ecosystem C balance. If primary production is more sensitive to water stress than respiration, ecosystems are likely to lose C with increasing droughts, as reduced photosynthesis does not equally reduce ecosystem respiration, leading to a net C loss (Liu et al., 2023). Moreover, the interplay between water and nutrient availability is a key factor that affects CUE. In nutrient-poor soils, water stress restricts nutrient uptake, hindering growth, and reducing C sequestration efficiency (Li et al., 2009). Understanding how soil moisture variability, driven by land-use change, influences plant water uptake and carbon assimilation is crucial for assessing impacts on both CUE and water use efficiency (WUE), defined as the ratio of gross primary productivity (GPP) to evapotranspiration (ET)) in dryland ecosystems (Beer et al., 2010; Hu et al., 2008; Tello-García et al., 2020). Conversely, nutrient-rich soils can help plants maintain higher photosynthetic efficiency and better withstand water stress, potentially enhancing NEP even under dry conditions (Paillassa et al., 2020; Sardans & Peñuelas, 2012). Water is needed to ensure soil hydrological connectivity, linking plant roots and microorganisms to nutrients essential for growth (Moyano et al., 2013), while in return, nutrients, particularly nitrogen (N) and phosphorus (P), are needed to produce

ODONGO ET AL. 2 of 21

osmolytes and enzymes that protect plants and microorganisms from osmotic stress and reactive oxygen species (Shanker et al., 2014). This is particularly important for semi-arid rangelands in Kenya where there is evidence that these ecosystems are nutrient limited (Carbonell et al., 2021; Leitner et al., 2024). Integrated management practices that address both water and nutrient limitations are therefore crucial for improving NEP and enhancing the resilience of dryland ecosystems to climatic variations. Understanding this interplay is essential, not only for assessing the direct impacts on C exchange processes between plants and soils but also for elucidating the consequences on water dynamics in the short and long term.

Despite the importance of dryland ecosystems, measurements of carbon and water flux dynamics in sub-Saharan Africa remain underrepresented in long-term eddy covariance networks. Existing measurements are often projector campaign-specific, such as CarboAfrica (Bombelli et al., 2009; Merbold et al., 2009), Adaptive Resilience of Southern African Ecosystems—(ARS AfricaE) (Berger et al., 2018), and the Safari2000 campaign (Scholes, 2005; Shugart et al., 2004) with continous observations largely concentrated in South Africa (Kutsch et al., 2008; Räsänen et al., 2017; Rybchak et al., 2024; Scholes, 2005). Limits our ability to generalize carbonwater dynamics in African drylands. Here, we address this gap by analyzing new flux data from two eddy covariance (EC) sites in East Africa: a grazed savanna rangeland and an adjacent dryland agricultural (cropland) site managed under conservation agriculture, following its conversion from rangeland in 2011, to investigate the differences in ecosystem carbon and water coupling between the two land use types. Our specific objectives were twofold: (a) to evaluate WUE of the rangeland and the cropland system during the peak growing season and the entire measurement period, and (b) to compare the CUE between the cropland and the rangeland during both the peak growing period and the entire measurement period, thereby capturing both phases of active vegetation and dormancy. The cropland site followed conservation agriculture principles, that included minimal soil disturbance (minimum-till) and crop diversification through rotation or intercropping (FAO, 2022; Hobbs et al., 2008). We hypothesized (a) that there would be higher WUE for the rangeland compared to the cropland due to its continuous vegetation cover, and (b) that the cropland would demonstrate higher CUE due to optimized agricultural practices, fertilization, and the selection of crops specifically aimed at achieving high yields and efficient C conversion into biomass.

#### 2. Methodology

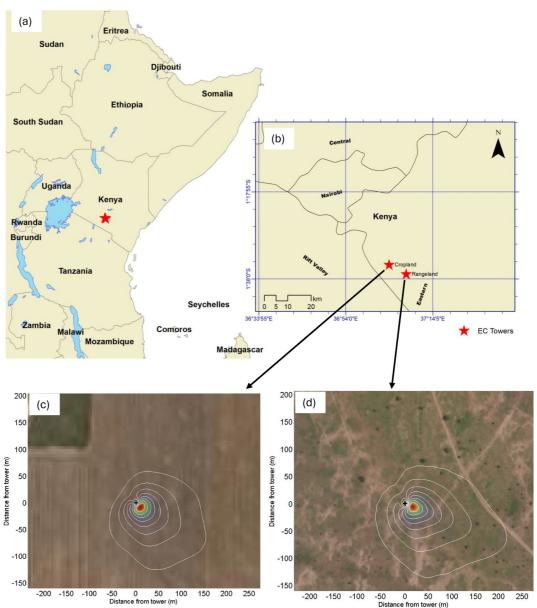
#### 2.1. Site Description

The flux measurements were conducted at two locations simultaneously: the Kapiti Research Station and Wildlife Conservancy—from now on referred to as "Kapiti" (1°36′50.40″S, 37°7′58.80″E, 1,667 m a.s.l.) managed by the International Livestock Institute (ILRI, 2019), and the Ausquest Ltd. farm (1°34′40.699″S, 37°04′01.301″E, 1,616 m a.s.l.), both located in the semi-arid drylands of Machakos county, Southern Kenya. The Ausquest farm is located about ~10 km to the Northwest of Kapiti (Figure 1). The region's climate is characteristic of semiarid savannas, marked by lower rainfall than potential ET rates. On average, the area receives about 550 mm of rainfall annually (ILRI, 2019; Leitner et al., 2024). 80% of the annual rainfall predominantly occurs in two seasons, forming a bimodal pattern: the first season spans from March to May and the second from October to December (Berliner & Kioko, 1999; Probert, 1992). The average annual temperature is around 20.2°C, with an annual variation of about 4°C (Carbonell et al., 2021; Leitner et al., 2024; Wolz et al., 2022).

Kapiti, covering approximately 14,000 ha, operates under a pastoral livestock management system. Here, cattle, sheep, goats, and camels are grazed and watered during daytime in the grassland and brought back to fenced enclosures (kraals or bomas) for the night (Leitner et al., 2024; Zhu et al., 2024). In addition to its role for livestock management and research, the station serves as a Wildlife Conservancy, hosting a wide variety of wildlife species including ungulates such as antelopes (eland, wildebeest, impala, gazelles), giraffes, and zebras, as well as carnivores such as lions, cheetahs, hyenas, and occasionally wild dogs. An eddy covariance (EC) station was installed at the end of 2018 to continuously observe the ecosystem-atmosphere exchange of CO<sub>2</sub> and water.

The Ausquest farm directly borders Kapiti and is a commercial agricultural operation covering approximately 1,101 ha of land. The area was a rangeland similar to Kapiti until 2011, when it was converted to dryland agriculture (pers. comm. Stuart Barden). The site adopts minimal tillage practices along with seasonal crop rotations. The farm is recognized for its diverse grain cultivation, including mung beans, seed beans, chickpeas, grain sorghum, barley, wheat and green grams, as well as forage sorghum. An EC system to measure CO<sub>2</sub> and water exchange was established at the farm in 2019. During the installation period, chickpeas were the primary

ODONGO ET AL. 3 of 21



**Figure 1.** Map showing the eddy covariance station sites in Kenya. Panel (a) shows the location of the monitoring sites in Kenya within Eastern Africa. Panel (b) provides a closer view of the southern part of Kenya, indicating the land use types at the EC sites. Panels (c, d) present detailed flux footprint climatology analyses (Kljun et al., 2015) using all the measured data, showing wind direction and distribution around the EC towers across different spatial scales. Contour lines in these panels depict the frequency of flux originating from various directions, highlighting the environmental dynamics at the sites.

crop grown in the monitored area. The farm used a seed rate of 80 kg ha<sup>-1</sup> and applied Diammonium Phosphate (DAP) fertilizer at a rate of 75–100 kg DAP ha<sup>-1</sup>, along with glyphosate herbicide spray. The EC setup provided data that covered the chickpea cropping season from March 2019 to 1 August 2019. During that period, the dry weight harvest was approximately 1.2 t ha<sup>-1</sup> of chickpea. After that, the EC tower malfunctioned due to excess water following heavy rainfall and required extensive repairs.

Soils on both tower locations are dark, clayey Vertisols (Chesworth, 2008; Leitner et al., 2024), commonly referred to as "black cotton soils", and lighter-textured Planosols (Gachene et al., in prep.). The vegetation at the rangeland site contained a rich variety of savanna grasses, such as *Cynodon dactylon, Bothriochloa insculpta*, *Aristida kenyensis, Themeda triandra*, *Panicum spp.*, and *Cenchrus mezianus*, legumes (e.g., Indigofera volkensii, Tephrosia pumila), forbs, and low densities of trees such as Vachellia drepanolobium and Balanites glabra,

ODONGO ET AL. 4 of 21

contributing to the area's biodiversity (Carbonell et al., 2021; Muthoka et al., 2022). Even though both sites were characterized by the same soil types, soil structure differed considerably due to the conversion from rangeland to cropland in 2011 at the Ausquest Ltd. farm.

#### 2.2. Instrumentation

The measurements presented in this study were taken from 13 March 2019 to 14 September 2019, when both eddy covariance (EC) towers were operational concurrently (Table S1 and Figure S3 in Supporting Information S1).

**Kapiti:** At Kapiti, a combination of an open-path infrared gas analyzer (LI-7500DS, LI-COR Biosciences, Lincoln, NE, USA) and a sonic anemometer (Gill Windmaster Pro sonic anemometer, Gill Instruments, Lymington, UK) was employed for measuring CO<sub>2</sub>, water vapor, sensible heat, and momentum fluxes. These instruments, set at a height of 4.3 m with a northward offset of 0°, operated at a sampling frequency of 10 Hz. The separation distances from the center of the gas analyzer's sampling volume to the anemometer were -5.0 cm northward, -20.0 cm eastward, and 0 cm vertically. The data acquisition was enabled using an embedded computer (LI-COR Biosciences, Lincoln, NE, USA). Meteorological measurements at this site included relative humidity and temperature gradients, measured at two-point heights of 2 and 4 m (Vaisala HMP155 sensors, Vaisala Oyj, Helsinki, Finland). Precipitation was recorded using a tipping bucket rain-gauge (LI-COR TR525 m, LI-COR Biosciences, Lincoln, NE, USA) at a height of 1.5 m. Shortwave and net radiation were measured with a net radiometer (CNR 4, Kipp & Zonen, Delft, The Netherlands) installed at a height of 4 m. Photosynthetic Photon Flux Density (PPFD) was measured using a quantum sensor (LI-190R, LI-COR Biosciences, Lincoln, NE, USA) installed at a height of 4 m. All these biometeorological data were stored on a datalogger (Sutron 9210 datalogger, Sutron Corporation, Sterling, VA, USA).

Ausquest farm: At the Ausquest farm, flux measurements in the cropland were conducted using a closed-path CO<sub>2</sub>/H<sub>2</sub>O gas analyzer (EC 155, Campbell Scientific, Logan, UT, USA) and a sonic anemometer (CSAT-3, Campbell Scientific, Logan, UT, USA) installed at a height of 3.2 m and North off-set at 115°. The sampling frequency was 10 Hz. The separation distance between the gas sampling tube and the center of the anemometer was 15.6 cm. The flow rate of the sampling system was 6.0 l min<sup>-1</sup>, with the inlet tube for the gas analyzer measuring approximately 64.5 cm in length and 2.2 mm in diameter. The longitudinal and transversal lengths of the setup were 12.0 and 1.0 cm respectively and the gas analyzer time response was 0.1 s. Meteorological measurements at this site included relative humidity and temperature measured at a height of 2.0 m (Vaisala HMP155 sensors, Vaisala Oyj, Helsinki, Finland). Precipitation was recorded using a tipping bucket rain-gauge (EML ARG100, Environmental Measurements Limited, NE, United Kingdom) at a height of 2.05 m. Radiation measurements, conducted at a height of 3.5 m, included incoming and outgoing Photosynthetic Photon Flux Density (PPFD) (LI-190 Quantum sensors, LI-COR Biosciences, Lincoln, NE, USA), shortwave radiation (Apogee SP-110 pyranometer, Apogee Instruments, Inc., Logan, UT, USA), and net radiation (NR-lite2 net radiometer, Kipp and Zonen, Delft, The Netherlands). The data acquisition was done with a datalogger (CDM-A116 with a 16-Channel 5V Analog to Input Module connected directly to a CR6 datalogger, Campbell Scientific, Logan, UT, USA).

#### 2.3. Processing of Eddy Covariance Data

The turbulent fluxes for both the open and closed path systems were calculated as 30-min block averages from the 10 Hz raw data. The process involved despiking (Vickers & Mahrt, 1997), double rotation of the wind coordinates (McMillen, 1988), and time lag compensation. For each averaging period, the time lag between the anemometer and gas analyzer signals was determined using a maximum covariance method. Subsequently, the fluxes were then corrected for frequency response to account for systematic losses at high and low frequencies (Moncrieff et al., 1997, 2004). These losses are due to insufficient response time of the instruments to capture all the high frequencies and averaging period not encompassing all the low frequency air flows (Moore, 1986). For the openpath system, the Webb-Pearman-Leuning (WPL) correction was applied to compensate for the effects of air density fluctuations on the measured CO<sub>2</sub> and H<sub>2</sub>O fluctuations (Webb et al., 1980). In the case of the closed-path EC 155 system, the CO<sub>2</sub> and H<sub>2</sub>O fluxes were calculated from instantaneous mixing ratio measurements. The EC155 outputs concentration measurements as mixing ratio, and mass—density concentrations are determined from the mixing ratio, and sample cell temperature and pressure. Spectral correction for the EC155 closed-path system were based on the analytical transfer function approach of Massman (2000). This approach corrected for

ODONGO ET AL. 5 of 21

instrument line averaging, sonic and gas analyzer lateral and longitudinal separation, tube attenuation for closed-path analyzer and high-pass filtering associated with block averaging and detrending (Novick et al., 2013). The rangeland flux data were processed using LI-COR EddyPro® software (v. 7.0.9) while the cropland flux data were processed using EasyFlux® PC software.

#### 2.4. Gap-Filling and Partitioning of the CO2 and Water Flux Data

The measured micrometeorological data had gaps during parts of the observation period due to system downtime, maintenance, or wildlife incidents. At both, the rangeland and cropland site, measurements of net ecosystem  $CO_2$  exchange (NEE) and latent energy (LE) exhibited gaps amounting to approximately 8.4% and 5.2% of the time, respectively (Table S2 in Supporting Information S1). Fingerprint plots of measured and gap filled NEE and LE are provided in the Figures S1 and S2 of Supporting Information S1. Additionally, fluxes classified as low-quality (flagged as 2 at the rangeland and 7–9 at the cropland site—according to the flux processing software outputs) were removed and replaced by gap filled data following the Marginal Distribution Sampling (MDS) method (Falge et al., 2001; Reichstein, Kätterer, et al., 2005) (Table S2 in Supporting Information S1).

The MDS method, a technique commonly employed for addressing data gaps, systematically evaluates the association between flux measurements and pivotal meteorological variables, such as global radiation, air temperature, and vapor pressure deficit, in conjunction with the flux values' temporal autocorrelation. When flux data are missing but corresponding meteorological information is available, the method fills these gaps by calculating the average flux value for analogous meteorological conditions identified within a 7-day period. If meteorological data are not available within this timeframe, the gap is filled by averaging flux values from the same time of day, initially spanning  $\pm 1$  hr from the missing point and extending the window as necessary. This procedure effectively utilizes linear interpolation, drawing on data points adjacent to the gap. The implementation of the MDS method was facilitated by the REddyProc (v. 1.3.2) open-source R package (Wutzler et al., 2018). Meteorological variables relevant for partitioning such as air temperature (Tair), vapor pressure deficit (VPD) and radiation ( $R_g$ ) were also gap-filled for missing data.

After completing the gap-filling process, the partitioning of net ecosystem  $CO_2$  exchange (NEE) into Gross Primary Production (GPP) and Ecosystem Respiration ( $R_{\rm eco}$ ) was conducted using the daytime method (DT) as outlined by Lasslop et al. (2010). This approach incorporates a two-part model: a rectangular hyperbola light response curve, as proposed by Falge et al. (2001), for the estimation of GPP, and the Lloyd and Taylor equation for calculating  $R_{\rm eco}$ , similar to the methodology used in the nighttime (NT) approach (Reichstein, Falge, et al., 2005).

#### 2.5. Calculation of Ecosystem Flux Metrics

The 30-min gap-filled fluxes (GPP, NEE,  $R_{\rm eco}$  and LE) were aggregated into daily totals. At each study site, these daily totals were then summed to calculate cumulative C fluxes over the entire measurement period (13th March 2019 to 14th September 2019). NEP was derived as the inverse of NEE, following the ecological sign convention, where positive NEP indicates net carbon uptake by the ecosystem, whereas negative values signify a net release of C (Xiao et al., 2013). This inversion is critical for understanding the directional flow of C within these ecosystems. To represent direct carbon flux dynamics, we retained NEE as it is the primary measured variable from the eddy covariance systems. For derived metrics such as CUE, we use NEP to align with ecological convention and accurately reflect net carbon uptake in the ecosystem. This approach ensures clarity between raw measurements and derived ecosystem efficiency calculations. CUE was computed as the ratio of NEP to GPP, providing an estimate of the efficiency with which assimilated carbon was retained in the ecosystem.

ET was computed from latent heat flux (LE) measurements using the formula:

$$ET [mm] = \frac{LE \times t}{L_{\nu} \times \rho_{w}}, \tag{1}$$

where LE is in W m<sup>-2</sup>, t is time period in seconds of the measurement (30-min × 60 s min<sup>-1</sup> = 1,800 s),  $L_v$  is the latent heat of vapourization of water in J kg<sup>-1</sup>, and  $\rho_w$  is the density of water in kg m<sup>-3</sup>. Nighttime ET was assumed negligible. WUE was then calculated as the ratio of cumulative GPP to cumulative ET.

ODONGO ET AL. 6 of 21

#### 2.6. Analytical Approach

Analytical periods were defined to compare ecosystem performance during periods of high productivity versus the full seasonal cycle. The peak growing season was determined using the 90th percentile threshold of daily NEE values, identifying days of maximum carbon uptake at both sites. The entire measurement period covered March–September 2019, spanning: early season (March–April: low rainfall and limited plant growth), peak growth (May–June corresponding to high precipitation and peak productivity), and post-harvest periods in the cropland, and continuous dynamics in the rangeland from (July–September). Flux measurements were first aggregated to daily totals and subsequently summed over the defined periods (peak growing period and full measurement period) to obtain cumulative totals for each flux variable. While the full-period metrics included phases with limited or no vegetation cover such as pre-emergence and post-harvest at the cropland, they are presented for completeness and to reflect overall ecosystem flux dynamics that consider both plant and microbial responses (for CUE) as well as background evaporation (for WUE). However, CUE and WUE values during the peak growing season were interpreted as more representative of vegetation-mediated resource-use efficiency. These cumulative totals formed the basis for statistical comparisons. Differences in the period totals of key ecosystem flux variables, including GPP,  $R_{\rm eco}$ , NEP, CUE, and WUE, between ecosystems and between periods were assessed using two-sample t-tests (ttest2) in MATLAB R2023a.

To examine ecosystem responses to extreme rainfall events, we applied a percentile-based thresholding approach, selecting events exceeding the 95th percentile of daily precipitation.  $R_{\rm eco}$  rates were extracted for the same days (i.e., day 0), capturing immediate pulse responses. These thresholds corresponded to rainfall amounts of 7.2–31.2 mm at the rangeland and 2.0–76.8 mm at the cropland and were used to evaluate respiration responses to high-intensity precipitation. While this approach captures extreme rainfall events relative to the distribution at each site, the absolute rainfall magnitudes differ between sites. Consequently, this method does not fully normalize cross-site comparisons. Alternative approaches, such as normalization by event magnitude or soil moisture response thresholds, could be considered in future analyses to improve the comparisons. In addition to high-intensity rainfall events, we also evaluated ecosystem responses during non-rainfall conditions, defined as days with zero recorded precipitation (PPT = 0 mm). This category captured all dry intervals throughout the measurement period, including both early season and in-season dry days, and was used to assess respiration dynamics in the absence of rainfall inputs.

To assess differences in ecosystem carbon use efficiency (CUE) between the two land-use types, we examined the daily relationships between GPP and  $R_{\rm eco}$ . This relationship provides insight inn how much of the carbon fixed through photosynthesis is respired back to the atmosphere, and thus directly reflects the efficiency of carbon retention at the ecosystem scale. To investigate these relationships, we fitted site-specific models to the daily aggregated data. For the cropland, a linear regression model was applied to represent the continuous coupling of GPP and  $R_{\rm eco}$ . For the rangeland, an exponential rise-to-maximum function was used to capture the observed saturation of  $R_{\rm eco}$  at higher GPP levels, indicating partial decoupling at high productivity. For the relationship between GPP and ET, linear regression models were applied for both the cropland and rangeland systems to assess water flux coupling. Model fits were evaluated using correlation coefficients (r), and sample sizes (N) were reported. To represent the expected range of observed values, 95% prediction intervals were calculated for both models and presented as shaded bands in the figures. Significance levels for all statistical tests were set at p < 0.05, with levels of significance indicated in the figures. Error bars in the figures represent the standard error of the aggregated totals for each period. This approach allowed us to directly compare how land use and its management influence carbon use efficiency (via GPP- $R_{\rm eco}$  coupling) and water-use coupling (via GPP-ET relationships).

To investigate how atmospheric water demand shapes ecosystem-scale WUE and GPP, we extracted VPD over the daytime window (10:00–16:00 hr) and computed the 90th percentile of the half-hourly VPD values (VPD $_{p90}$ ) as our metric of peak evaporative demand. We retained only days meeting quality criteria: GPP > 0, ET > 0, and photosynthetically active radiation >50  $\mu$ mol m $^{-2}$  s $^{-1}$ . To characterize the WUE-VPD and GPP-VPD relationship, we then binned the daily VPD $_{p90}$  into fixed classes (0–1, 1–2, 2–3, 3–4 kPa), computed within-bin means and standard errors of WUE and GPP, and overlaid the daily observations distinguishing growing-season versus non-growing-season days.

ODONGO ET AL. 7 of 21

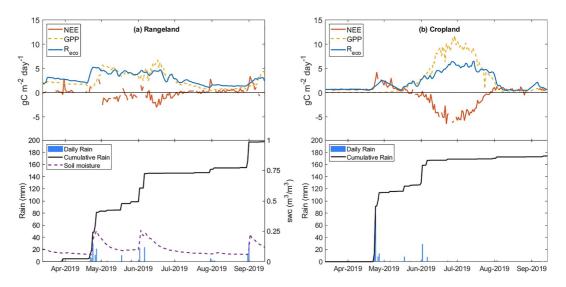


Figure 2. Daily C fluxes (GPP, Reco, NEE) and meteorological variables (Soil water content, daily and cumulative precipitation) for the (a) rangeland and (b) cropland sites. NEE is presented as the directly measured flux, with positive values indicating net ecosystem carbon loss. Sample size: daily observations from 13 March to 14 September 2019 (N = 185).

#### 3. Results

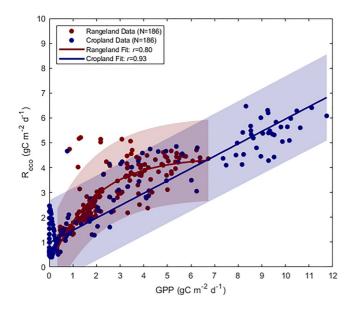
#### 3.1. C Exchange

Despite being of similar magnitude, the timing and total amount of rainfall slightly differed between the two study sites, which resulted in distinct C flux dynamics (Figure 2). The rangeland site exhibited an immediate increase in  $R_{\rm eco}$  following early rainfall events, and  $R_{\rm eco}$  remained elevated throughout much of the growing season, even during periods without rain, before gradually declining as precipitation decreased around June.  $R_{\rm eco}$  then peaked again in response to late season rainfall events in September. In contrast, despite substantial early rainfall events at the cropland site,  $R_{\rm eco}$  displayed a delayed response because of the initial absence of vegetation cover before planting. The increase in  $R_{\rm eco}$  became more pronounced only during the period of active crop growth, coinciding with canopy development.

The cropland site was characterized by bare soil until emergence of chickpea plants at the end of May 2019, and consequently both GPP and  $R_{\rm eco}$  were low in the first 4 weeks of the growing season (Figure 2b). With the emergence of chickpeas,  $R_{\rm eco}$  started to increase from mid-May simultaneously with increasing GPP, which reached a peak of ~12 g C m<sup>-2</sup> d<sup>-1</sup> before senescence in early July 2019, after which  $R_{\rm eco}$  declined again, too. By mid-June 2019, GPP had surpassed  $R_{\rm eco}$  leading to a net uptake of C in the cropland. In contrast to the cropland, which was bare at the beginning of the observations, the rangeland maintained a continuous vegetation cover, characterized by a mix of perennial and seasonal plant species that contributed to a stable and sustained  $R_{\rm eco}$  rate throughout the study period. Consequently, the rangeland exhibited higher  $R_{\rm eco}$  rates than the cropland from the beginning of the measurements on 13-Mar-2019 until 12-Jun-2019 (Figure 2a). The relationship between GPP and  $R_{\rm eco}$  was stronger and more linear in the cropland than in the rangeland (Figure 3). The daily maximum GPP from the rangeland site was 6.7 g C m<sup>-2</sup> which was only about half of what was observed at the cropland. While the daily maximum rangeland  $R_{\rm eco}$  did not exceed 5.2 g C m<sup>-2</sup>, the cropland  $R_{\rm eco}$  continued to increase linearly with GPP up to a maximum of 6.5 g C m<sup>-2</sup> until early July.

Initially, during the early part of the season in March and April 2019, prior to the onset of rains and canopy development,  $R_{\rm eco}$  consistently exceeded GPP (Figure 2) at both the rangeland and cropland site. The mean  $R_{\rm eco}$  rate for the rangeland during this dry period was  $\sim 2.7 \pm 1$  g C m<sup>-2</sup> d<sup>-1</sup>. The non-rainy periods showed a relatively narrow interquartile range of  $R_{\rm eco}$  for the rangeland, reflecting consistent C emission rates with little variability. In contrast, the cropland had a lower mean  $R_{\rm eco}$  rate of  $2.2 \pm 2$  g C m<sup>-2</sup> d<sup>-1</sup>, with higher variability, as indicated by the wider interquartile range and the presence of extreme values (Figure 4a).

ODONGO ET AL. 8 of 21



**Figure 3.** Relationship between daily GPP and  $R_{\rm eco}$  at the rangeland and cropland sites during the full measurement period. Data points represent daily sums. The rangeland data are fitted with an exponential rise-to-maximum function, highlighting a plateau of  $R_{\rm eco}$  at higher GPP levels, indicating partial decoupling. Cropland data are fitted with a linear model, reflecting continuous coupling. Shaded areas represent 95% prediction intervals, indicating the expected range of observed values.

Following the onset of the rains in late April 2019, higher rates of C release were recorded at both sites. The rangeland site showed significant C emissions during rainfall events above the 95th percentile (Rangeland: 7.2–31.2 mm; Cropland: 2.0–76.8 mm), with a mean emission rate of  $3.9 \pm 1.3$  g C m<sup>-2</sup> d<sup>-1</sup>. The interquartile range for the rangeland was higher during the high rainfall events than for the cropland site but was comparable to the rangeland non-rainy days (Figure 4).

At the cropland site,  $R_{\rm eco}$  rates during rainfall events averaged ~1.9  $\pm$  0.67 g C m<sup>-2</sup> d<sup>-1</sup>. Although there was an increase in  $R_{\rm eco}$  compared to the fluxes observed during the non-rainy periods, the variability in respiration rates of the cropland site was less pronounced during rainfall events (Figure 4b). Cumulative C emissions from the rangeland (35 g C m<sup>-2</sup>) following 95th percentile rain events were twice as high as emissions from the cropland site during the same period (17.5 g C m<sup>-2</sup> d<sup>-1</sup>), even though both sites received similar amounts of rainfall (164 mm at the cropland vs. 168 mm at the rangeland over the entire observation period). A two-tailed *t*-test confirmed that  $R_{\rm eco}$  was significantly higher (p < 0.01) at the rangeland than at the cropland for both rainy and non-rainy days.

Throughout the 185-day measurement period (March to mid-September 2019), NEE accumulated to 14 g C m<sup>-2</sup> at the rangeland site compared to -69 g C m<sup>-2</sup> at the cropland site (Figure 5a). These values reflect net C exchange during the seasonal measurement window and do not capture fluxes occurring before planting or after crop harvest. The cumulative GPP was comparable at both sites, totaling 452 g C m<sup>-2</sup> at the rangeland site and 469 g C m<sup>-2</sup> at the cropland site (Figure 5b). However, the cumulative  $R_{\rm eco}$  at the rangeland site reached 527 g C m<sup>-2</sup>, which was 21% higher than the 415 g C m<sup>-2</sup> observed at the cropland site (Figure 5c).

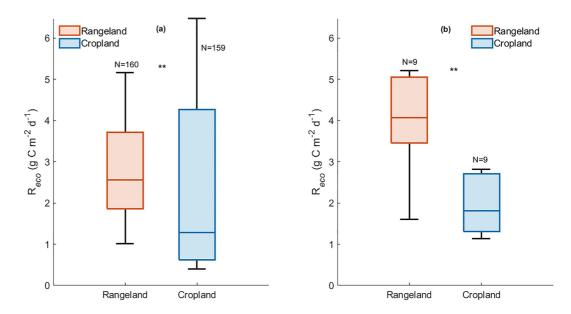
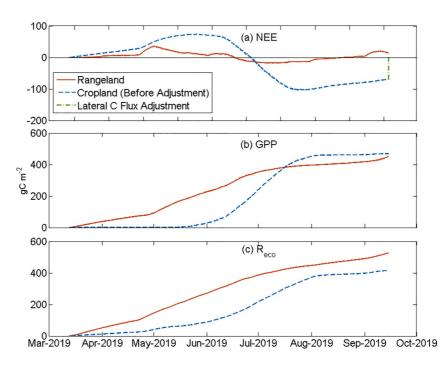


Figure 4. Mean ecosystem respiration ( $R_{\rm eco}$ ) at the rangeland and cropland sites (a) during non-rainy days (i.e., all days with rainfall = 0 throughout the entire observation period) and (b) following daily rainfall above the 95th percentile (7.2–31.2 mm for the rangeland and 2.0–76.8 mm for the cropland). Mean  $R_{\rm eco}$  was significantly higher in the rangeland compared to the cropland in both cases (\*\* indicates significant p < 0.01, two-tailed t-test).

ODONGO ET AL. 9 of 21



**Figure 5.** Cumulative C fluxes for the rangeland and cropland sites (a) NEE, (b), GPP, (c)  $R_{\rm eco}$ . Note NEE is presented as the directly measured flux, with positive values indicating net C loss. Please note that we only observed one rainy season in a bimodal system, while the C exchange during the second season could not be measured due to sensor malfunction.

Consequently, the rangeland site acted as a small  $CO_2$  source (+14 g C m<sup>-2</sup>) while the cropland site functioned as a  $CO_2$  sink (-69 g C m<sup>-2</sup>). However, after accounting for the lateral C flux (~75 g C m<sup>-2</sup>) due to the chickpea harvest, which was reported to be 1,200 kg FW ha<sup>-1</sup> at a moisture content of 11% (pers. comm. Stuart Barden), and considering a legume C fraction of 49% of dry matter (Kuyah et al., 2023) and harvest index of 56% (Patil et al., 2016), the net C balance at the cropland was reduced to +6 g C m<sup>-2</sup>, indicating that the cropland was a small C source as well. In contrast, the rangeland did not experience much C offtake, as there was no harvest other than anticipated redistribution of C through wildlife and livestock grazing activities.

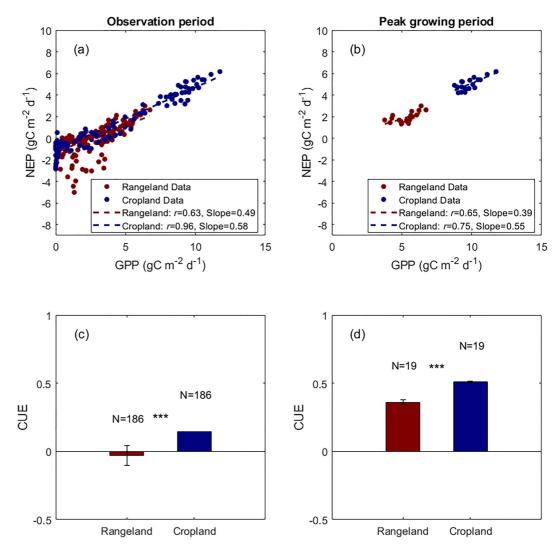
#### 3.2. Carbon Use Efficiency

The rangeland had a mean CUE of  $-0.03 \pm 0.07$  (s.e.m) (Figure 6). The negative mean CUE stems from the rangeland ecosystem being a net C source over the measurement period (NEE = 14 g C m<sup>-2</sup>), with C release through respiration exceeding C fixation via photosynthesis. However, the relatively large standard error of the mean that is larger than the mean CUE itself indicates substantial variability in the data (Figure 6). Furthermore, even though the mean CUE was negative, instances occurred when the rangeland acted as a C sink. More specifically, the rangeland was a C sink during the peak growing season and consequently, CUE was positive then  $(0.36 \pm 0.02 \text{ s.e.m})$ .

Conversely, the cropland site showed a mean CUE of  $0.15 \pm 25.6$  (s.e.m), as it was a net C sink over the study period that rarely acted as a source. Nevertheless, similar to the rangeland, the cropland also exhibited a widely varying standard error of the mean for CUE. During the peak growing season, the CUE increased to  $0.51 \pm 0.01$  (s.e.m), suggesting that the cropland was particularly efficient at converting assimilated C into biomass, more so than the rangeland during the same period. However, please note that a large fraction of the fixed C was transported out of the system in the form of crop harvest. The steeper slopes of the correlations between NEP and GPP both during the entire observation period and the peak growing period indicated that the cropland had a consistently higher NEP response to GPP compared to the rangeland. However, a slight decrease in slope is observed in both systems during the peak growing period.

ODONGO ET AL. 10 of 21

from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2024JG008623 by Schweizerische Akademie Der, Wiley Online Library on [28/10/2025]. See the Terms and Conditions (https://onlinelibrary.wile



**Figure 6.** Comparison of NEP and CUE between rangeland and cropland sites. (a, b) show the relationship between GPP and NEP for the whole observation period and the peak growing season (90th percentile of NEE) (c) CUE calculated for the entire observation period, showing significantly higher CUE in cropland compared to rangeland (\*\*\* indicates p < 0.001, two-tailed t-test) (d) CUE during the peak growing period, similarly showing significantly higher CUE in cropland compared to rangeland (p < 0.001, two-tailed t-test). Total daily observations (N) are indicated on each bar. Error bar for the cropland observation period is not displayed as it was too large (s.e.m = 25.6).

#### 3.3. Water Use Efficiency

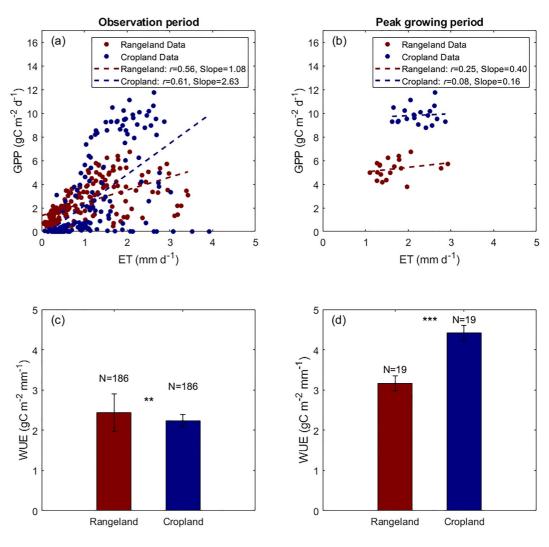
During the entire observation period the rangeland exhibited a significantly higher ecosystem water use efficiency (WUE) (2.  $43 \pm 0.46$  (s.e.m) g C m<sup>-2</sup> mm<sup>-1</sup> H<sub>2</sub>O) compared to the cropland (2.24 ± 0.15 g C m<sup>-2</sup> mm<sup>-1</sup> H<sub>2</sub>O) (p < 0.05). However, when investigating the peak growing season only, the cropland exhibited a significantly (p < 0.001) higher WUE (4.42 ± 0.19 (s.e.m) g C m<sup>-2</sup> mm<sup>-1</sup> H<sub>2</sub>O) compared to the rangeland (3.17 ± 0.19 (s.e.m) g C m<sup>-2</sup> mm<sup>-1</sup> H<sub>2</sub>O) (Figure 7)). The rate of increase of GPP per unit increase of ET was higher for the cropland compared to the rangeland during the entire observation period as indicated by the steeper slope of the correlation between GPP and ET (Figure 7a). In contrast, during the peak growing period, the slopes for both systems were less steep (0.4 and 0.16 for the rangeland and cropland, respectively).

To further explore differences in flux sensitivity to atmospheric demand, we examined both WUE and GPP as functions of daytime VPDp90 (Figure 8). Across both ecosystems, binned WUE and GPP responses to daytime VPD<sub>p90</sub> revealed contrasting sensitivities and strong seasonality. In the rangeland (Figures 8a–8c), full observation period WUE showed a slight upward trend with increasing VPD<sub>p90</sub>, rising from  $\sim$ 2.5 g C mm<sup>-1</sup> at low

ODONGO ET AL.

. 2025, 10, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2024JG008623 by Schweizerische

Akademie Der, Wiley Online Library on [28/10/2025]. See the Terms and Conditions



**Figure 7.** Comparison of GPP and WUE between rangeland and cropland systems during the observation period and peak growing season. (a) Relationship between ET and GPP for rangeland and cropland during the entire observation period. (b) Relationship between ET and GPP during the peak growing period (90th percentile NEE threshold). (c) WUE calculated for the entire observation period, showing significant high WUE in rangeland than cropland (\*\* indicates p < 0.05, two-tailed t-test). (d) WUE during the peak growing period, showing significantly higher WUE in cropland compared to rangeland (\*\*\* indicates p < 0.001, two-tailed t-test). The number of observations (N) is indicated on each bar.

VPD to  $\sim 3.8~g$  C mm<sup>-1</sup> at the highest VPD bin; however, when only peak growing season days were considered, WUE instead dropped from  $\sim 4.8$  to  $\sim 3.2~g$  C mm<sup>-1</sup>. Rangeland GPP likewise decreased moderately with VPD<sub>p90</sub>, with mean rates dropping from  $\sim 3.2$  to  $\sim 2.1~g$  C m<sup>-2</sup> d<sup>-1</sup> across the VPD range in the full record, and from  $\sim 5.8$  to  $\sim 5.0~g$  C m<sup>-2</sup> d<sup>-1</sup> during peak growth. By contrast, cropland WUE (Figures 8b–8d) declined steadily with VPD<sub>p90</sub> in both the full and peak-growing periods, from  $\sim 3.0$  to  $\sim 0.2~g$  C mm<sup>-1</sup> over the observed VPD bins and from  $\sim 6.0$  to  $\sim 2.5~g$  C mm<sup>-1</sup> during peak growth. Cropland GPP fell sharply as well, with full observation period means falling from  $\sim 4.5~g$  C m<sup>-2</sup> d<sup>-1</sup> at low VPD<sub>p90</sub> to near zero at high VPD, and peak growing season GPP declining from  $\sim 10.0$  to  $\sim 9.5~g$  C m<sup>-2</sup> d<sup>-1</sup> only at the lowest bins.

## 4. Discussion

## 4.1. Contrasting CO<sub>2</sub> Response Between Rangeland and Cropland

Our observation period, which captured the early non-rainy season (March–April), the main rainy period (May–June) followed by transition to non-rainy period (July–September), revealed differences in CO<sub>2</sub> dynamics between rangeland and cropland. Rangeland C fluxes were more variable, with large rainfall events triggering

ODONGO ET AL. 12 of 21

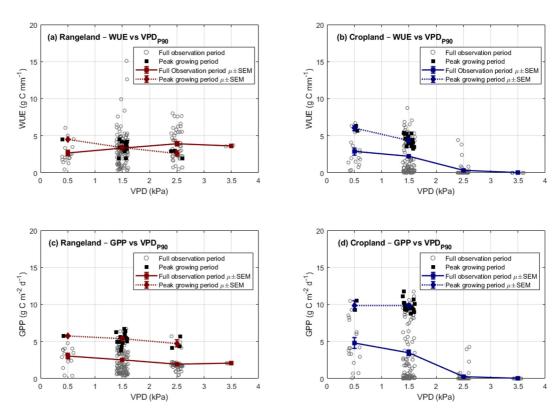


Figure 8. Binned relationships of ecosystem water-use efficiency (WUE) and gross primary productivity (GPP) with daytime vapor-pressure deficit (VPD $_{90}$ ; 10:00–16:00 hr) at the rangeland (left column) and cropland (right column) sites. Panels (a) and (b) show WUE versus VPD $_{90}$  and panels (c) and (d) show GPP versus VPD $_{90}$ . In each panel, individual daily values of WUE or GPP corresponding to the 90th-percentile daytime VPD are plotted as open gray circles (full observation period) or filled black squares (peak-growing-season days). Bin-averaged means  $\pm$  SEM for the full observation period are drawn as solid lines with filled circle markers, and bin-averaged means  $\pm$  SEM for the peak season only are drawn as dotted lines with filled diamond markers.

emissions exceeding 4.0 g C m $^{-2}$  d $^{-1}$ . One possible explanation for this might be the sustained presence of vegetation cover in rangelands along with living roots, which continuously supply labile C through root exudation and plant litter (Sayer et al., 2007; Wang, Lai, et al., 2015). This supports microbial activity leading to sustained respiration rates. In contrast, the cropland site had limited vegetation cover during the early part of the season, as planting is typically timed with the anticipated onset of rains. As a result, the soil remained largely bare during initial rainfall events, which likely contributed to the lower  $R_{\rm eco}$  observed during this period. The increase in  $R_{\rm eco}$  in the cropland coincided with chickpea emergence and canopy development from late May onward (Figure S7 in Supporting Information S1), reflecting expected increases in autotrophic and microbial respiration associated with crop growth.

Other than the notable differences in C emissions before and after rainfall events (Figure 4), the influence of management practices and nutrient availability, especially N, likely played a crucial role in determining the difference in C fluxes between rangeland and cropland (Wang, Zhang, et al., 2015). On the ecosystem scale, N inputs have been shown to enhance NEP and explain C allocation patterns (Du, 2023; Hagh-Doust et al., 2023; Janssens et al., 2010). The fraction of GPP retained as NEP (as indicated by the slopes) was higher in the cropland compared to the rangeland, both during the observation period and the peak growing period. This suggests that a larger portion of the C fixed through photosynthesis (GPP) was retained as NEP in the cropland, implying higher CUE relative to the rangeland. This was likely due to farm management and application of DAP fertilizer that increased N availability. In contrast, N limitation in the rangeland might have led to a larger proportion of its GPP being released through  $R_{\rm eco}$  because plants and microorganisms did not have enough N to incorporate the fixed C into their biomass.

ODONGO ET AL. 13 of 21

Rangelands contain a mix of grasses, forbs and shrubs that produce plant litter with a high carbon-to-nitrogen (C:N) ratio, which is more resistant to decomposition (Piñeiro et al., 2010). In contrast, fertilized croplands receive N fertilizer as well as inputs of N-rich plant residues with a lower C:N that decompose more readily (Yan et al., 2017). These patterns are supported by supplementary soil data (Figure S6 in Supporting Information S1), which show that rangeland soils had consistently higher %C and, in most soil depth layers, higher %N than the cropland. Compounded by the typical N limitation in rangeland soils, microbial communities in these environments tend to respire more  $CO_2$  per unit of C assimilated compared to those in N-rich environments like croplands (Manzoni et al., 2012). This is because N-limited microbes require more energy and respire more  $CO_2$  to access the nutrients they need (Manzoni et al., 2012; Sinsabaugh et al., 2013).

Comparing the GPP- $R_{\rm eco}$  relationship indicated that for GPP < 7 g C m<sup>-2</sup> d<sup>-1</sup>, a larger fraction of GPP was released through  $R_{\rm eco}$  in the rangeland compared to the cropland. However, when cropland GPP increased >7 g C m<sup>-2</sup> d<sup>-1</sup>, this corresponded with increased  $R_{\rm eco}$  rates, probably because N fertilization (a) boosted photosynthesis and with that belowground C allocation (Keller et al., 2023), and (b) enhanced the overall metabolic activity of plants and soil microbes, sustaining high respiration (Bossolani et al., 2023; Chen et al., 2019). In contrast, the rangeland did not reach such high GPP values, and its  $R_{\rm eco}$  tended to level off (decouple) with increasing GPP, likely due to nutrient limitation as well as adaptive strategies of rangeland vegetation that aims to minimize water loss.

Furthermore, it is known that soil biogeochemical processes are primarily driven by a small fraction of physiologically active soil microbes, depending on the changing environmental conditions (Allison et al., 2010; Blagodatskaya et al., 2011; Frey et al., 2013; Salazar-Villegas et al., 2016; Sulman et al., 2014; Wieder et al., 2013). While the rangeland has vegetation cover throughout the seasons, the cropland was bare at the onset of the rains and remained without cover after crop harvest. Considering that microbial respiration responds rapidly to changing environmental conditions, the absence of C input from root exudation during the dry period potentially leads to a reduced microbial population in the cropland. In contrast, the microbial population of the rangeland were likely higher during the dry period because of presence of active plant cover that continuously provides a proportion of active microbes with soil C inputs throughout the transition period long after the cropland has been harvested and stopped allocating any C belowground.

In summary, the findings advance our understanding of ecosystem function in East Africa drylands by showing how contrasting land use and management shape C dynamics based on concurrent eddy covariance observations. Despite comparable GPP across both systems, distinct land use management regimes, ranging from fertilization and minimum tillage in cropland to continuous grazing in rangeland, led to divergent C dynamics. The cropland exhibited higher CUE and a tighter GPP- $R_{\rm eco}$  coupling, suggesting enhanced C retention under optimized agricultural conditions. In contrast, the rangeland showed lower CUE and partial decoupling of GPP and  $R_{\rm eco}$ , reflecting nutrient constraints and water-saving strategies of native vegetation.

#### 4.2. Ecosystem Management and Carbon Dynamics

The rangeland site acted as a moderate C source ( $+14 \, \mathrm{g} \, \mathrm{C} \, \mathrm{m}^{-2}$ ), whereas the cropland site initially functioned as a C sink ( $-69 \, \mathrm{g} \, \mathrm{C} \, \mathrm{m}^{-2}$ ). However, when accounting for the lateral C flux due to the harvest of chickpeas, the net C balance for the cropland site shifted to being a small C source ( $+6 \, \mathrm{g} \, \mathrm{C} \, \mathrm{m}^{-2}$ ), too. The rangeland, however, did not experience lateral C flux other than C redistribution due to livestock and wildlife grazing within the system. Since the C fluxes reported here reflect only the seasonal measurement window (March to September), full-year C budgets cannot be inferred directly. Longer-term, continuous measurements would be required to quantify net annual C exchange more accurately at both sites. Furthermore, it is important to note that this study did not account for C fluxes associated with methane (CH<sub>4</sub>), which could significantly influence the overall C dynamics, particularly in the rangeland environment.

Moreover, it should be noted that the conversion of rangeland to cropland in 2011 had likely resulted in significant initial C losses due to soil disturbance and biomass removal. This historical C loss of land conversion should be considered when evaluating the long-term C dynamics and sequestration potential of croplands compared to grasslands, as it has been shown to contribute up to 37% to the total long-term C balance (Tang et al., 2019). While the rangeland showed a slight net C release over the observation period, its C dynamics were less influenced by lateral fluxes compared to croplands because the grassland biomass that was grazed by livestock and wildlife was deposited in the form of manure within the same ecosystem (Leitner et al., 2024). In addition, previous work has

ODONGO ET AL. 14 of 21

shown that the export of nutrients via sold livestock in Kapiti is small compared to the internal redistribution (Carbonell et al., 2021).

This underscores the importance of including lateral C fluxes in C balance assessments, as neglecting these can lead to an overestimation of the net C sequestration potential of agricultural systems. Additionally, the historical C losses from land conversion highlight the need for careful consideration of land-use changes in C accounting across longer time scales than a few months or even few years. In addition, for a complete picture, the GHG emissions originating from fertilizer production and application, fuel for machinery, and other management practices in the cropland as well as  $CH_4$  and  $N_2O$  emission from grazing livestock in the rangeland (Leitner et al., 2024; Wolz et al., 2022; Zhu et al., 2024) need to be considered. While this was beyond the scope of the current study, it is important to emphasize that understanding these dynamics is crucial for developing accurate C budgets and effective land management strategies to mitigate climate change.

#### 4.3. Comparison of CUE in Rangelands and Croplands

The rangeland exhibited a negative mean CUE over the entire season, suggesting that it was a net C source, which is in line with the cumulative net C release we observed. However, the substantial intra-seasonal variability points to periods where the rangeland has acted as a C sink, particularly during the peak of the growing season. This finding is consistent with the notion that semi-arid rangelands exhibit fluctuating C dynamics, influenced by seasonal changes in plant growth and microbial activity (Liang et al., 2021). The positive CUE observed during the peak growing season supports this, highlighting the impact of increased photosynthetic activity in these periods.

In contrast, the cropland maintained a predominantly positive CUE values across the observation period, with mean CUE significantly higher than in the rangeland. This suggested that the cropland functioned as a net C sink during most of the growing season. This is likely attributable to the efficient use of C for growth, amplified by fertilizer use, which alleviated crop N limitation, and minimum tillage practices, which enhance soil structure and moisture retention (Rahman et al., 2021). The higher CUE during the peak growing season compared to the rangeland further suggests that crop management strategies are effectively optimized for C sequestration, a trend observed in various studies on dryland agriculture (Guillen-Cruz et al., 2022). However, it is important to note that full-period CUE values at the cropland included pre-emergence and post-harvest phases, when photosynthetic uptake was minimal. These values reflect broader ecosystem dynamics but may not accurately represent plant-level efficiency. Peak growing period CUE offers a more reliable indicator of carbon use during periods of active crop growth. Management that is N fertilization also increased the metabolic activity of chickpea and soil microbes, leading to sustained higher respiration rates compared to the rangeland (Figure 3). Still, our observations only resemble a snapshot within a single year, and we argue for continuous multi-year observations in order to observe trends in CUE for rangelands and croplands.

When compared with other reported values, our ecosystem CUE shows clear differences. The rangeland mean CUE of -0.03 reflected its status as a net C source over the full observation period. While negative CUE values are not typical for many semi-arid rangelands, previous work has shown that these ecosystems can switch between sink and source states depending on rainfall pulses and seasonal moisture availability (e.g., Fernández-Martínez, Vicca, Janssens, Sardans, et al., 2014; Liu et al., 2022; Manzoni et al., 2018). The positive CUE we observed during the peak growing season (0.36) supports this pattern, indicating that rangelands can act as temporary C sinks under favorable conditions. By contrast, the cropland maintained a positive mean CUE (0.15) and reached 0.51 during peak growth, values consistent with agricultural systems where management inputs (fertilizer, reduced tillage) enhance carbon retention efficiency (Guillen-Cruz et al., 2022; Rahman et al., 2021). These sitelevel patterns suggest that while rangelands are highly sensitive to seasonal moisture fluctuations, croplands under conservation management achieve higher and more stable CUE during active growth phases, though this comes with the trade-off of lateral C export via harvest.

#### 4.4. Comparison of WUE in Rangelands and Croplands

The cropland was bare before planting and vegetation cover occurred only after germination. In contrast, the natural vegetation cover in the rangeland was permanently present and only varied in its activity seasonally. This likely led to different rates of evaporation and transpiration between rangeland and cropland (Figure 7; also see Figures S4 and S5 in Supporting Information S1) (Horton et al., 1996; O'Brien et al., 2018). Also, the growth stage

ODONGO ET AL. 15 of 21

of the crop in the cropland likely affected both GPP and ET, leading to large variability in the estimated WUE. More specifically, before and during planting, ET was primarily driven by soil evaporation, while after crop emergence, transpiration from the growing crops became the dominant pathway of water loss. Nitrogen fertilization has also been found to increase the ratio of water lost by transpiration compared to evaporation, and to improve WUE for both grain and dry matter production (Li et al., 2009). Our initial hypothesis suggested that the rangelands would exhibit higher WUE compared to dryland agricultural systems over the entire season, reflecting adaptations such as deep rooting systems and leaf morphologies designed to optimize water use. This hypothesis is supported by our results, which show significantly higher WUE in the rangeland over the full observation period. However, during the peak growing season, the cropland demonstrated significantly greater WUE than the rangeland, likely due to optimized transpiration during active canopy development.

Rangeland vegetation did not achieve quite as high GPP rates relative to the cropland due to nutrient limitation and possibly also the adaptive strategies of rangeland vegetation that aim to minimize water and nutrient loss. This suggests that while semi-arid rangeland plants are adapted for overall WUE, crops, likely due to targeted agricultural practices such as fertilization, may have the capacity to achieve higher WUE when conditions are optimal for growth (Flexas & Carriquí, 2020). This suggests that during the active growth phase, the cropland ecosystem was more efficient at converting water into biomass. WUE values calculated over the full observation period at the cropland site include pre-emergence and post-harvest phases, when vegetation cover was minimal and evaporation dominated water loss. These full-period values reflect broader ecosystem water dynamics, particularly the role of soil evaporation during non-vegetated phases, which tends to lower ecosystem-level WUE compared to periods of active transpiration (Tang et al., 2014). However, conservation practices at the site tha include minimum tillage, crop rotation, and post-harvest residue retention are known to suppress soil evaporation and improve water retention during these intervals (Adil et al., 2022; Zhang et al., 2007). In addition, we want to point out that, while full period WUE is an indicator of system-level efficiency, peak growing period WUE offers a clearer indication of plant-mediated efficiency. In contrast, the variability in WUE of the cropland throughout the whole season, suggested by the marginally higher standard error, may be reflective of the seasonal nature of agricultural production. Once crops were harvested, the WUE of the cropland diminished due to the reduced plant activity and the exposed soil surface, which increased evaporation rates.

Across both sites, ecosystem WUE and GPP declined with rising daytime VPD during the defined growing season, and in cropland this negative slope was evident even when the full observation period was considered. In the rangeland, the full-period data suggested a weak WUE increase, but when restricted to peak growth the relationship also turned negative. These results suggest that, in our semi-arid setting, high VPD often coincides with low soil moisture, leading to stronger suppression of GPP than ET (Figure 8) and ultimately reduced WUE (Roby et al., 2020; Yuan et al., 2019). This contrasts with many temperate, water-abundant sites where WUE typically increases with VPD (Beer et al., 2009; Yi et al., 2024). However, our findings are consistent with recent observations from other dryland ecosystems. For example, Roby et al. (2020) showed in semi-arid Arizona that drier air reduced photosynthesis more strongly than respiration and ET during rainfall "pulse events", leading to lower ecosystem WUE. Similarly, Maluleke et al. (2025) reported contrasting responses at two South African shrublands: a grassy site where WUE increased with VPD and temperature but declined after rainfall, and an arid site where WUE remained comparatively stable even under high VPD. They argued, consistent with other studies (Brümmer et al., 2012; Eamus et al., 2013; Grossiord et al., 2020; Liu et al., 2020; Novick et al., 2016; Tarin et al., 2020; Yang et al., 2016), that the balance between GPP and ET suppression under water limitation largely governs WUE outcomes. Our results fit within this broader dryland evidence, highlighting that in strongly waterlimited systems, rising VPD often reduces rather than enhances WUE.

In the cropland, steep decline was most pronounced at VPD levels >1.0 kPa and temperatures exceeding  $20^{\circ}$ C (Figure 8b and Figure S9 in Supporting Information S1), where WUE dropped close to zero. This pattern reflects crop phenology and reduced canopy cover during early and late phases of the growing season, when evaporation dominated water loss and photosynthetic uptake was minimal. In contrast, the rangeland maintained moderate WUE even under elevated atmospheric demand, likely due to the continuous presence of vegetation and potential structural or physiological adaptations for water conservation. These findings suggest that while croplands can achieve high WUE under favorable growth conditions, their efficiency is tightly constrained by the timing of crop development and rainfall distribution, whereas rangelands exhibit more stable, though generally lower, WUE across seasons. Our WUE values (rangeland:  $2.43 \pm 0.46$  g C kg $^{-1}$  H $_2$ O; cropland:  $2.24 \pm 0.15$  g C kg $^{-1}$  H $_2$ O) were higher than those reported by Maluleke et al. (2025) for South African drylands ( $\sim 1.1-1.3$  g C kg $^{-1}$  H $_2$ O)

ODONGO ET AL. 16 of 21

21698961, 2025, 10, Downloaded

over multi-season records reported in their study. However, a similar range of WUE values was observed in a semi-arid Australian Mulga woodland (1.47–2.89 g C kg $^{-1}$  H $_2$ O) (Tarin et al., 2020). During the peak growing season, our cropland (4.42  $\pm$  0.19 g C kg $^{-1}$  H $_2$ O) and rangeland (3.17  $\pm$  0.19 g C kg $^{-1}$  H $_2$ O) values reached the upper end of dryland reports and overlap the temperate range (Beer et al., 2009). We note that our comparison should be interpreted cautiously caused by the relatively short observation period of 185 days compared to multiyear data sets in other studies.

#### 5. Conclusions

This study provides insights into the distinct C and water dynamics of semi-arid savannas by comparing observations from a rangeland with observations from an adjacent dryland agricultural system in Kenya. We observed that both systems exhibited near C neutrality but with notable differences in their seasonal C and water dynamics. Our findings corroborate the crucial role of nutrient limitation for C fluxes, which was reflected in the consistently higher CUE of the cropland suggesting effective C sequestration, driven by efficient C use for growth, enhanced by fertilizer application and minimum tillage practices. Furthermore, our study emphasizes the critical need to include lateral C fluxes in C balance assessments to avoid overestimating the sequestration potential of agricultural systems. Further studies should also consider emissions and C loss through grassland conversion to cropland as well as livestock GHG emission for the rangeland to give a complete picture.

Our results highlight how contrasting land use and management strategies influence water and C exchange in semi-arid East African ecosystem. The higher water and carbon use efficiencies observed in the cropland during the growing season point to the potential of agricultural practices that optimize resource use under favorable conditions. In contrast, the lower but more consistent efficiency in the rangeland likely reflects long-term adaptation to variable and resource-limited environments. These findings emphasize the importance of evaluating ecosystem processes across full seasonal cycles, including phases of bare soil or reduced biological activity, to fully capture the complete dynamics of C and water exchange in drylands. Such insights can help guide land management strategies that aim to balance productivity, ecological resilience, and climate mitigation in water-limited systems.

#### **Inclusion in Global Research Statement**

The authors would like to thank the colleagues of the Kapiti Research Station and Wildlife Conservancy, particularly Nelson Kipchirchir and Nehemiah Kimengich, for their support during field and lab work. Similarly, we are greatly thankful for the support provided by Stuart Barden, owner of Ausquest Farms Ltd, and David Otieno, Ausquest farm manager, for granting us access to the fields, providing us with agronomic information, and for assistance with field security. We are grateful to the two anonymous reviewers for their constructive feedback, which greatly improved the quality of this work.

#### **Data Availability Statement**

All code and data for this study have been archived under a CC-BY 4.0 license on Zenodo (https://doi.org/10.5281/zenodo.16993625). The EastAfricaFluxData v1.0.0 release includes both the fully processed eddy-covariance flux and meteorology time-series (Data set; Odongo (2025a)) and the analysis scripts and software tools (Software; Odongo (2025b)). The final, fully processed KE-Kpt and KE-Aq1 data sets have been submitted under a CC-BY license to the FLUXNET Data System Initiative and will be made publicly available with DOIs upon completion of processing (FLUXNET Data System Initiative, 2025).

#### References

Adil, M., Zhang, S., Wang, J., Shah, A. N., Tanveer, M., & Fiaz, S. (2022). Effects of fallow management practices on soil water, crop yield and water use efficiency in winter wheat monoculture system: A meta-analysis. Frontiers in Plant Science, 13, 825309. Volume 13. https://doi.org/10.3389/fpls.2022.825309

Alkemade, R., Reid, R. S., van den Berg, M., de Leeuw, J., & Jeuken, M. (2013). Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *Proceedings of the National Academy of Sciences*, 110(52), 20900–20905. https://doi.org/10.1073/pnas.1011013108

Allard, V., Soussana, J. F., Falcimagne, R., Berbigier, P., Bonnefond, J. M., Ceschia, E., et al. (2007). The role of grazing management for the net biome productivity and greenhouse gas budget (CO<sub>2</sub>, N<sub>2</sub>O and CH<sub>4</sub>) of semi-natural grassland. *Agriculture, Ecosystems & Environment*, 121(1), 47–58. https://doi.org/10.1016/j.agee.2006.12.004

Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, 3(5), 336–340. https://doi.org/10.1038/ngeo846

Acknowledgments

The Eddy Covariance equipment used in this research at Kapiti was provided by the UK's Natural Environmental Research Council (NERC) via the UK's National Centre for Earth Observation (NCEO). MJW was supported by NERC NC funding (NE/R016518/1) and TPD by a grant from the UK Space Agency for the project "PRISE: A Pest Risk Information Service." VO, SML and LM were supported by the ESSA project (Earth observation and environmental sensing for climate-smart sustainable agropastoralism ecosystem transformation in East Africa) funded by the European Union through the EU-DeSIRA programme. Furthermore, we acknowledge financial support of the CGIAR Research Initiatives Livestock and Climate and Mitigate+: Low-Emission Food Systems, which are supported by contributors to the CGIAR Trust Fund, LM acknowledges funding received from the European Union's Horizon Europe Programme (Grant agreement number 101058525) for the project "Knowledge and climate services from an African observation and Data research Infrastructure (KADI)."

ODONGO ET AL. 17 of 21

21698961



# Journal of Geophysical Research: Biogeosciences

- 10.1029/2024JG008623
- Beer, C., Ciais, P., Reichstein, M., Baldocchi, D., Law, B. E., Papale, D., et al. (2009). Temporal and among-site variability of inherent water use efficiency at the ecosystem level. *Global Biogeochemical Cycles*, 23(2). https://doi.org/10.1029/2008GB003233
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., et al. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. Science, 329(5993), 834–838. https://doi.org/10.1126/science.1184984
- Berardi, A. (Ed.) (2006). Savannas and dry forests: Linking people with nature (1st ed. ed.). Routledge. https://doi.org/10.4324/9781315243788
- Berger, C., Bieri, M., Bradshaw, K., Brümmer, C., Clemen, T., Hickler, T., & Agrarklimaschutz, I. f. (2018). ARS AfricaE—Adaptive resilience of Southern African ecosystems: Final joint project report (public version): Funded under the SPACES—Science partnerships for the adaption/adjustment to complex Earth system processes in Southern Africa under the bmbf's research for sustainable development (FONA) framework programme: Project duration (reporting period): 1.8.2014–31.1.2018. Institut für Agrarklimaschutz.
- Berliner, D., & Kioko, J. (1999). The effect of long-term mowing and ungulate exclusion on grass species composition and soil nutrient status on the Athi-Kapiti plains, central Kenya. *African Journal of Range and Forage Science*, 16(2–3), 62–70. https://doi.org/10.2989/10220119909485720
- Béziat, P., Ceschia, É., & Dedieu, G. (2009). Carbon balance of a three crop succession over two cropland sites in South West France. Agricultural and Forest Meteorology, 149(10), 1628–1645. https://doi.org/10.1016/j.agrformet.2009.05.004
- Biederman, J. A., Scott, R. L., Bell, T. W., Bowling, D. R., Dore, S., Garatuza-Payan, J., et al. (2017). CO<sub>2</sub> exchange and evapotranspiration across dryland ecosystems of Southwestern North America. *Global Change Biology*, 23(10), 4204–4221. https://doi.org/10.1111/gcb.13686
- Blagodatskaya, E., Yuyukina, T., Blagodatsky, S., & Kuzyakov, Y. (2011). Turnover of soil organic matter and of microbial biomass under C3–C4 vegetation change: Consideration of <sup>13</sup>C fractionation and preferential substrate utilization. *Soil Biology and Biochemistry*, 43(1), 159–166. https://doi.org/10.1016/j.soilbio.2010.09.028
- Bombelli, A., Henry, M., Castaldi, S., Adu-Bredu, S., Arneth, A., de Grandcourt, A., et al. (2009). An outlook on the Sub-Saharan Africa carbon balance. *Biogeosciences*, 6(10), 2193–2205. https://doi.org/10.5194/bg-6-2193-2009
- Bossolani, J. W., Leite, M. F. A., Momesso, L., ten Berge, H., Bloem, J., & Kuramae, E. E. (2023). Nitrogen input on organic amendments alters the pattern of soil–microbe-plant co-dependence. Science of the Total Environment, 890, 164347. https://doi.org/10.1016/j.scitotenv.2023.164347
- Brümmer, C., Black, T. A., Jassal, R. S., Grant, N. J., Spittlehouse, D. L., Chen, B., et al. (2012). How climate and vegetation type influence evapotranspiration and water use efficiency in Canadian forest, peatland and grassland ecosystems. *Agricultural and Forest Meteorology*, 153, 14–30. https://doi.org/10.1016/j.agrformet.2011.04.008
- Carbonell, V., Merbold, L., Díaz-Pinés, E., Dowling, T. P. F., & Butterbach-Bahl, K. (2021). Nitrogen cycling in pastoral livestock systems in Sub-Saharan Africa: Knowns and unknowns. Ecological Applications, 31(6), e02368. https://doi.org/10.1002/eap.2368
- Chen, W., Huang, D., Liu, N., Zhang, Y., Badgery, W. B., Wang, X., & Shen, Y. (2015). Improved grazing management may increase soil carbon sequestration in temperate steppe. *Scientific Reports*, 5(1), 10892. https://doi.org/10.1038/srep10892
- Chen, Z., Xu, Y., Castellano, M. J., Fontaine, S., Wang, W., & Ding, W. (2019). Soil respiration components and their temperature sensitivity under chemical fertilizer and compost application: The role of nitrogen supply and compost substrate quality. *Journal of Geophysical Research: Biogeosciences*, 124(3), 556–571. https://doi.org/10.1029/2018JG004771
- Chesworth, W. (2008). Encyclopedia of soil science. In W. Chesworth (Ed.), Encyclopedia of soil science. Springer Netherlands. https://doi.org/10.1007/978-1-4020-3995-9
- Dobson, A., Hopcraft, G., Mduma, S., Ogutu, J. O., Fryxell, J., Anderson, T. M., et al. (2022). Savannas are vital but overlooked carbon sinks. Science, 375(6579), 392. https://doi.org/10.1126/science.abn4482
- Du, E. (2023). Effects of nitrogen deposition on forest ecosystems. In H. Akimoto & H. Tanimoto (Eds.), Handbook of air quality and climate change (pp. 923–945). Springer Nature Singapore. https://doi.org/10.1007/978-981-15-2760-9\_27
- Eamus, D., Cleverly, J., Boulain, N., Grant, N., Faux, R., & Villalobos-Vega, R. (2013). Carbon and water fluxes in an arid-zone Acacia savanna woodland: An analyses of seasonal patterns and responses to rainfall events. *Agricultural and Forest Meteorology*, 182–183, 225–238. https://doi.org/10.1016/j.agrformet.2013.04.020
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., et al. (2001). Gap filling strategies for long term energy flux data sets. Agricultural and Forest Meteorology, 107(1), 71–77. https://doi.org/10.1016/S0168-1923(00)00235-5
- FAO. (2022). Conservation agriculture. In Food and agriculture organisation of the United Nations. Retrieved from https://www.fao.org/conservation-agriculture/en/
- Feng, Y., Wu, J., Li, M., Chen, B., Tilahun, M., & Zhang, X. (2024). Carbon use efficiency of alpine grasslands affected by grazing exclusion and local environmental context in Tibet, China. *Global Ecology and Conservation*, 56, e03275. https://doi.org/10.1016/j.gecco.2024.e03275
- Fernández-Martínez, M., Vicca, S., Janssens, I. A., Luyssaert, S., Campioli, M., Sardans, J., et al. (2014a). Spatial variability and controls over biomass stocks, carbon fluxes, and resource-use efficiencies across forest ecosystems. *Trees*, 28(2), 597–611. https://doi.org/10.1007/s00468-013-0975-9
- Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., et al. (2014b). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change*, 4(6), 471–476. https://doi.org/10.1038/nclimate2177
- Flexas, J., & Carriquí, M. (2020). Photosynthesis and photosynthetic efficiencies along the terrestrial plant's phylogeny: Lessons for improving crop photosynthesis. *The Plant Journal*, 101(4), 964–978. https://doi.org/10.1111/tpj.14651
- FLUXNET Data System Initiative. (2025). KE-Kpt (Kapiti) and KE-Aq1 (Ausquest) eddy-covariance flux data [Dataset]. Submitted under CC-BY; DOI pending, Puplisher, Europe-FluxData portal. http://archive.sciendo.com/INTAG/intag.2017.32.issue-4/intag-2017-0043/intag-2017-0043.pdf
- Frey, S. D., Lee, J., Melillo, J. M., & Six, J. (2013). The temperature response of soil microbial efficiency and its feedback to climate. *Nature Climate Change*, 3(4), 395–398. https://doi.org/10.1038/nclimate1796
- Gao, J., & Carmel, Y. (2020). A global meta-analysis of grazing effects on plant richness. Agriculture, Ecosystems & Environment, 302, 107072. https://doi.org/10.1016/j.agee.2020.107072
- Ghimire, R., Aryal, D. R., Hanan, N. P., Boufous, S., Burney, O., Idowu, O. J., et al. (2024). Carbon sequestration through sustainable land management practices in arid and semiarid regions: Insights from New Mexico. Agrosystems, Geosciences & Environment, 7(4), e70019. https://doi.org/10.1002/agg2.70019
- Gourlez de la Motte, L., Jérôme, E., Mamadou, O., Beckers, Y., Bodson, B., Heinesch, B., & Aubinet, M. (2016). Carbon balance of an intensively grazed permanent grassland in southern Belgium. *Agricultural and Forest Meteorology*, 228–229, 370–383. https://doi.org/10.1016/j.agrformet.2016.06.009
- Graversen, A. E. L., Banta, G. T., Masque, P., & Krause-Jensen, D. (2022). Carbon sequestration is not inhibited by livestock grazing in Danish salt marshes. *Limnology & Oceanography*, 67(S2), S19–S35. https://doi.org/10.1002/lno.12011
- Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., et al. (2020). Plant responses to rising vapor pressure deficit. New Phytologist, 226(6), 1550–1566. https://doi.org/10.1111/nph.16485

ODONGO ET AL. 18 of 21

21698961,

- Guillen-Cruz, G., Torres-Arreola, R., Sanchez-Mejia, Z., & Flores-Renteria, D. (2022). The effect of conventional and sustainable agricultural management practices on carbon and water fluxes in a Mexican semi-arid region. *PeerJ*, 10, e14542. https://doi.org/10.7717/peerj.14542
- Hagh-Doust, N., Mikryukov, V., Anslan, S., Bahram, M., Puusepp, R., Dulya, O., & Tedersoo, L. (2023). Effects of nitrogen deposition on carbon and nutrient cycling along a natural soil acidity gradient as revealed by metagenomics. New Phytologist, 238(6), 2607–2620. https://doi.org/10.1111/nph.18897
- Han, X., Fang, F., Bai, C., Du, K., Zhu, Y., & Liu, W. (2024). Dynamics of carbon and water fluxes over cropland and agroforest ecosystems on the Southern Chinese Loess Plateau. *Forests*, 15(5), 774. https://doi.org/10.3390/f15050774
- Hobbs, P. R., Sayre, K., & Gupta, R. (2008). The role of conservation agriculture in sustainable agriculture. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1491), 543–555. https://doi.org/10.1098/rstb.2007.2169
- Horton, R., Bristow, K. L., Kluitenberg, G. J., & Sauer, T. J. (1996). Crop residue effects on surface radiation and energy balance Review. Theoretical and Applied Climatology, 54(1), 27–37. https://doi.org/10.1007/BF00863556
- Hu, Z., Yu, G., Fu, Y., Sun, X., Li, Y., Shi, P., et al. (2008). Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China. Global Change Biology, 14(7), 1609–1619. https://doi.org/10.1111/j.1365-2486.2008.01582.x
- ILRI. (2019). Kapiti research station: A livestock, environmental and agricultural research station in southeastern Kenya. https://hdl.handle.net/10568/107222
- Janssens, I. A., Dieleman, W., Luyssaert, S., Subke, J. A., Reichstein, M., Ceulemans, R., et al. (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, 3(5), 315–322. https://doi.org/10.1038/ngeo844
- Jérôme, E., Beckers, Y., Bodson, B., Heinesch, B., Moureaux, C., & Aubinet, M. (2014). Impact of grazing on carbon dioxide exchanges in an
- intensively managed Belgian grassland. Agriculture, Ecosystems & Environment, 194, 7–16. https://doi.org/10.1016/j.agee.2014.04.021 Keller, A. B., Walter, C. A., Blumenthal, D. M., Borer, E. T., Collins, S. L., DeLancey, L. C., et al. (2023). Stronger fertilization effects on aboveground versus belowground plant properties across nine U.S. grasslands. Ecology. 104(2), e3891. https://doi.org/10.1002/ecv.3891
- Kljun, N., Calanca, P., Rotach, M. W., & Schmid, H. P. (2015). A simple two-dimensional parameterisation for Flux Footprint Prediction (FFP). Geoscientific Model Development, 8(11), 3695–3713. https://doi.org/10.5194/gmd-8-3695-2015
- Kutsch, W. L., Hanan, N., Scholes, B., McHugh, I., Kubheka, W., Eckhardt, H., & Williams, C. (2008). Response of carbon fluxes to water
- relations in a savanna ecosystem in South Africa. *Biogeosciences*, 5(6), 1797–1808. https://doi.org/10.5194/bg-5-1797-2008 Kuyah, S., Muoni, T., Bayala, J., Chopin, P., Dahlin, A. S., Hughes, K., et al. (2023). Grain legumes and dryland cereals contribute to carbon
- Kuyah, S., Muoni, T., Bayala, J., Chopin, P., Dahlin, A. S., Hughes, K., et al. (2023). Grain legumes and dryland cereals contribute to carbon sequestration in the drylands of Africa and South Asia. Agriculture, Ecosystems & Environment, 355, 108583. https://doi.org/10.1016/j.agee. 2023.108583
- Lajtha, K., & Silva, L. (2022). Grazing cattle, well-managed or not, is unlikely to increase soil carbon sequestration. Proceedings of the National Academy of Sciences, 119(30), e2203408119. https://doi.org/10.1073/pnas.2203408119
- Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneth, A., Barr, A., et al. (2010). Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation. Global Change Biology, 16(1), 187–208. https://doi.org/10.1111/j.1365-2486.2009.02041.x
- Leitner, S. M., Carbonell, V., Mhindu, R. L., Zhu, Y., Mutuo, P., Butterbach-Bahl, K., & Merbold, L. (2024). Greenhouse gas emissions from cattle enclosures in semi-arid Sub-Saharan Africa: The case of a rangeland in South-central Kenya. *Agriculture, Ecosystems & Environment*, 367, 108980. https://doi.org/10.1016/j.agee.2024.108980
- Leu, S., Ben-Eli, M., & Mor-Mussery, A. (2021). Effects of grazing control on ecosystem recovery, biological productivity gains, and soil carbon sequestration in long-term degraded loess farmlands in the Northern Negev, Israel. *Land Degradation & Development*, 32(8), 2580–2594. https://doi.org/10.1002/ldr.3923
- Li, S.-X., Wang, Z.-H., Malhi, S. S., Li, S.-Q., Gao, Y.-J., & Tian, X.-H. (2009). Chapter 7 nutrient and water management effects on crop production, and nutrient and water use efficiency in dryland areas of China In. Advances in agronomy, Academic Press. https://doi.org/10.1016/S0065-2113(09)01007-4, (pp. 223–265).
- Liang, M., Feng, X., & Gornish, E. S. (2021). Rainfall pulses mediate long-term plant community compositional dynamics in a semi-arid rangeland. *Journal of Applied Ecology*, 58(4), 708–717. https://doi.org/10.1111/1365-2664.13780
- Liu, C., Sun, G., McNulty, S. G., Noormets, A., & Fang, Y. (2017). Environmental controls on seasonal ecosystem evapotranspiration/potential evapotranspiration ratio as determined by the global eddy flux measurements. *Hydrology and Earth System Sciences*, 21(1), 311–322. https://doi.org/10.5194/hess-21-311-2017
- Liu, X., Feng, X., & Fu, B. (2020). Changes in global terrestrial ecosystem water use efficiency are closely related to soil moisture. Science of the Total Environment, 698, 134165. https://doi.org/10.1016/j.scitotenv.2019.134165
- Liu, Z., Chen, Z., Yu, G., Yang, M., Zhang, W., Zhang, T., & Han, L. (2022). Ecosystem carbon use efficiency in ecologically vulnerable areas in China: Variation and influencing factors. Frontiers in Plant Science, Volume 13, 13, 1062055. https://doi.org/10.3389/fpls.2022.1062055
- Liu, Z., Chen, Z., Yu, G., Zhang, W., Zhang, T., & Han, L. (2023). The role of climate, vegetation, and soil factors on carbon fluxes in Chinese drylands. Frontiers in Plant Science, 14, 1060066. https://doi.org/10.3389/fpls.2023.1060066
- López-Ballesteros, A., Beck, J., Bombelli, A., Grieco, E., Lorencová, E. K., Merbold, L., et al. (2018). Towards a feasible and representative Pan-African research infrastructure network for GHG observations. *Environmental Research Letters*, 13(8), 085003. https://doi.org/10.1088/1748-9326/aad66c
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., et al. (2007). CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a global database. Global Change Biology, 13(12), 2509–2537. https://doi.org/10.1111/j.1365-2486.2007.01439.x
- Maluleke, A., Feig, G., Brümmer, C., Jaars, K., Hamilton, T., & Midgley, G. (2025). Paired eddy covariance site reveals consistent net C sinks over three growing seasons in an African arid and grassy Shrubland. *Agricultural and Forest Meteorology*, 372, 110705. https://doi.org/10.1016/j.agrformet.2025.110705
- Manzoni, S., Čapek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., et al. (2018). Reviews and syntheses: Carbon use efficiency from organisms to ecosystems Definitions, theories, and empirical evidence. *Biogeosciences*, 15(19), 5929–5949. https://doi.org/10.5194/bg-15-5929-2018
- Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytologist, 196(1), 79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x
- Massman, W. J. (2000). A simple method for estimating frequency response corrections for eddy covariance systems. Agricultural and Forest Meteorology, 104(3), 185–198. https://doi.org/10.1016/S0168-1923(00)00164-7
- McMillen, R. T. (1988). An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorology*, 43(3), 231–245. https://doi.org/10.1007/BF00128405
- McNaughton, S. J. (1985). Ecology of a grazing ecosystem: The Serengeti. *Ecological Monographs*, 55(3), 260–294. https://doi.org/10.2307/1942578

ODONGO ET AL. 19 of 21

21698961

- Medina-Roldán, E., Paz-Ferreiro, J., & Bardgett, R. D. (2012). Grazing exclusion affects soil and plant communities, but has no impact on soil carbon storage in an upland grassland. *Agriculture, Ecosystems & Environment, 149*, 118–123. https://doi.org/10.1016/j.agee.2011.12.012
- Merbold, L., Ardö, J., Arneth, A., Scholes, R. J., Nouvellon, Y., de Grandcourt, A., et al. (2009). Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosciences*, 6(6), 1027–1041. https://doi.org/10.5194/bg-6-1027-2009
- Merbold, L., Scholes, R., Acosta, M., Beck, J., Bombelli, A., Fiedler, B., et al. (2021). Opportunities for an African greenhouse gas observation system. *Regional Environmental Change*, 21(4), 104. https://doi.org/10.1007/s10113-021-01823-w
- Mgalula, M. E., Wasonga, O. V., Hülsebusch, C., Richter, U., & Hensel, O. (2021). Greenhouse gas emissions and carbon sink potential in Eastern Africa rangeland ecosystems: A review. *Pastoralism*, 11(1), 19. https://doi.org/10.1186/s13570-021-00201-9
- Moncrieff, J., Clement, R., Finnigan, J., & Meyers, T. (2004). Averaging, detrending, and filtering of eddy covariance time series. In X. Lee, W. Massman, & B. Law (Eds.), *Handbook of micrometeorology: A guide for surface flux measurement and analysis* (pp. 7–31). Springer Netherlands. https://doi.org/10.1007/1-4020-2265-4\_2
- Moncrieff, J. B., Massheder, J. M., de Bruin, H., Elbers, J., Friborg, T., Heusinkveld, B., et al. (1997). A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, 188–189, 589–611. https://doi.org/10.1016/S0022-1694 (96)03194-0
- Moore, C. J. (1986). Frequency response corrections for eddy correlation systems. Boundary-Layer Meteorology, 37(1), 17–35. https://doi.org/10.1007/BF00122754
- Moyano, F. E., Manzoni, S., & Chenu, C. (2013). Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. Soil Biology and Biochemistry, 59, 72–85. https://doi.org/10.1016/j.soilbio.2013.01.002
- Muthoka, J. M., Antonarakis, A. S., Vrieling, A., Fava, F., Salakpi, E. E., & Rowhani, P. (2022). Assessing drivers of intra-seasonal grassland dynamics in a Kenyan Savannah using digital repeat photography. *Ecological Indicators*, 142, 109223. https://doi.org/10.1016/j.ecolind.2022. 109223
- Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., et al. (2016). The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change*, 6(11), 1023–1027. https://doi.org/10.1038/nclimate3114
- Novick, K. A., Walker, J., Chan, W. S., Schmidt, A., Sobek, C., & Vose, J. M. (2013). Eddy covariance measurements with a new fast-response, enclosed-path analyzer: Spectral characteristics and cross-system comparisons. *Agricultural and Forest Meteorology*, 181, 17–32. https://doi.org/10.1016/j.agrformet.2013.06.020
- O'Brien, P. L., Acharya, U., Alghamdi, R., Niaghi, A. R., Sanyal, D., Wirtz, J., et al. (2018). Hydromulch application to bare soil: Soil temperature dynamics and evaporative fluxes. *Agricultural & Environmental Letters*, 3(1), 180014. https://doi.org/10.2134/ael2018.03.0014
- Odongo, V. O. (2025a). EastAfricaFluxData v1.0.0 Initial public release of EastAfricaFluxData [Dataset]. Zenodo. https://doi.org/10.5281/zenodo.16993625
- Odongo, V. O. (2025b). EastAfricaFluxData v1.0.0 Initial public release of EastAfricaFluxData [Software]. Zenodo. https://doi.org/10.5281/zenodo.16993625
- Paillassa, J., Wright, I. J., Prentice, I. C., Pepin, S., Smith, N. G., Ethier, G., et al. (2020). When and where soil is important to modify the carbon and water economy of leaves. New Phytologist, 228(1), 121–135. https://doi.org/10.1111/nph.16702
- Patil, S. L., Loganandhan, N., & Ramesha, M. N. (2016). Evaluation of chickpea varieties under compartmental bunding in rainfed situation. Legume Research, 39(6), 890–895. https://doi.org/10.18805/lr.v0iOF.9379
- Piñeiro, G., Paruelo, J. M., Oesterheld, M., & Jobbágy, E. G. (2010). Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology & Management*, 63(1), 109–119. https://doi.org/10.2111/08-255.1
- Probert, M. E. (1992). A search for strategies for sustainable dryland cropping in semi-arid eastern Kenya: Proceedings of a symposium held in Nairobi, Kenya, 10–11 December 1990. Australian Centre for International Agricultural Research. [Canberra].
- Rahman, M. D. M., Aravindakshan, S., Hoque, M. A., Rahman, M. A., Gulandaz, M. A., Rahman, J., & Islam, M. T. (2021). Conservation Tillage (CT) for climate-smart sustainable intensification: Assessing the impact of CT on soil organic carbon accumulation, greenhouse gas emission and water footprint of wheat cultivation in Bangladesh. *Environmental and Sustainability Indicators*, 10, 100106. https://doi.org/10.1016/j. indic.2021.100106
- Räsänen, M., Aurela, M., Vakkari, V., Beukes, J. P., Tuovinen, J. P., Van Zyl, P. G., et al. (2017). Carbon balance of a grazed savanna grassland ecosystem in South Africa. *Biogeosciences*, 14(5), 1039–1054. https://doi.org/10.5194/bg-14-1039-2017
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., et al. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, 11(9), 1424–1439. https://doi.org/10.1111/j. 1365-2486.2005.001002.x
- Reichstein, M., Kätterer, T., Andrén, O., Ciais, P., Schulze, E. D., Cramer, W., et al. (2005). Temperature sensitivity of decomposition in relation to soil organic matter pools: Critique and outlook. *Biogeosciences*, 2(4), 317–321. https://doi.org/10.5194/bg-2-317-2005
- Ritchie, M. E., & Penner, J. F. (2020). Episodic herbivory, plant density dependence, and stimulation of aboveground plant production. *Ecology and Evolution*, 10(12), 5302–5314. https://doi.org/10.1002/ece3.6274
- Roby, M. C., Scott, R. L., & Moore, D. J. P. (2020). High vapor pressure deficit decreases the productivity and water use efficiency of rain-induced pulses in Semiarid ecosystems. *Journal of Geophysical Research: Biogeosciences*, 125(10), e2020JG005665. https://doi.org/10.1029/2020JG005665
- Rybchak, O., du Toit, J., Delorme, J.-P., Jüdt, J.-K., Bieri, M., Midgley, G., et al. (2024). Livestock grazing and biodiversity: Effects on CO<sub>2</sub> exchange in semi-arid Karoo ecosystems, South Africa. *Science of the Total Environment*, 910, 168517. https://doi.org/10.1016/j.scitotenv. 2023.168517
- Salazar-Villegas, A., Blagodatskaya, E., & Dukes, J. S. (2016). Changes in the size of the active microbial pool explain short-term soil respiratory responses to temperature and moisture. Frontiers in Microbiology, 7, 524. https://doi.org/10.3389/fmicb.2016.00524
- Sardans, J., & Peñuelas, J. (2012). The role of plants in the effects of global change on nutrient availability and stoichiometry in the plant-soil system. *Plant physiology*, 160(4), 1741–1761. https://doi.org/10.1104/pp.112.208785
- Sayer, E. J., Powers, J. S., & Tanner, E. V. J. (2007). Increased litterfall in tropical forests boosts the transfer of soil CO<sub>2</sub> to the atmosphere. *PLoS One*, 2(12), e1299. https://doi.org/10.1371/journal.pone.0001299
- Scholes, R. J. (2005). SAFARI 2000 woody vegetation characteristics of Kalahari and Skukuza sites. ORNL Distributed Active Archive Center. https://doi.org/10.3334/ORNLDAAC/777
- Shanker, A. K., Maheswari, M., Yadav, S. K., Desai, S., Bhanu, D., Attal, N. B., & Venkateswarlu, B. (2014). Drought stress responses in crops. Functional & Integrative Genomics, 14(1), 11–22. https://doi.org/10.1007/s10142-013-0356-x
- Shugart, H. H., Macko, S. A., Lesolle, P., Szuba, T. A., Mukelabai, M. M., Dowty, P., & Swap, R. J. (2004). The SAFARI 2000 Kalahari transect wet season Campaign of year 2000. Global Change Biology, 10(3), 273–280. https://doi.org/10.1111/j.1365-2486.2004.00732.x

ODONGO ET AL. 20 of 21

21698961

10.1029/2024JG008623



# Journal of Geophysical Research: Biogeosciences

- Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L., & Richter, A. (2013). Carbon use efficiency of microbial communities: Stoichiometry, methodology and modelling. *Ecology Letters*, 16(7), 930–939. https://doi.org/10.1111/ele.12113
- Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E., & Pacala, S. W. (2014). Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. Nature Climate Change, 4(12), 1099–1102. https://doi.org/10.1038/nclimate2436
- Tadey, M., & Souto, C. P. (2016). Unexpectedly, intense livestock grazing in arid rangelands strengthens the seedling vigor of consumed plants. Agronomy for Sustainable Development, 36(4), 63. https://doi.org/10.1007/s13593-016-0400-z
- Tang, S., Guo, J., Li, S., Li, J., Xie, S., Zhai, X., et al. (2019). Synthesis of soil carbon losses in response to conversion of grassland to agriculture land. Soil and Tillage Research, 185, 29–35. https://doi.org/10.1016/j.still.2018.08.011
- Tang, X., Li, H., Desai, A. R., Nagy, Z., Luo, J., Kolb, T. E., et al. (2014). How is water-use efficiency of terrestrial ecosystems distributed and changing on Earth? *Scientific Reports*, 4(1), 7483. https://doi.org/10.1038/srep07483
- Tarin, T., Nolan, R. H., Medlyn, B. E., Cleverly, J., & Eamus, D. (2020). Water-use efficiency in a semi-arid woodland with high rainfall variability. *Global Change Biology*, 26(2), 496–508. https://doi.org/10.1111/gcb.14866
- Tello-García, E., Huber, L., Leitinger, G., Peters, A., Newesely, C., Ringler, M.-E., & Tasser, E. (2020). Drought- and heat-induced shifts in vegetation composition impact biomass production and water use of alpine grasslands. *Environmental and Experimental Botany*, 169, 103921. https://doi.org/10.1016/j.envexpbot.2019.103921
- UNCCD, UNEP, & UNDP. (2009). Climate change in the African drylands: Options and opportunities for adaptation and mitigation, United Nations Development Programme (UNDP), (p. 54).
- Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., et al. (2000). Respiration as the main determinant of carbon balance in European forests. *Nature*, 404(6780), 861–865. https://doi.org/10.1038/35009084
- Vickers, D., & Mahrt, L. (1997). Quality control and flux sampling problems for tower and aircraft data. *Journal of Atmospheric and Oceanic Technology*, 14(3), 512–526. https://doi.org/10.1175/1520-0426(1997)014<0512;QCAFSP>2.0.CO;2
- Wang, J. J., Lai, L. M., Zhao, X. C., Jiang, L. H., Wang, Y. J., Zhou, J. H., et al. (2015). Litter priming and trenching greatly affect soil respiration in a mature subtropical evergreen broadleaf forest in Southwestern China. Contemporary Problems of Ecology, 8(4), 486–494. https://doi.org/ 10.1134/S1995425515040150
- Wang, Y.-P., Zhang, Q., Pitman, A. J., & Dai, Y. (2015). Nitrogen and phosphorous limitation reduces the effects of land use change on land carbon uptake or emission. *Environmental Research Letters*, 10(1), 014001. https://doi.org/10.1088/1748-9326/10/1/014001
- Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density effects due to heat and water vapour transfer. Ouarterly Journal of the Royal Meteorological Society, 106(447), 85–100. https://doi.org/10.1002/qj.49710644707
- Wieder, W. R., Bonan, G. B., & Allison, S. D. (2013). Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change*, 3(10), 909–912. https://doi.org/10.1038/nclimate1951
- Wilsey, B. J., Parent, G., Roulet, N. T., Moore, T. R., & Potvin, C. (2002). Tropical pasture carbon cycling: Relationships between C source/sink
- strength, above-ground biomass and grazing. *Ecology Letters*, 5(3), 367–376. https://doi.org/10.1046/j.1461-0248.2002.00322.x

  Wolz, K., Leitner, S., Merbold, L., Wolf, B., & Mauder, M. (2022). Enteric methane emission estimates for Kenyan cattle in a nighttime enclosure using a backward Lagrangian stochastic dispersion technique. *Theoretical and Applied Climatology*, 147(3), 1091–1103. https://doi.org/10.
- worz, K., Letiner, S., Meroold, L., Worr, B., & Mauder, M. (2022). Enteric methane emission estimates for Kenyan cattle in a nighttime enclosure using a backward Lagrangian stochastic dispersion technique. *Theoretical and Applied Climatology*, 147(3), 1091–1103. https://doi.org/10.1007/s00704-021-03868-7
- Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L., et al. (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences*, 15(16), 5015–5030. https://doi.org/10.5194/bg-15-5015-2018
- Xia, J., Niu, S., Ciais, P., Janssens, I. A., Chen, J., Ammann, C., et al. (2015). Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proceedings of the National Academy of Sciences*, 112(9), 2788–2793. https://doi.org/10.1073/pnas.1413090112
- Xiao, J., Sun, G., Chen, J., Chen, H., Chen, S., Dong, G., et al. (2013). Carbon fluxes, evapotranspiration, and water use efficiency of terrestrial ecosystems in China. Agricultural and Forest Meteorology, 182–183, 76–90. https://doi.org/10.1016/j.agrformet.2013.08.007
- Yan, D., Li, J., Pei, J., Cui, J., Nie, M., & Fang, C. (2017). The temperature sensitivity of soil organic carbon decomposition is greater in subsoil than in topsoil during laboratory incubation. *Scientific Reports*, 7(1), 5181. https://doi.org/10.1038/s41598-017-05293-1
- Yang, Y., Guan, H., Batelaan, O., McVicar, T. R., Long, D., Piao, S., et al. (2016). Contrasting responses of water use efficiency to drought across global terrestrial ecosystems. *Scientific Reports*, 6(1), 23284. https://doi.org/10.1038/srep23284
- Yi, K., Novick, K. A., Zhang, Q., Wang, L., Hwang, T., Yang, X., et al. (2024). Responses of marginal and intrinsic water-use efficiency to changing aridity using FLUXNET observations. *Journal of Geophysical Research: Biogeosciences*, 129(6), e2023JG007875. https://doi.org/ 10.1029/2023JG007875
- Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., et al. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. Science Advances, 5(8), eaax1396. https://doi.org/10.1126/sciadv.aax1396
- Zhang, L., Xiao, J., Zheng, Y., Li, S., & Zhou, Y. (2020). Increased carbon uptake and water use efficiency in global semi-arid ecosystems. Environmental Research Letters, 15(3), 034022. https://doi.org/10.1088/1748-9326/ab68ec
- Zhang, S., Simelton, E., Lövdahl, L., Grip, H., & Chen, D. (2007). Simulated long-term effects of different soil management regimes on the water balance in the loess Plateau, China. Field Crops Research, 100(2), 311–319. https://doi.org/10.1016/j.fcr.2006.08.006
- Zhou, Y., Ma, J., Ma, J., Lu, Q., Wang, G., Shen, Y., & Ma, H. (2024). Extending grazing time during the warm season can reduce P limitation and increase the N cycling rate in arid desert steppes. *Science of the Total Environment*, 941, 173664. https://doi.org/10.1016/j.scitotenv.2024. 173664
- Zhu, Y., Butterbach-Bahl, K., Merbold, L., Oduor, C. O., Gakige, J. K., Mwangi, P., & Leitner, S. M. (2024). Greenhouse gas emissions from sheep excreta deposited onto tropical pastures in Kenya. Agriculture, Ecosystems & Environment, 359, 108724. https://doi.org/10.1016/j.agee. 2023.108724
- Zhu, Y., Merbold, L., Leitner, S., Xia, L., Pelster, D. E., Diaz-Pines, E., et al. (2020). Influence of soil properties on N<sub>2</sub>O and CO<sub>2</sub> emissions from excreta deposited on tropical pastures in Kenya. Soil Biology and Biochemistry, 140, 107636. https://doi.org/10.1016/j.soilbio.2019.107636

#### **References From the Supporting Information**

- Foken, T., Göockede, M., Mauder, M., Mahrt, L., Amiro, B., & Munger, W. (2004). Post-field data quality control. In X. Lee, W. Massman, & B. Law (Eds.), *Handbook of micrometeorology: A guide for surface flux measurement and analysis* (pp. 181–208). Springer Netherlands. https://doi.org/10.1007/1-4020-2265-4\_9
- Mauder, M., & Foken, T. (2004). Documentation and instruction manual of the eddy-covariance software package TK3.
- Wang, B., Zha, T. S., Jia, X., Wu, B., Zhang, Y. Q., & Qin, S. G. (2014). Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences*, 11(2), 259–268. https://doi.org/10.5194/bg-11-259-2014

ODONGO ET AL. 21 of 21