Responses and feedbacks of African dryland ecosystems to environmental changes

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Abstract

Drylands occupy 43% of the African continent and play an important role in the global carbon cycle and in supporting local livelihoods. Understanding how dryland ecosystems respond to environmental changes, both structurally and functionally, is of great significance for sustainable dryland management. In this article, we review the current remote sensing-based knowledge on African dryland ecosystem dynamics and the main drivers of changes. Global CO₂ enrichment, changes in rainfall regimes, and a decline in fire activity have collectively driven vegetation greening, woody plant increase and carbon dynamics in African drylands over recent decades, challenging the long-held desertification narrative. Here we also highlight the importance of rainfall-vegetation-fire feedbacks in enhancing dryland ecosystem resilience and predicting future ecosystem responses.

Key words: African drylands; savanna; ecosystem dynamics; drivers; woody encroachment; rainfall-vegetation-fire feedback loops
Introduction

Drylands are regions with an aridity index (i.e. the ratio of mean annual rainfall to mean annual potential evapotranspiration) below 0.65 and are characterized by scarce and highly variable rainfall [1]. Inhabited drylands (primarily including arid, semi-arid, and dry sub-humid areas) in Africa cover 11% of the Earth’s land surface, 27% of the global drylands, and 43% of the African continent (Fig. 1) [2]. Drylands in Africa support 325 million people whose livelihoods depend heavily on the ecosystem services. Therefore, understanding how drylands in Africa respond to climate change and human pressure is extremely important for sustainable management in the context of global environmental changes.

The vegetation of drylands in Africa is largely characterized by savannas and open shrublands, with a dynamic assemblage of trees and grasses [3], regulated by the availability of resources (i.e. water, soil nutrients) and disturbance regimes (i.e. fire, herbivory) [4-6]. A large proportion of research has documented that rainfall regimes (i.e. amount, intensity, frequency, and seasonality of rainfall) are the main drivers of vegetation composition and growth in African drylands [7,8]. Furthermore, fire and herbivory regulate the competition of grasses and woody plants at the local scale [4,9]. Moreover, human activities (i.e. land conversion, farming, de- and afforestation) play an increasingly prominent role for ecosystem properties in the Anthropocene [10,11]. However, the interactions/feedbacks between resources, ecosystems, and disturbances are complex and not yet fully understood which poses great challenges for understanding how dryland ecosystem structure and function might respond to global environmental changes.

Given the capability of large spatial coverage and long-term observations, satellite remote sensing has been instrumental in monitoring the dynamics of dryland ecosystems and in elucidating the driving mechanisms. In this review, we frame the main drivers impacting on dryland ecosystems in Africa in terms of resource availability and disturbance. In placing this within a Resource-Ecosystem-Disturbance framework, we present an overview of the structural (i.e. vegetation greenness, the composition of grasses and woody plants) and functional (i.e. carbon stocks, green biomass) dynamics of dryland ecosystems and highlight the important role of rainfall-
vegetation-fire feedback loops in understanding how dryland ecosystems respond to global environmental changes.

Fig. 1. Drylands in Africa based on the aridity index. Hyper-arid areas were excluded in this study. (https://figshare.com/articles/Global_Aridity_Index_and_Potential_Evapotranspiration_on_ET0_Climate_Database_v2/7504448/3).

Drivers of dryland ecosystem changes

Drylands in Africa are projected to expand in the coming century [12], and a thorough understanding of ongoing environmental changes in dryland ecosystems is urgently needed for future sustainable management. The Resource-Ecosystem-Disturbance framework includes five fundamental elements: rainfall regimes, soil properties, ecosystem structure and function, fire regimes, and human management (Fig. 2). Each of these elements has its own properties and they interact with each other through complex positive or negative feedback loops. Rather than attempting to synthesize all possible inter-relationships among these five elements, here we focus on understanding how dryland ecosystems respond to environmental change.

Elevated atmospheric CO$_2$ has a positive impact on water use efficiency and thus can
increase photosynthetic activity and carbon sequestration [11,13]. In drylands, resource availability (i.e. water, soil nutrients) as well as disturbance regimes (i.e. fire, herbivory) regulate ecosystem structure, function, and dynamics (Fig. 2). Recent findings based on Earth observations and field data suggest that the alteration of rainfall regimes (i.e. amount, frequency, intensity, and seasonality) is an important determinant of ecosystem structural and functional changes across African drylands, and that changes towards more intensive, less evenly distributed rainfall events has promoted woody over herbaceous vegetation in recent decades [7,8,11,14]. Soil nutrient availability also can interact with rainfall to influence tree-grass dynamics in savanna ecosystems [9,15]. In the future, CO$_2$ fertilization effects on aboveground biomass accumulation may slow down due to nutrient constraints [16]. Although the availability of resources determines overall ecosystem properties and dynamics, disturbances such as fire and herbivory explain the spatial variation in vegetation dynamics [17]. Such disturbances are fundamental to nutrient recycling, niche partitioning [18] and the maintenance of multiple stable states [19]. Fire regimes and herbivory promote alternative biome states (i.e. forest-savanna-grass mosaic) by stabilizing feedbacks [19]. Frequent fires keep the system open and enable a dominance of shade-intolerant flammable grasses that enhance fires, while in more closed systems, shade limits the growth of grasses, lowering dry fuel load which reduces fires and contributes to woody plant increase [19,20]. Browsers may enhance the effect of fire on trees because they reduce woody biomass, thus indirectly stimulating grass growth. Grazers may facilitate woody plant increase by reducing the fuel load and hence the fire frequency [22,23]. Moreover, vegetation in savanna ecosystems may respond non-linearly to human disturbances. For example, increased population may initially reduce tree cover but the later introduction of agroforestry practices may increases tree cover again. In some arid and semi-arid areas, tree cover on agricultural land may even exceed the natural tree cover, although the depletion of forests in more humid areas cannot be compensated [17,21].

In summary, it is widely agreed that rising atmospheric CO$_2$, changes in resource availability (water, soil nutrients), coupled with disturbances (fire, herbivory) shape African dryland ecosystem dynamics, yet quantifying the importance of these drivers...
and understanding the extent to which they interact with each another remains challenging.

Fig. 2. A conceptual framework of drivers-responses-feedbacks in African dryland ecosystems. Here we present the driving mechanism of dryland ecosystems (center) from the perspective of resource availability (left side) and disturbance (right side). Specifically, rainfall regimes (dark blue box), soil properties (light blue box), fire regimes (orange box), and human activities (brown box) together drive ecosystem structural and functional dynamics (green box) in African drylands. We also highlight the rainfall-vegetation-fire feedback loops in drylands where rainfall promotes fire through fuel load (blue arrow) while fire suppresses rainfall by increasing surface albedo (orange arrow).

Ecosystem structural and functional dynamics in African drylands

Dryland ecosystems dominate the inter-annual changes in the global carbon sink [24,25]. Monitoring the spatio-temporal dynamics of dryland ecosystem structure and function is therefore essential to understand dryland carbon sequestration potentials. In this section, we review the progress made in monitoring dryland ecosystem structural and functional dynamics across Africa.
Changes in vegetation greenness

Spectral vegetation indices, of which the most widely used is the Normalized Difference Vegetation Index (NDVI) [26], have played an important role in inferring changes in dryland vegetation across a wide range of spatio-temporal scales, acting as proxies for leaf area index, fractional vegetation cover, and photosynthetic capacity [26]. Monitoring vegetation greenness is an important indicator of photosynthetic activity and therefore availability of green biomass that is used for livestock fodder [27]. While satellite records reported an overall greening trend in African drylands over recent decades [13], changes in vegetation greenness are spatially heterogeneous [14]. Moreover, vegetation greening or browning is often a matter of observation period and associated interpretations of such changes to represent “recovery” or “degradation” are not always appropriate and oversimplified [28]. Satellite observations and long-term field data generally show a positive trend in rainfall and vegetation greenness over the last decades of the 20th century across much of the Sahel (“re-greening Sahel” after the drought years of 1970s and 1980s) and this has been interpreted as an increase in biomass [29]. However, the rainfall recovery in the Sahel does not benefit herbaceous vegetation to the same extent as woody vegetation, which appears to be favored by strongly increased early/late rains [8]. Additionally, vegetation greening has been prevalent in water-limited southern Africa, which is associated with an increase in woody cover driven by an increase in rainfall and augmented by CO₂ fertilization [11,14,17]. In contrast, East Africa has been detected as a hotspot of vegetation browning caused by increased soil water deficit in recent decades [14]. Vegetation trends are, however, rarely linear [31] due to the strong effect of El Niño-Southern Oscillation (ENSO) in controlling seasonal and inter-annual rainfall in this region [32].

Woody plant increase

Woody-grass interactions in savanna ecosystems are typically regarded as being competitive, yet tree-grass assemblages coexist in a range of rainfall conditions.
increase in woody plants has been widely reported in African drylands over past decades [11,33]. While southern Africa experiences woody encroachment at the expense of herbaceous vegetation [17, 34], the woody vegetation in the Sahel shows a general shift towards drought resistant shrubs at the expense of trees [29]. Moreover, recently accelerating encroachment rates have also been noted across all three continents in which savannas occur [33]. Emerging remote sensing datasets have advanced the monitoring of African ecosystems. For example, vegetation optical depth (VOD) from passive microwave remote sensing measures vegetation water content which can be related to the total aboveground biomass of both woody and leafy components [35,36]. Considering both NDVI and VOD records together can distinguish leafy and woody components to obtain a more accurate assessment of woody vegetation changes in drylands [14,37]. The widely observed increase in woody plant cover in tropical drylands globally is mirrored in trends of increasing leaf area index/vegetation greenness in African drylands [7,37], thereby challenging long-held desertification narratives [38].

The drivers and effects of woody plant increase in African drylands have also been the subject of recent studies [5,7,11,17,39]. There is a consensus that global drivers such as CO₂ fertilization, changes in rainfall regimes along with a decline in fires and overgrazing facilitate woody plant increase [7,9,17]. In contrast to herbaceous vegetation, woody plants can benefit from a higher variability and intensity of rainfall [7] and a higher atmospheric CO₂ level benefits mostly C₃ trees and shrubs [9,17]. Decreased fire activity facilitates the establishment of woody vegetation at the expense of herbaceous plants, which in turn reduces fuel load and further enhance woody plant growth [40]. However, in areas with high human population growth rates, deforestation caused by the increasing demand for agricultural and forest products (including fuelwood collection) still prevails [11]. At the continental scale, human population growth is found to offset the climate-driven increase in woody vegetation in African drylands [11].

The effects of woody plant increase on African drylands are still largely controversial [40-42]. On the one hand, rangeland degradation due to the encroachment of unpalatable bushes replacing pasture grasses negatively impacts livestock production and pastoral livelihoods [39]. Moreover, bush encroachment has
been found to threaten the preservation of savanna ecosystems and its endemic biodiversity [40], and impact litter decomposition rates and soil organic matter [43]. On the other hand, woody plant encroachment may be linked to increased long term carbon accumulation [17], which may help balancing carbon losses from deforestation. Overall, woody encroachment leads to substantial changes in nutrient cycling, carbon dynamics, biodiversity, and human well-being, but the effects can be local, difficult to generalize and should not systematically be equated with the structural and functional degradation of ecosystems [42].

**Carbon dynamics in African drylands**

Aboveground carbon is stored in both green (herbaceous vegetation and woody foliage) and woody (trunks, branches) biomass. While inter-annual dynamics are largely controlled by changes in green biomass, woody biomass represents a long term carbon stock that is vulnerable to disturbance such as fire and deforestation. Woody cover estimates derived from VOD have also exhibited significant increases in African drylands during 1992-2011 [11]. This increase in woody cover is not necessarily coupled with an increase in plant density, but may also be linked to increased woody plant foliage production. Recent studies, using time-series of VOD derived from low-frequency passive microwaves (1.4 GHz) to quantify annual aboveground biomass carbon changes, document a climate-induced carbon loss in African drylands during 2010-2016 [35,36]. This shows that the greening observed over the past three decades did not continue in recent years. While African drylands were identified as an important carbon sink with a peak in the extremely wet year of 2011, the recent extreme El Niño event of 2015–2016 led to drylands being identified as a carbon source [35]. More recent studies suggest that the carbon stock of African drylands (shrublands and savanna) in 2017 had almost recovered to the pre–2015–2016 El Niño state [44]. These dynamics suggest that ENSO largely modulates the inter-annual variations and long term trends in vegetation productivity in African drylands and also highlight the marked resilience of dryland ecosystems to prolonged water stress [44,45].

African drylands hold a large proportion of the continental carbon stock, of which
a considerable proportion comes from soil carbon [46]. The high potential for carbon 
storage in soils contributes to ecosystem resilience and mitigates climate change and 
therefore, knowledge of the amount, distribution, and dynamics of soil carbon in 
African drylands is crucial for understanding the carbon cycle. Widespread woody 
plant increase is often associated with an increase in aboveground carbon biomass 
[17], yet the effects on soil carbon are less clear. Woody encroachment reduces the 
proportion of herbaceous biomass, which may impact the plant decomposition rate 
and soil organic matter content [40]. Nevertheless, the effects of woody 
encroachment on soil carbon need more observational evidence, as soil carbon 
responses to woody encroachment vary along rainfall gradients, and with soil 
properties and plant functional types [48].

Rainfall-vegetation-fire feedback loops

The importance of rainfall and fire on ecosystem structural and functional changes 
in African drylands are well documented, yet the interplay between vegetation 
dynamics, rainfall, and fire are rarely investigated. Rainfall regulates fuel load and 
fuel flammability [49], which largely controls the spatio-temporal dynamics of fires in 
African drylands [50]. Most importantly, the effects of rainfall on fire are spatio-
temporally varied: short rainfall periods - especially during or just before the fire 
season commences - moisten the fuel, while longer rainfall periods, including rainfall 
of the preceding one or two wet seasons (around 8 months or 20 months), favor an 
accumulation of fuel load [50]. Overall, rainfall facilitates fire activity in xeric areas 
where the fire fuel loads limits fire activity. Contrarily, rainfall suppresses fire in mesic 
regions where fires are limited by fuel flammability. Therefore, fires in African 
drylands are likely to reduce in projected warming and drought scenarios, decreasing 
productivity and limiting fuel to support fire activity. Moreover, ongoing cropland 
expansion can reduce fire activity, which may break the natural linkage between fire 
and rainfall. It is thus possible that climate change and land conversion will further 
reduce fire activity in African drylands.

Fires are widespread in African drylands and mediate land-atmosphere feedbacks 
by modifying vegetation cover, albedo, and the partitioning of net radiation into
sensible and latent heat fluxes [51,52]. Rainfall controls savanna fires through
availability and flammability of fuel, in turn altering fire regimes with further
feedback to rainfall. Recently, fire-induced rainfall changes have attracted more
attention from researchers [52-55]. Observational evidence of rainfall suppression by
fire has been reported in African drylands, of which changes in albedo after fire have
been regarded as the primary cause [53-55]. Fire induced lowering of the surface
albedo is a well-known phenomenon [51,56], and new studies in African drylands
[52,57] show that fire results in an immediate darkening (ash and charcoal
deposition) followed by persistent brightening (vegetation and ground condition
deterioration), which increases mean surface albedo and, in turn, decreases surface
net radiation and evapotranspiration. Such changes in the surface energy balance
may result in a drier, more stable boundary layer that suppresses convective rainfall
[53-55]. In summary, more rainfall facilitates fire (via fuel), yet increased fire activity
may decrease rainfall (via albedo).

Conclusions

African drylands are particularly sensitive to environmental changes and play an
important role in carbon dynamics while supporting local livelihoods. Our Resource-
Ecosystem-Disturbance framework highlights the inter-linkages between rainfall, soil,
vegetation, fire, and human management and helps to understand how dryland
ecosystems’ structure and functioning respond to global environmental changes.
Moreover, our framework and the negative rainfall-vegetation-fire feedback loops
are widely applicable for semi-arid and dry sub-humid regions where trees and
grasses have a balanced coexistence, yet the framework is not equally relevant for
very dry areas.

Over past decades, global CO$_2$ fertilization, resource availability (i.e. water, soil
nutrients), and disturbances (i.e. fire, herbivory) together drive vegetation greening,
woody plant increase and carbon dynamics in African drylands. However, the
projected warming and increased frequency of droughts may cause a shift in
vegetation composition with negative effects on biodiversity and the terrestrial
carbon sink [58-59]. Moreover, it remains unclear whether increases in water use
efficiency associated with elevated atmospheric CO\textsubscript{2} may mitigate the effects of droughts. Currently, our understanding of the discussed drivers and their interactions is either limited to local scale field studies or ecosystem models. While these models are able to quantify interactions between drivers and predict future scenarios at large scales, the quality of such predictions depends partly on the input data. The increasing availability of high quality remote sensing data and artificial intelligence technologies open new doors for improved data-informed modelling by use of data assimilation schemes to better understand mechanisms and develop more realistic long-term projections applicable for sustainable management plans. Although new satellite data-sets and methods have improved our understanding, there is also a critical need to maintain/build a long-term ground observation network to complement, calibrate and evaluate model and remote sensing based data.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
-● of outstanding interest


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** This article introduces the concept of alternative biome state (ABS) – an alternative framework to that of climate determinism and succession for exploring forest and nonforest mosaics, and highlights fire and herbivory as the key processes promoting ABS.

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● This paper summarizes the past achievements and current progress in remote sensing of dryland ecosystems, discusses the major challenges of remote sensing in monitoring dryland structural and functional dynamics, proposes future research directions and the opportunities in remote sensing to deal with pervious challenges.


** This paper reveals the nonlinear dynamics of fires in Africa supposedly following the oscillating variations of precipitation (ENSO-induced) concealed by linear trend estimators, develops a change typology on fire evolution in space and over time, and highlights the relationship between fire and precipitation are spatio-temporally varied.


** This paper investigates the impact of fire on local precipitation using satellite observations and suggests that fire suppresses precipitation by reducing the evapotranspiration resulting from a decrease in surface net radiation.

