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Tagesson, Torbern; Fensholt, Rasmus; Guiro, Idrissa; Rasmussen, Mads Olander; Huber, Silvia; Mbow, Cheikh; García, Monica; Horion, Stephanie; Sandholt, Inge; Holm-Rasmussen, Bo; Goettsche, Frank M.; Ridler, Marc-Etienne; Boke-Olén, Niklas; Olsen, Jorgen Lundegard; Ehammer, Andrea; Madsen, Mathias; Olesen, Folke S.; Ardö, Jonas

Published in:
Global Change Biology

DOI:
10.1111/gcb.12734

2015

Document Version:
Publisher’s PDF, also known as Version of record

Link to publication

Citation for published version (APA):

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Ecosystem properties of semiarid savanna grassland in West Africa and its relationship with environmental variability

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Abstract

The Dahra field site in Senegal, West Africa, was established in 2002 to monitor ecosystem properties of semiarid savanna grassland and their responses to climatic and environmental change. This article describes the environment and the ecosystem properties of the site using a unique set of in situ data. The studied variables include hydroclimatic variables, species composition, albedo, normalized difference vegetation index (NDVI), hyperspectral characteristics (350–1800 nm), surface reflectance anisotropy, brightness temperature, fraction of absorbed photosynthetic active radiation (FAPAR), biomass, vegetation water content, and land-atmosphere exchanges of carbon (NEE) and energy. The Dahra field site experiences a typical Sahelian climate and is covered by coexisting trees (~3% canopy cover) and grass species, characteristicizing large parts of the Sahel. This makes the site suitable for investigating relationships between ecosystem properties and hydroclimatic variables for semiarid savanna ecosystems of the region. There were strong interannual, seasonal and diurnal dynamics in NEE, with high values of ~7.5 g C m⁻² day⁻¹ during the peak of the growing season. We found neither browning nor greening NDVI trends from 2002 to 2012. Interannual variation in species composition was strongly related to rainfall distribution. NDVI and FAPAR were strongly related to species composition, especially for years dominated by the species Zornia glochidiata. This influence was not observed in interannual variation in biomass and vegetation productivity, thus challenging dryland productivity models based on remote sensing. Surface reflectance anisotropy (350–1800 nm) at the peak of the growing season varied strongly depending on wavelength and viewing angle thereby having implications for the design of remotely sensed spectral vegetation indices covering different wavelength regions. The presented time series of in situ data have great potential for dryland dynamics studies, global climate change related research and evaluation and parameterization of remote sensing products and dynamic vegetation models.

Keywords: dryland, eddy covariance, evapotranspiration, latent heat flux, net ecosystem exchange, Sahel, savanna, sensible heat flux

Introduction

Savannas cover approximately one-sixth of the world’s land surface and 15.1 million km² or 50% of the African continent (Grace et al., 2006). The African Sahel is a region dominated by semiarid grass savannas with shrubs and low tree coverage. Located at the Saharan desert border (Fig. 1), the productivity of these ecosystems is heavily influenced by water availability (Hill & Hanan, 2011). Rainfall declined by ~25% during the 20th century in the region, which is one of the largest
negative trends in the global record (Hulme et al., 2001; Dai et al., 2004; Trenberth et al., 2007). The mean temperature in the region increased by up to 1.3 °C during the same period (Hulme et al., 2001; Trenberth et al., 2007). As a result, the region has experienced several severe droughts since the end of the 1960s (Lebel et al., 2009). However, since the mid-1980s rainfall has steadily increased (Lebel et al., 2009), and there is an ongoing debate whether the region experiences a greening or a browning trend (Dardel et al., 2014). Studies have reported a decline in vegetation productivity (e.g. Adeel et al., 2005), whereas studies based on remotely sensed advanced very high resolution radiometer (AVHRR) data show increased vegetation productivity in the Sahel (e.g. Anyamba & Tucker, 2005; Fensholt et al., 2013).

The population in the Sahel is strongly dependent on rain-fed agriculture and seasonal pasture lands for extensive grazing. The Sahelian dryland ecosystems and its population are thereby particularly vulnerable to land degradation and to the impact of climate variability (Abdi et al., 2014). A range of possible climate feedback mechanisms could arise from these ecosystems, such as changes in albedo, evapotranspiration, and land-atmosphere exchange of carbon dioxide. Future climate scenarios project an increase in temperature and a decrease in rainfall for the western Sahel region (Roehrig et al., 2013). The long-term responses of savanna ecosystems and their resilience to climatic and environmental changes are therefore important to understand, to better quantify and predict the effects of potential climate change.

There are limited in situ data available from semiarid savanna grasslands in general and from the African continent in particular. In situ data sets from the Sahel covering hydroclimatic variables and ecosystem properties are very rare, and to our knowledge the only sites covering a large array of ecosystem properties are the AMMA-CATCH observatories (Cappelaere et al., 2009; Mougin et al., 2009) and Demokeya (Ardô et al., 2008; Ardô, 2013). In situ data are necessary to assess dynamic responses of ecosystems to changing environmental conditions on fine spatial and temporal scales. In addition, in situ measurements are important for the parameterization and evaluation of remote sensing products and dynamic vegetation models. Hence, there is an increasing demand for in situ data regarding environmental variables and ecosystem properties resulting in research data exchange programs such as SpecNet and FLUXNET (Baldocchi et al., 2001; Gamon et al., 2010).

Remote sensing methods have proven to be a useful tool for studies of ecosystem properties of the Sahel region. There are, however, several sources of uncertainty associated with remote sensing products, such as sensor noise and degradation, calibration errors, atmospheric perturbations (water vapor, aerosols, clouds, scattering, etc.), retrieval algorithm errors, adjacency effects, scaling issues and anisotropic effects. Anisotropic effects are a function of viewing/illumination geometry, and can cause substantial bias in remote sensing products if not accounted for (e.g. Eklundh et al., 2007; Fensholt et al., 2010). However, anisotropic effects can also be seen as an additional information source and it has been shown that the directional properties of vegetated land surface reflectance contain information about vegetation structure (Kimes, 1983; Chen et al., 2003).

To gain insight into properties of semiarid savanna ecosystems and their response to climatic and environmental change, the Dahra field site in Senegal, West Africa, was established as an in situ research site in 2002. The main aim of this article is to describe the hydroclimatic conditions (meteorological and hydrological variables) and the ecosystem properties (species composition, albedo, normalized difference vegetation
indices (NDVI), spectral characteristics, surface reflectance anisotropy, fraction of absorbed photosynthetic active radiation (FAPAR), biomass, vegetation water content, and land-atmosphere exchange of energy and carbon) of the site using a unique set of in situ data. A further objective is to identify how the dynamics of the ecosystem properties are related to the hydroclimatic variables and to each other.

Materials and methods

Site description

The Dahra field site is located in the semiarid central part of Senegal (15.40°N, 15.43°W) within the Sahelian ecoclimatic zone (Fig. 1). The climate at the site is typical of hot semiarid regions, with daily average air temperature at 2 m height ranging between 15.9 and 39.9 °C (Fig. 2a). Annual rainfall ranged between 169 mm for 2002 and 650 mm for 2010 (Fig. 2c; Table 1), indicating that Dahra experiences a typical sahelian climate, which is defined by the 100 mm and 700 mm isohyets (Prince et al., 1995). More than 93% of the rain falls during the rainy season from July to October, with August being the wettest month. The growing season is relatively short, coinciding with the rainy reason.

The site is a typical low tree and shrub savanna environment with the coexistence of trees and a continuous but strongly seasonal grass cover. In 2008, the tree canopy cover was ~3% of the ground surface with Balanites aegyptiaca, Acacia tortilis, and Acacia senegal as the most dominant species (Table S3) (Rasmussen et al., 2011b). All three tree species exist throughout the Sahel, and Balanites aegyptiaca, and Acacia tortilis throughout most African arid and semiarid regions (von

![Fig. 2](image-url)
Maydell, 1986). The average tree height was 5.2 m and the breast height diameter was 0.15 m (Table S3). The five most common herbaceous species were Zornia latifolia, Aristida adscensionis, Cenchrus biflorus, Dactylocenium aegyptium, and Eragrostis tremula, all of which are found across the western Sahel (a complete description of species composition is given in Table S4). The land is used as grazed rangeland. Effective LAI of the vegetation was measured in 2002 and ranged between 0.05 and 0.79, peaking at the end of August (Figure S2) (Fensholt et al., 2004). The soil is sandy luvic arenosol with negligible amounts of organic material and low clay content (Clay = 0.35%, silt = 4.61%, and sand = 95.04%). To limit the uncertainty in the evaluation and parameterization of remote sensing products and models, criteria for the site selection were that the field site had to be flat with homogeneous vegetation cover within a radius of at least 3 km (Fensholt et al., 2004). The Dahra site is located in the ‘Centre de Recherche Zootechnique (CRZ)’ managed by the Institut Sénégalais de Recherche Agronomique (ISRA).

The site is equipped with three towers: a meteorological tower with meteorological, hydrological and radiation sensors, a flux tower with an eddy covariance (EC) system for CO₂, H₂O and energy flux measurement, and a land surface temperature tower equipped with infrared thermometers (Fig. 1). A thorough description of measurements of hydroclimatic variables, edaphic conditions, brightness temperature, biomass, species composition, hyperspectral reflectance, and land-atmosphere exchange of CO₂ and energy is given in the supplementary material.

**Data analysis**

**Surface albedo, reflectance, NDVI, and FAPAR.** Broadband surface albedo was estimated as reflected total solar irradiance divided by incoming total solar irradiance. The reflectance corresponding to different wavelengths and different viewing angles was estimated by dividing reflected radiance by incoming radiance for each wavelength and angle combination. The reflectance estimates in the near infrared (NIR) and red bands were used to calculate the NDVI as:

\[
NDVI = \frac{\rho_{\text{NIR}} - \rho_{\text{red}}}{\rho_{\text{NIR}} + \rho_{\text{red}}} \tag{1}
\]

where \(\rho_{\text{NIR}}\) and \(\rho_{\text{red}}\) are the reflectance in the NIR and the red bands, respectively. The FAPAR was estimated by:

\[
FAPAR = \frac{\text{PAR}_\text{inc} - \text{PAR}_\text{ref} - (1 - 2a_{\text{soil}}) \times \text{PAR}_\text{transmit}}{\text{PAR}_\text{inc}} \tag{2}
\]

where \(\text{PAR}_\text{inc}\) is incoming photosynthetic active radiation (PAR), \(\text{PAR}_\text{ref}\) is reflected PAR, \(2a_{\text{soil}}\) is PAR albedo of the soil, and \(\text{PAR}_\text{transmit}\) is PAR transmitted through the vegetation.

**Surface reflectance anisotropy.** To assess the anisotropic effects on the hyperspectral surface reflectance (350–1800 nm), we calculated the anisotropy factor (ANIF) (Sandmeier et al., 1998):

\[
ANIF(\lambda, \theta) = \frac{\rho(\lambda, \theta)}{\rho(\lambda)} \tag{3}
\]

where \(\rho\) is reflectance for the different wavelengths (\(\lambda\)) and the different viewing angles (\(\theta\)), and \(\rho(\lambda)\) is the nadir reflectance. We used the median reflectance for each wavelength (350–1800 nm) measured between 12:00 and 14:00 hours from the peak of the growing season 2011. The peak of the growing season was defined as the maximum of the 15 days around the DOY of maximum NDVI. Maximum biomass and vegetation water content is the maximum value measured. DW is dry weight. – means no data

### Table 1
Annual values of ecosystem properties and hydroclimatic variables. Start of rainy season is the day of the year (DOY) when the first rain arrived. However, for some years there was a minor rain fall a few weeks before the actual start of the rainy season, a so called false start of the rainy season. These rain falls are not included in the start of the rainy season. End of the rainy season is defined as the last DOY with rain fall. Maximum NDVI is the maximum normalized difference vegetation index. Peak FAPAR is the median fraction of photosynthetically active radiation absorbed by the vegetation for the peak of the growing season. The peak of the growing season was defined as the average of the 15 days around the DOY of maximum NDVI. Maximum biomass and vegetation water content is the maximum value measured. DW is dry weight. – means no data.

<table>
<thead>
<tr>
<th>Year</th>
<th>Annual rainfall (mm)</th>
<th>Start rainy season (DOY)</th>
<th>End rainy season (DOY)</th>
<th>Number of species</th>
<th>Maximum NDVI</th>
<th>Peak FAPAR</th>
<th>Maximum biomass (g DW m⁻²)</th>
<th>Maximum vegetation water content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>169</td>
<td>186</td>
<td>304</td>
<td>–</td>
<td>0.65</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2003</td>
<td>346</td>
<td>178</td>
<td>303</td>
<td>–</td>
<td>0.59</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2004</td>
<td>323</td>
<td>192</td>
<td>311</td>
<td>–</td>
<td>0.62</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2005</td>
<td>488</td>
<td>178</td>
<td>334</td>
<td>–</td>
<td>0.56</td>
<td>0.72</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2006</td>
<td>232</td>
<td>193</td>
<td>279</td>
<td>22</td>
<td>0.82</td>
<td>0.81</td>
<td>150</td>
<td>76</td>
</tr>
<tr>
<td>2007</td>
<td>333</td>
<td>191</td>
<td>283</td>
<td>–</td>
<td>0.66</td>
<td>0.67</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2008</td>
<td>302</td>
<td>167</td>
<td>328</td>
<td>31</td>
<td>0.64</td>
<td>0.75</td>
<td>418</td>
<td>68</td>
</tr>
<tr>
<td>2009</td>
<td>504</td>
<td>174</td>
<td>274</td>
<td>36</td>
<td>0.59</td>
<td>0.56</td>
<td>289</td>
<td>67</td>
</tr>
<tr>
<td>2010</td>
<td>650</td>
<td>174</td>
<td>267</td>
<td>36</td>
<td>0.68</td>
<td>0.62</td>
<td>471</td>
<td>66</td>
</tr>
<tr>
<td>2011</td>
<td>486</td>
<td>176</td>
<td>278</td>
<td>35</td>
<td>0.64</td>
<td>0.53</td>
<td>223</td>
<td>73</td>
</tr>
<tr>
<td>2012</td>
<td>606</td>
<td>176</td>
<td>289</td>
<td>32</td>
<td>0.61</td>
<td>0.49</td>
<td>206</td>
<td>65</td>
</tr>
</tbody>
</table>
gradient estimated fluxes are given in the supplementary material. To be able to estimate daily values of net ecosystem exchange of carbon dioxide (NEE; \( \mu mol \ m^{-2} \ s^{-1} \)), sensible heat flux (H; \( W \ m^{-2} \)) and latent heat flux (LE; \( W \ m^{-2} \)), gap-filling is needed. Gaps shorter than and equal to 3 days in NEE were filled using four different approaches: (i) gaps shorter than 2 h were filled using linear interpolation (Falge et al., 2001); (ii) daytime gaps longer than 2 h were filled using the Misterlich function fitted to half-hourly NEE estimates in 7-day gliding windows:

\[
NEE = -(F_{\text{csat}} + R_d) \times (1 - e^{-\left(\frac{F_{\text{PAR}}}{F_{\text{PAR}} - R_d}\right)}) + R_d
\]

where \( F_{\text{csat}} \) is the CO\(_2\) uptake at light saturation, \( R_d \) is dark respiration and \( z \) is the quantum efficiency or the initial slope of the light response curve (Falge et al., 2001); (iii) the nighttime gaps were filled using average NEE measured during that night; and (iv) remaining gaps were filled using mean diurnal variation 7-day gliding windows (Falge et al., 2001). Gaps in H and LE shorter than 2 h were filled using linear interpolation. Remaining gaps shorter than or equal to 3 days were filled using mean diurnal variation 7-day gliding windows (Falge et al., 2001).

**Results and discussions**

**Species composition**

The numbers of grass and herbaceous species identified for the different years ranged between 22 and 36 (Table 1). The interannual variability in number of herbaceous species was correlated with the start of the rainy season and to annual rainfall (Table 2). The year 2006 had the lowest diversity in species composition (Table 1, Table S4). The dominant species in 2006 was

### Table 2

Matrix of correlation coefficient (raw 1) and sample size (raw 2) between interannual variation in hydroclimatic variables and ecosystem properties. Rainfall is annual, soil moisture and soil temperature is averaged for the peak of the growing season and measured at 5 cm depth, air temperature and relative humidity were also averaged for the peak of the growing season, and measured at ~2 m height (for exact measurement height, see supplementary material). FAPAR is the median fraction of photosynthetically active radiation absorbed by the vegetation for the peak of the growing season. The peak of the growing season was defined as the average of the 15 days around the DOY of maximum NDVI. The low number of statistically significant correlations is caused by the few number of years measured. Maximum NDVI, biomass and vegetation water content is the maximum values measured. DW is dry weight.

<table>
<thead>
<tr>
<th></th>
<th>Number of species</th>
<th>Peak Albedo</th>
<th>Maximum NDVI</th>
<th>Peak FAPAR</th>
<th>Maximum Biomass (g DW m(^{-2}))</th>
<th>Maximum Vegetation water content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall</td>
<td>0.78</td>
<td>-0.13</td>
<td>-0.39</td>
<td>-0.63</td>
<td>0.30</td>
<td>-0.69</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>0.83*</td>
<td>-0.24</td>
<td>-0.64</td>
<td>-0.35</td>
<td>0.35</td>
<td>-0.28</td>
</tr>
<tr>
<td>Soil temperature</td>
<td>0.40</td>
<td>-0.77</td>
<td>-0.49</td>
<td>-0.81</td>
<td>-0.11</td>
<td>-0.58</td>
</tr>
<tr>
<td>Air temperature</td>
<td>0.80</td>
<td>-0.39</td>
<td>-0.61</td>
<td>-0.78*</td>
<td>0.12</td>
<td>-0.43</td>
</tr>
<tr>
<td>Air humidity</td>
<td>-0.65</td>
<td>0.58</td>
<td>0.31</td>
<td>0.92†</td>
<td>0.05</td>
<td>0.36</td>
</tr>
<tr>
<td>Start of rainy season</td>
<td>-0.98†</td>
<td>0.39</td>
<td>0.57</td>
<td>0.62</td>
<td>-0.49</td>
<td>0.73</td>
</tr>
<tr>
<td>Number of species</td>
<td>-0.32</td>
<td>-0.84*</td>
<td>-0.84*</td>
<td>0.53</td>
<td>-0.62</td>
<td></td>
</tr>
<tr>
<td>Albedo</td>
<td>-0.34</td>
<td>0.55</td>
<td>-0.15</td>
<td>0.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NDVI</td>
<td>0.51</td>
<td>-0.30</td>
<td>0.70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FAPAR</td>
<td>-0.13</td>
<td>0.62</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>-0.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Statistical significance according a 0.05 threshold.
†Statistical significance according a 0.01 threshold.
an annual legume, *Zornia glochidiata* of the *Fabaceae* family, and, in comparison to the other years, only few of the dominant species were annual grasses of the *Poaceae* family (Table S4). Most of the years had a dominant species of the *Zornia* genus. However, under certain rainfall conditions *Zornia glochidiata* can become very dominant and it can produce continuous mats of leaf layers during the rainy season (Burkill, 1995). The year 2006 was the driest of all years, from which species composition was measured, and it also had a so called false start of the rainy season (there was rainfall on ~14 June, 28 days before the main part of the rainy season started). A false start of the rainy season can strongly influence the plant community in that some species (the dominant for the other years) are specialized to grow quickly at the beginning of the rainy season (Elberse & Breman, 1989, 1990; Mbow et al., 2013), and possibly these species did not survive the dry period after the false start of the rainy season. Other factors which were not measured but can strongly influence the species composition in the Sahel are grazing, species composition of the seeds from the previous year, nutrient availability, disturbance history, fire, and herbivory (Hiernaux, 1998; Hérault & Hiernaux, 2004; Hiernaux et al., 2009).

**Hyperspectral reflectance**

To study the dynamics in spectral reflectance, the ratio between daily median reflectance for each wavelength (350–1800 nm) and the average reflectance for the entire measurement period for each wavelength was calculated (Fig. 3b). As variability in visible (VIS, 350–700 nm) reflectance is mostly affected by changes in leaf pigments (Asner, 1998), there was stronger absorption after bud burst, than at the start of the rainy season and during the dry season (Fig. 3). To reduce excessive heating of the leaves, a large fraction of NIR radiation is reflected in green vegetation and the NIR reflectance is affected mostly by changes in LAI, canopy architecture, and by the spongy mesophyll layer in green leaves (Asner, 1998). The strongest NIR absorption was seen at the end of the rainy season and at the beginning of the dry season, when LAI was at its maximum. The amount of litter decreased over the dry season because of grassing and decomposition and NIR reflectance thereby increased toward the end of the dry season (Fig. 3b). Clear seasonal variation depending on phenology was also visible in the water absorption region around 1450 nm. Reflectance in the short-wave infrared part of the spectrum (1400–1800 nm) was also affected by leaf phenology and vegetation water content, which most likely increased the absorption in these wavelength bands (e.g. Carter, 1991).

**Surface reflectance anisotropy**

The surface reflectance anisotropy increased with increasing sensor viewing angle for observations made during the rainy season (Fig. 4). With increasing sensor

![Fig. 3 Reflectance spectrum of the ground surface; (a) median spectra from two different periods are shown, one from the peak of the growing season 2011 with dense vegetation (black) and one from the dry season 2012 (day of year 71–85) with sparse or no vegetation (gray). (b) The ratio between daily median reflectance for each wavelength (350–1800 nm) and the average reflectance for the entire measurement period 2011–2012 for each wavelength. The black lines in (b) indicate the start and end of the rainy seasons (first and final day of rainfall). Only data measured with the sensor pointing nadir were used.](image-url)
viewing angle, more top of the vegetation canopy is viewed and soil and shading effects decrease, which thereby increases ANIFs with sensor viewing angle (Kimes, 1983). The ANIF for the blue, red and the SWIR bands were less than one whereas the ANIF for green and NIR were close to or exceeded the nadir value of 1. Green plant leaves absorb incident energy in the blue, red, and SWIR wavelengths, while the green and NIR energy is mostly reflected or transmitted in the mesophyll of the plant material (Kimes, 1983). The shift in anisotropy for different wavelength regions could have implications for the design of remotely sensed spectral vegetation indices covering different wavelengths.

For most years, there was an effect of surface reflectance anisotropy on NDVI at the Dahra site (Figure S1). Generally, NDVI increases with viewing angle as only the top part of the canopy is seen (Kimes, 1983) whereas soil background has a larger influence for the nadir pointing estimates (Fensholt et al., 2006). This mainly affects the NDVI for larger viewing zenith angles (Huber et al., 2014), which explains why the NDVI measured at 22.5° and 23° off-nadir viewing angles were most similar to the nadir estimates. Measuring with a hemispherical sensor not only increases the footprint but also adds this effect to the NDVI estimates, explaining the slightly higher NDVI values for the hemispherical sensor. No anisotropic effects were seen for the years 2004 and 2005. Unfortunately, we do not have species composition estimates from these years and we do not have NDVI obtained at different sensor viewing angles from 2006. It could be that the

![Fig. 4 Surface reflectance anisotropy factors (ANIF) for the wavelengths between 350 and 1800 nm measured at the peak of the growing season 2011. The different lines are nadir (black), 15°W (dark blue), 15°E (light blue), 30°W (dark red), 30°E (light red), 45°W (dark green), 45°E (light green).](image)

![Fig. 5 Time series 2002–2012 of albedo, NDVI, and FAPAR; (a) daytime median albedo, (b) daytime median normalized difference vegetation index (NDVI) measured at nadir hemispherically with a Moderate Resolution Imaging Spectroradiometer (MODIS) sensor response configuration (from which the longest time series is available), and (c) daytime median fraction of photosynthetically active radiation absorption (FAPAR). The median values were taken from between 10:00 and 16:00 hours for each day.](image)
years 2004 and 2005 were dominated by planophile species, as was 2006, whereas the other years were dominated by erectophile species. Planophile species show weaker anisotropic effects than erectophile species (Kimes, 1983).

Albedo, NDVI, and FAPAR

The annual variability in the daily albedo (median value between 10:00 and 16:00 hours) was distinct, with values between 0.25 and 0.4. There was a clear effect of ground vegetation on surface albedo (Fig. 5a). During dry seasons, albedo was similar to desert sand of the Sahara (0.4) (Tetzlaff, 1983), whereas during the growing season it was similar to grass (0.25) (Jones & Vaughan, 2010), and values were within the range typical of other sites in the Sahel (Samain et al., 2008; Mougin et al., 2009).

NDVI ranged between 0.02 and 0.82, with strong seasonal dynamics following the phenology of the green vegetation (Fig. 5b). The highest and lowest maximum NDVI were measured in 2006 and 2005, respectively (Table 1). There was strong interannual variability in dry season NDVI (Fig. 5b), which can be explained by variability in the signal from surrounding evergreen trees and remaining dry biomass during the dry season.

June 3 2009 had the largest fraction of PAR incident transmitted to the soil (99.6%). Median PAR albedo measured between 10:00 and 16:00 hours that day (0.20) was assumed to be the albedo and used in the FAPAR calculations [Eqn (2)]. The FAPAR ranged between 0.01 and 0.86, with high values at the rainy season and low values during the dry season (Fig. 5c).

Time series of vegetation indices are the main tool for detecting trends in land surface condition of drylands using remote sensing (e.g. Tucker et al., 1991; Prince & Goward, 1995; de Jong et al., 2013; Dardel et al., 2014). There are reports of declining vegetation productivity since the mid-1980s (Adeel et al., 2005; Cappelaere et al., 2009), whereas others found a greening trend of the Sahel for the same period (e.g. Eklundh & Olsson, 2003; Anyamba & Tucker, 2005; Mougin et al., 2009; Fensholt et al., 2013; de Jong et al., 2013). For the AMMA-CATCH observatory in Niger, Cappelaere et al. (2009) attributed the decreased vegetation productivity to the strong human impact (land use change, increased grazing, wood cutting, and decreased fertility) affecting the land, whereas de Jong et al. (2013) showed that greenness trends in the Sahel region were explained by climatic effects. Based on AVHRR data for the period 2002-2011, Dardel et al. (2014) showed a greening trend for the Gourma region in Mali, explained by that the vegetation reacted to more favorable rainfall. However, they showed a browning trend for the Fakara region in Niger, possibly explained by a reduction in available land for pastoral use and a decline in soil fertility. At Dahra no trend in maximum in situ NDVI was observed between 2002 and 2012 [sample size 11, Sen’s slope 0.0002 (not significant at 95% confidence interval)], i.e. there was no browning or greening trend (Fig. 5b). During this period, there was an increasing trend in rainfall (Sen’s slope 23.87 mm yr⁻¹), but it was not significant. There were no clear trends in the other hydroclimatic variables (Fig. 2).

There were strong negative correlations between both maximum NDVI and peak of the growing season FAPAR with the number of species (Table 2). This was due to the year 2006 where Zornia glochidiata was the dominant species covering the ground with thick planophile leaves, which led to high values of NDVI, leaf area index (LAI) and FAPAR while at the same time reducing the number of species considerably (Mbow et al., 2013).

There was no connection between either soil moisture or annual rainfall and maximum NDVI and peak of the growing season FAPAR (Table 2), which is surprising given the well-documented correlation between primary productivity and rainfall for semiarid savanna ecosystems in general (e.g. Hill & Hanan, 2011). A possible explanation can be alleviated water stress...
conditions for vegetation growth; rainfall has been relatively high during the study period, and during the rainy seasons soil moisture was always above the permanent wilting point (2.78%), indicating no water stress for the plants. On the other hand, peak of the growing season FAPAR was strongly negatively correlated with peak of the growing season air temperature and strongly positively correlated with peak of the growing season air humidity (Table 2). This may indicate that for high temperatures and low air humidity, plants close their stomata to limit water losses, while at the same time reducing PAR absorption.

Several studies from semiarid areas and other ecosystem types have shown linear correlations between FAPAR and NDVI (e.g. Myneni & Williams, 1994; Fensholt et al., 2004; Tagesson et al., 2012). Our result only showed a weak nonsignificant correlation between annual maximum NDVI and the peak of the growing season FAPAR (Table 2). However, the correlations in the cited studies were based on seasonal variation in FAPAR by the photosynthetic tissues. We measured FAPAR for the entire plant community, and it was linearly correlated with NDVI during the vegetative phase (beginning of the growing season until the day of year (DOY) with maximum NDVI), but not during senescence and the dry season (Fig. 6). During the vegetative phase basically all PAR was absorbed by the green vegetation, which explains why the two metrics correlate well during this part of the phenological development. Our results highlight potential difficulties when using

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**Fig. 7** Half-hourly estimates of land-atmosphere exchange of carbon dioxide and energy; (a) net ecosystem exchange of CO$_2$ (NEE) 2010–2012; (b) sensible heat flux (H) 2004–2012 measured with the eddy covariance (EC) method (black dots), and the gradient method (gray dots); (c) latent heat flux (LE) measured with the EC method (black dots), and residuals (net radiation – H – ground heat flux) measured with the gradient method (gray dots); and (d) ground heat flux (G) 2004–2012. The full lines indicate the start (first day of rainfall) and the dotted lines indicate the end of the rainy seasons (final day of rainfall). R means rainy season and D means dry season.
remotely sensed NDVI for estimating FAPAR over a full growing season including the period of senescence. There is an ongoing debate within the FAPAR community, whether FAPAR should be measured for the entire plant or if a method for estimating FAPAR for the green fraction of the vegetation only should be defined (CEOS LPV FAPAR sub-group, 2014).

Properties of the grass and herbaceous vegetation
Vegetation water content was highest in 2006 and lowest in 2012, whereas the lowest and highest amount of dry biomass was measured in 2006 and 2010, respectively (Table 1, Figure S3). There were no correlations between maximum aboveground biomass and any of the environmental variables (Table 2). In 2008 and 2010 there was substantially more maximum biomass in comparison to the other years (Table 1), yet none of the measured environmental variables deviate for these years in comparison to the other years. We can thereby not draw any conclusion about what caused these high productivity years. Factors that were not measured but can cause interannual variability in biomass are grazing, disturbance, or herbivory (Hiernaux, 1998; Hérault & Hiernaux, 2004; Hiernaux et al., 2009). Biomass was similar to that at other Sahelian sites for all years except these two peak years (Mougín et al., 2009).

Remotely sensed NDVI and FAPAR is often used as input data to estimate biomass and vegetation productivity (e.g. Boelman et al., 2003; Tagesson et al., 2012). However, our results indicate no such relationships (Table 2). Again, the explanation could be the species *Zornia glochidiata*, a planophile annual legume covering the surface with thick leaves: this increased the LAI, NDVI, and FAPAR, but since these species do not grow very high, they have a low biomass. The profound effect that the interannual variability in species composition has on the relationship between vegetation indices (NDVI, FAPAR, and LAI) and biomass/NPP poses a substantial challenge to accurate satellite-based biomass/NPP estimates in drylands using production efficiency models based on input from optical remote sensing (Mbow et al., 2013). Another factor influencing NPP and biomass is the dependence of most herbaceous species on previous year’s seeds, and herbivory or rainfall can have strong effects on the seed stocks (Hiernaux et al., 2009; Mougín et al., 2009).

Net ecosystem exchange of carbon dioxide
Strong interannual, seasonal, and diurnal dynamics in CO₂ flux were seen in NEE (Fig. 7a). The fluxes were highest during the rainy season (average NEE = 1.9 g C m⁻² day⁻¹) and lowest during the dry season (average NEE = 0.2 g C m⁻² day⁻¹). NEE peaked at ~7.5 g C m⁻² day⁻¹ during the growing season 2010, which was considerably higher than for other studied semiarid sites in Africa (Verhœuf et al., 1996; Veenendaal et al., 2004; Brümmer et al., 2008; Kutsch et al., 2008; Boulain et al., 2009; Sjöstom et al., 2009). For most of these sites, lower rainfall, lower LAI, or sparser vegetation could possibly explain lower NEE values (Verhœuf et al., 1996; Veenendaal et al., 2004; Boulain et al., 2009; Sjöstom et al., 2009). However, the study sites of Kutsch et al. (2008) and Brümmer et al. (2008) had similar or larger amounts of rainfall and LAI than Dahra, but they also had higher fluxes than at the other sites, but they were still substantially lower than at Dahra. The level of the NEE values at Dahra were instead similar to the level of tropical C₄ wetland plants, humid tropical grassland, and temperate C₄ grassland species (Kim et al., 1992; Dugas et al., 1999; Morison et al., 2000; Merbold et al., 2009; Saunders et al., 2012). Several factors can substantially impact the observed fluxes, such as radiation regime, soil type, site history (cultivation, fire sequences, and disturbances), vegetation age, species composition, and moisture and nutrient conditions (Hill & Hanan, 2011). The soil nutrient concentration was indeed relatively high in the area (0.40 ± 0.10 mg N g⁻¹ soil; 3.2 ± 1.0 g C kg⁻¹ soil at 0–20 cm depth in February 2011).

Half-hourly NEE was strongly correlated with PAR following the Misterlich light response function [Eqn (4); Fig. 8; Table 3] for all days except DOY 158, and DOY 177–179 in 2012. PAR is a strong factor controlling photosynthesis (e.g. Lambers et al., 1998; Tagesson & Lindroth, 2007), and it overruled the influence of all other environmental variables on half-hourly NEE. At DOY 158 in 2012, during the end of the dry season, there was only little vegetation productivity. At the beginning of the rainy season (DOY 177–179, 2012), just after the first rainfall, there was a large positive burst in

![Fig. 8](image-url)
CO₂ flux indicating a strong increase in ecosystem respiration (CO₂ uptake being defined as negative and CO₂ release as positive). This ecosystem respiration flux masked the minor vegetation productivity at the beginning of the growing season, which explains the lack of correlation between NEE and PAR for this period.

**Brightness temperatures**

There are relatively large differences in daily averages of brightness temperature (BT) for the three present surface types, i.e. the sunlit and shaded patches containing a mixture of grass and soil and the tree crown (Fig. 9). As to be expected, the unshaded grass and soil patch showed the largest diurnal and seasonal variability, with the highest temperatures during dry seasons when solar exposure was highest (early summer). During the rainy season, the variation in BT was much lower due to the dense grass cover and availability of moisture at the surface for evapotranspiration. For the shaded grass and soil patch and for the (evergreen) tree crown, the seasonal variation in BT was much lower and the two had almost identical BT during the dry season whereas the tree canopy was generally slightly cooler than the shaded grass patch during the rainy season. The availability of measurements from three different surface types, combined with detailed spatial information about the surroundings, provide a unique dataset for evaluating large scale satellite-based land surface temperature products in a savanna landscape (Rasmussen et al., 2011a).

**Energy fluxes**

H was lower during the rainy season (EC estimated average H: 28 W m⁻²) than in the dry season (EC...
estimated average H: 54 W m\(^{-2}\)), whereas LE was higher during the rainy season (EC estimated average LE: 122 W m\(^{-2}\)) in comparison to the dry season (EC estimated average LE: 47 W m\(^{-2}\)) (Fig. 7b and c). The measured values of the energy fluxes and their temporal patterns were similar to other savanna sites (e.g. Aradö et al., 2008; Brümmer et al., 2008; Mougin et al., 2009).

Previously it has been found that H and LE are strongly affected by phenology, soil type, lateral water distribution, and surface temperature (e.g. Stisen et al., 2008; Cappelaere et al., 2009; Timouk et al., 2009). LE and H were coupled to phenology and rainfall patterns also at the Dahra site: LE was considerably higher, whereas H was lower during the rainy season than during the dry season (Fig. 7b and c). H was strongly affected by solar irradiance and brightness temperature (Fig. 10a, b, d, and e). The large scatter could be due to the long period included in the relationships (giving diurnal-, intra-, and interannual variability 2010–2012) and variability in other environmental variables affecting the fluxes. There was a boundary line for maximum H set up by soil moisture, since at high soil moisture values potential H decreased as more energy was used for LE (Fig. 10c and f). There was no difference in the relationships between H and environmental variables for the rainy and dry season. None of the environmental variables alone could explain LE, yet still affecting it by setting potential boundary lines (Fig. 11). Surprisingly, LE was not correlated with soil moisture at 0.05 m depth. An explanation could be direct wet soil and canopy evapotranspiration of minor rainfall events that do not increase the soil moisture at 0.05 m depth.

Theoretically, the residual of the energy balance (net radiation – H – ground heat flux) should be attributed to the LE (when LE is not measured) and it is often used as a proxy for evapotranspiration in model evaluations (e.g. Stisen et al., 2008). However, LE and the residual are not measuring the same. A comparison between eddy covariance estimated LE and gradient estimated residuals generated a root mean square error

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**Fig. 10** Sensible heat flux (H) against environmental variables; H measured with the eddy covariance method against solar radiation (E), brightness temperature (BT) and soil moisture at 5 cm depth [SWC, soil volumetric water content (m\(^3\) m\(^{-3}\) × 100)] for the dry and rainy season.
Fig. 11 Latent heat flux (LE) against environmental variables; LE measured with the eddy covariance method against solar radiation (E), brightness temperature (BT), and soil moisture at 5 cm depth [SWC, soil volumetric water content (m$^3$ m$^{-3}$ $\times$ 100)] for the dry and rainy season.
References


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Supporting Information

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

**Figure S1.** Daily values of in situ measured normalized difference vegetation index (NDVI) for different viewing angles; (a) NDVI measured at nadir with 60° instantaneous field of view (IFOV) (black) and hemispherical (gray), (b) NDVI measured at nadir with 60° IFOV (black), measured at 22.5° off-nadir angle toward E with 60° IFOV (blue), measured at 22.5° off-nadir angle toward W with 60° IFOV (red), (c) NDVI measured at nadir with 60° IFOV (black), measured at 45° off-nadir angle toward E with 25° IFOV (blue), measured at 45° off-nadir angle toward W with 25° IFOV (red), and (d) NDVI measured at nadir (black) with 25° IFOV and at 23° off-nadir angle toward NW with 25° IFOV (gray). The NDVI values are the median from between 10:00 and 16:00 hours each day.

**Figure S2.** Time series 2002 of in situ measured effective leaf area index (LAI). DOY is day of year.

**Figure S3.** Time series 2006–2012 of average estimates of (a) aboveground dry biomass (DW), (b) net primary productivity (NPP), and (c) relative water content in the harvested plants (VWC).

**Figure S4.** Friction velocity ($u^*$) modeled with equation S1 against friction velocity measured by the sonic anemometer.

**Figure S5.** Density scatter plot for evaluation of gradient estimated sensible heat flux (H) 2010–2012. Half-hourly H measured with the gradient method against half-hourly H measured with the eddy covariance (EC) method. The black line is the one-to-one ratio.

**Figure S6.** Density scatter plot for evaluation of gradient estimated residuals 2010–2012. Half-hourly residual measured with the gradient method against half-hourly LE measured with the eddy covariance (EC) method. The black line is the one-to-one ratio.

**Table S1.** Periods during which hydroclimatic variables have been measured 2002–2012 at the Dahra field site. $T_{air}$ and $T_{soil}$ are air and soil temperature, RH is relative humidity, W is wind speed, SWC is soil moisture, and BT is the brightness temperature, G is ground heat flux. Height is measurement height (m) and angle is the sensor view zenith angle (°). Soil moisture was measured in volumetric water content (%). CS215, 107 and A100R are made by Campbell Scientific Inc. (North Logan, USA), ML2X is made by Delta T devices (Cambridge, UK), HFP001 is made by Hukselux Thermal Sensors B.V. (Delft, Netherlands), ARG1000 is made by Wattera (Burnaby, Canada), the Miniature Infrared (MI) sensors are made by Raytek CO. (Santa Cruz, CA, USA), and the IRTS-P are made by Apogee Electronics (Santa Monica, CA, USA). – means no data.

**Table S2.** Periods during which reflected and incoming radiation have been measured using different bands and different sensor response configurations 2002–2012. Height is measurement height (m), IFOV is the instantaneous field of view, angle is view angle of the sensor, inc. is incoming, ref. is reflected, trans. is transmitted, NIR is near infrared, PAR is photosynthetically active radiation, irr. is irradiance, Hemi. is hemispherically, Rad. is radiation, Meris is the medium resolution imaging spectroradiometer, MODIS is the moderate resolution imaging spectroradiometer, AVHRR is the advanced very high resolution radiometer, and MSG is the Meteosat Second Generation. SKR1800, SKR1850A, and SKP 215 are made by Skye instruments Ltd. (Llandrindod Wells, UK), and SP Lite and NR2Lite is produced by Kipp & Zonen (Delft, The Netherlands).

**Table S3.** Dominant tree species at Dahra in 2008 and their mean heights and mean diameters at breast height (DBH).

**Table S4.** Grass and herbaceous species composition at the Dahra field site in 2006, and 2008–2012.

**Table S5.** Height (m) of the sensors measuring air temperature and wind speed used in the gradient calculations of sensible heat flux. DOY is day of year.