

On regreening and degradation in Sahelian watersheds

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Over many decades our understanding of the impacts of intermittent drought in water-limited environments like the West African Sahel has been influenced by a narrative of overgrazing and human-induced desertification. The desertification narrative has persisted in both scientific and popular conception, such that recent regional-scale recovery ("regreening") and local success stories (community-led conservation efforts) in the Sahel, following the severe droughts of the 1970s-1980s, are sometimes ignored. Here we report a study of watershed-scale vegetation dynamics in 260 watersheds, sampled in four regions of Senegal, Mali, and Niger from 1983-2012, using satellite-derived vegetation indices as a proxy for net primary production. In response to earlier controversy, we first examine the shape of the rainfall-net primary production relationship and how it impacts conclusions regarding greening or degradation. We conclude that the choice of functional relationship has little quantitative impact on our ability to infer greening or degradation trends. We then present an approach to analyze changes in long-term (decade-scale) average rain-use efficiency (an indicator of slowly responding vegetation structural changes) relative to changes in interannual-scale rainfall sensitivity (an indicator of landscape ability to respond rapidly to rainfall variability) to infer trends in greening/degradation of the watersheds in our sample regions. The predominance of increasing rain-use efficiency in our data supports earlier reports of a "greening" trend across the Sahel. However, there are strong regional differences in the extent and direction of change, and in the apparent role of changing woody and herbaceous components in driving those temporal trends.

Sahel | desertification | rain-use efficiency | drylands | West Africa

The Sahel (Fig. S1) extends east-west across Africa between the Sahara desert to the north and the humid savanna to the south. It is one of the world's largest water-limited environments (WLE). The region is often considered to be particularly vulnerable to climate change and human activities (1, 2). Herders and farmers in the Sahel have long recognized the importance of short-term rainfall variability on farm and livestock production, with drought being the principal cause of food insecurity (3). Rainfall largely controls net primary productivity (NPP), forage availability, and livestock carrying capacity (1), and is a primary driver of carbon cycling (4, 5). Climate variability (within and between seasons) in WLE such as the Sahel modifies the structure, composition, and diversity of vegetation via changes in NPP and recruitment-mortality dynamics of woody and herbaceous plants (6, 7).

The degradation of the Sahel has been greatly debated within the scientific community. In the 1930s, after a visit to West Africa, Stebbing was one of the first to conclude that the Sahara desert was expanding south into the Sahel and that the cause of degradation was human activity (8). With above-average rainfall in the region in the 1950s and 1960s, these concerns diminished for a while. In the 1970s and 1980s, however, severe drought and famine in the Sahel, coincident with influential ideas on the potential for human mismanagement of common land (9) and the potential for amplifying feedbacks between grazing and drought (10), led to widespread acceptance in both scientific and popular imagination of Sahelian "desertification" as a pervasive and irreversible process (11, 12). In the 1990s, however, an alternative picture emerged as political ecologists and others began to question the "received wisdom" of human-induced desertification (e.g., refs. 13 and 14), perhaps motivated by recognition of the positive role of social institutions in the management of common pool resources (15) and by the recognition that degradation and recovery of Sahelian vegetation is a normal consequence of drought cycles, with or without human agency (16–19).

In the last 20 y, remote-sensing studies have documented an apparent increase in vegetation productivity in the Sahel using satellite measurements of vegetation greenness (i.e., normalized difference vegetation index, NDVI) as a proxy for NPP (20–22). Independent studies have also documented farmer strategies to restore landscape-scale function, in particular through planting of trees and soil conservation actions (23, 24). Other authors, however, have used both satellite and field data to argue that the apparent "regreening" of the Sahel may still hide real degradation in the form of ecosystem ability to use available rainfall (i.e., rain-use efficiency), or in the structure and species composition of the vegetation (25–29).

Meanwhile, in the popular press and often in the environmental and development literature, the reports of recovery are sometimes forgotten (30–32), to the extent that popular opinion in the West—and indeed very often in Africa—holds fast to pessimistic images of overgrazing, degradation, sand storms, and sand-dunes "marching" south from the Sahara towards the sea. The differences in perception of recent changes highlight the need to quantify the extent of recovery (or otherwise) in Sahelian systems since the droughts of the 1970s and 1980s and the extent to which vegetation changes in the Sahel respond proportionally to climate variations.

Many studies have shown that the interannual variability of NPP in WLE is positively correlated with the interannual variability of rainfall (33–35). In addition, the rain-use efficiency (RUE; the slope of the relationship between NPP and rainfall) quantifies an ecosystem's ability to use rainfall and may therefore be a useful indicator of ecosystem health or degradation. However, the use of RUE has been dominated by two contrasting schools of thought. Many authors assume that RUE will be constant with interannual

Significance

For decades, the science and policy narrative relating to the West African Sahel has focused on perceptions of overgrazing and human-induced desertification. More recent reports of regional-scale recovery ("regreening") following the severe droughts of the 1970s and 1980s are sometimes ignored. This study provides a satellite-based evaluation of changes in watershed-scale vegetation conditions in four regions of the Sahel from 1983–2012. Though the results support earlier reports of a "greening" trend, our approach identified strong regional differences in the extent and direction of change, and in the apparent role of woody and herbaceous components in driving the temporal trend.

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variation in rainfall if ecosystem conditions are constant. In this situation, changing RUE can be used directly to diagnose changes in vegetation, reflecting long-term degradation or recovery (20, 21). Meanwhile, based on physical and physiological logic, others argue for an underlying nonlinear relationship between NPP and rainfall, with NPP initially increasing with rainfall before saturating at higher rainfall as light or nutrients become limiting (25, 27). In this situation, we no longer expect a constant RUE (calculated simply as NPP/rainfall), which compromises (or at least complicates) its utility as a degradation indicator. In all cases, however, if the functional relationship between NPP and rainfall is known, or can be derived from observations, then temporal trends in residuals from the fitted relationship can be used to infer changing ecosystem condition. This is the basis for the "residual trend" approach used by several authors to diagnose changing ecosystem health in the Sahel and other regions (36, 37).

The aim of this study is to quantify the changes in vegetation condition in the Sahel based on assessments of long-term satellite-derived greenness sensitivity to rainfall. We explore changes at watershed scales in four test regions across the Sahel and examine the form (linear, nonlinear) of functional relationships between this proxy for NPP and rainfall. We then propose a new approach to the diagnosis of trends in vegetation condition that relates short-term and long-term NPP-rainfall sensitivity to changes in herbaceous and woody plants, respectively. We address the following research questions: (i) What is the shape of the rainfall-NPP relationship and its relevance to the ongoing debate of regreening of the Sahel? (ii) How has NPP varied as a function of rainfall since the 1980s drought in the Sahel? (iii) Can changes in short- and long-term NPP sensitivity to rainfall inform our understanding of changing vegetation structure in different regions of the Sahel?

We based our study on a 30-y (1983–2012) African Rainfall Climatology (ARC) rainfall database (38) in combination with a merged NDVI dataset from Moderate Resolution Imaging Spectroradiometer (MODIS) (39) and Advanced Very High Resolution Radiometer (AVHRR) (40). Annual integrals of NDVI during the growing season (from June to October) are used as a proxy for NPP (20–22) over 260 watersheds located in four regions of Senegal, Mali, and Niger (Fig. S1).

Results

Modeling the Relationship Between Seasonal Rainfall and Integrated NDVI. Using the seasonal sum of rainfall (iR) and seasonal sum of the normalized difference vegetation index (iNDVI), we tested multiple candidate functional models (linear and nonlinear for each of the 260 watersheds) (Table 1). The Corrected Akaike Information Criteria (cAIC) for linear, log-linear, quadratic, and hyperbolic functions indicate three behaviors of the rainfall–NPP relationship (Fig. 1*A*): (i) a linear relationship at 128 watersheds best described by the linear model; (ii) a saturating relationship at 130 watersheds best described by the log-linear model (84 watersheds), the hyperbolic model (38 watersheds), or the quadratic model (8 watersheds); and (iii) a concave up relationship at two watersheds best described by the quadratic model.

We now examine the extent to which the choice of functional relationship impacts conclusions regarding long-term trends in vegetation condition inferred using the trend-in-residuals approach (ResTrend) (36, 37). We note that temporal trends in residuals occur if productivity in later years is greater than (+ve trends) or less than (-ve trends) the productivity predicted by the fitted full time-series model. Such trends are interpreted to imply changes in vegetation structure (e.g., density of trees or the fractional cover of herbaceous sward) that go beyond simple proportional responses to interannual variability in rainfall.

During the period 1983–2012, considering the best model for each watershed indicates: (*i*) a greening trend at 218 (84%) watersheds, but with only 43 of those watersheds (17%) experiencing significant increases; and (*ii*) a degradation trend at 42 watersheds (16%), with only one of those watersheds (<1%) experiencing a significant decline (Fig. 1B and Table S1). This

Table 1. Functional models relating seasonal rainfall to
vegetation productivity in the Sahel, with reference to earlier
research adopting the different forms

Model	Form	Source
Linear	iNDVI = $a + bi$ R	20–22
Log-linear	iNDVI = a + bln(iR)	37
Quadratic	iNDVI = $a + bi$ R + ci R ²	25–27
Hyperbolic	iNDVI = $a + b/i$ R	44

*i*NDVI denotes the seasonal integrated NDVI and *i*R the seasonal integrated rainfall.

proportion of watersheds experiencing greening or degradation remains approximately the same irrespective of the choice of functional relationship. Hence, although important as a reflection of our process-level understanding, the choice of functional relationship has little qualitative or quantitative impact on detection of landscape-scale trends in greening or degradation. Although we conclude from this analysis that most watersheds in our sample have relatively stable or greening vegetation, we derive little insight into the contributing processes. In the following sections we demonstrate an approach to use long- and short-term RUE trends to diagnose changes in woody and herbaceous vegetation.

Long- and Short-Term Sensitivity of WLE to Rainfall. The interannual variability of *i*NDVI is positively correlated with the interannual variability of rainfall across the Sahelian region (Fig. S2). When considering all annual scale data for all 260 watersheds, *i*NDVI increases with *i*R (Fig. 24), but with substantial variations among watersheds and regions in short-term (i.e., interannual) and long-term (i.e., interdecadal) NDVI sensitivity to rainfall (S_S and S_L , respectively) (Fig. 2*B*).

We interpret $S_{\rm L}$ and $S_{\rm S}$ as follows: $S_{\rm L}$ (long-term mean *i*NDVI/ iR) (dashed lines in Fig. 2B) reflects long-term greenness per unit rainfall. $S_{\rm L}$ is thus an index of the efficiency with which a landscape is able to use rainfall in vegetation production. Although soil and geomorphological characteristics can affect landscape reflectances and the NDVI (and thus also $S_{\rm L}$), we anticipate that S_{L} will be correlated with vegetation density and fractional cover, in particular the density and canopy cover of trees and the extent of the herbaceous sward (i.e., areas of the landscape where herbaceous plants typically grow, as distinct from bare ground areas where herbaceous vegetation cannot quickly establish after rainfall because of soil crusting, erosion, or seed bank limitations). In contrast, S_{S} (the slope of *i*NDVI response to interannual variations in rainfall in color-scale of points in Fig. 2B) is an expression of the more rapid greenness response of a landscape to years that are wetter or drier than the mean. Whereas the establishment and mortality of trees and the denudation/recolonization of bare ground are relatively slow processes (i.e., $S_{\rm L}$), the growth of herbaceous vegetation within the established sward (whether annual or perennial) can typically respond rapidly to wet and dry years (33-35). The magnitude of $S_{\rm S}$ is, therefore, likely to be correlated with extent and density of herbaceous vegetation and it's plasticity to interannual rainfall variability via the bud and seed banks of perennial and annual herbaceous vegetation, respectively.

Distinct regional differences in S_S and S_L are evident (Fig. 2B), with the two western regions (Senegal and western Mali) having higher S_L than the eastern regions (eastern Mali and Niger), indicating generally higher greenness per unit rainfall in the western Sahel relative to the eastern regions. In contrast, the interannual rainfall sensitivity (S_S) is generally higher in Senegal and eastern Mali, relative to western Mali and Niger, reflecting the lower tree cover and higher importance of herbaceous vegetation in the drier northern Sahel, relative to the southern Sahel. Comparing the drier regions (i.e., Senegal and eastern Mali), the patterns in S_L and S_S are consistent with field

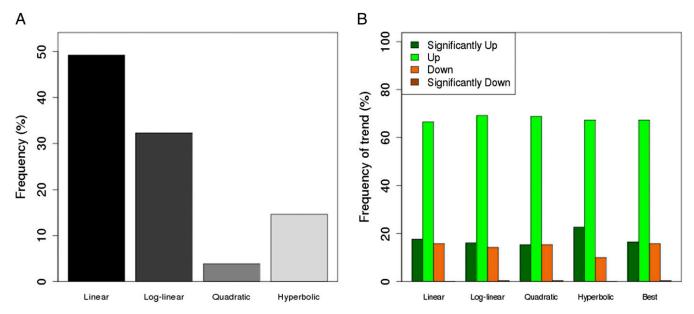


Fig. 1. Sahelian rainfall–NDVI functional relationships and inferred trends in greening or degradation. (*A*) Best-fit functional models for 260 watersheds in Senegal, Mali, and Niger based on the cAIC. (*B*) Trends in vegetation condition through time in the same watersheds assessed using the residual-trend approach (36, 37), where "up" indicates increasing RUE (i.e., improving vegetation) and "down" indicates decreasing RUE (i.e., degradation). Inferences in *B* are reported using the linear and nonlinear functional relationships, as well as using the best models for each watershed shown in *A*. In general, although the majority of watersheds show modest (nonsignificant) improvements, relatively few watersheds show strong upward or downward trends. The choice of functional relationship has little impact on these results.

observations of better vegetation condition in Senegal relative to eastern Mali (22, 41). Similarly, the distinctive geomorphological pattern of plateau and valleys in southwestern Niger results in considerable run-off and bare soil exposure (42). This finding, together with intense anthropological influences in the highly populated area near Niamey, could explain both the low S_L and low S_S of watersheds in the southwestern Niger region.

Diagnosing Change in Vegetation Conditions: A Conceptual Framework.

The increasing duration of the environmental satellite data record makes change detection possible. We use changes in long-term sensitivity (ΔS_L ; i.e., temporal change in S_L) relative to changes in short-term sensitivity (ΔS_S ; i.e., temporal change in S_S) to diagnose trends in vegetation condition between the first (1983–1992) and last decades (2003–2012) of the satellite time-series (Fig. 3). This process provides an opportunity to compare conditions during and immediately after the Sahelian drought with more average rainfall conditions in recent years. The benefit of focusing on change detection within individual watersheds (rather than comparing between watersheds) is that sources of variability in satellite greenness (e.g., soil reflectance properties and geomorphology discussed above) are minimized, allowing more confident inference of watershed-specific change through time.

In the conceptual representation of temporal shifts in $S_{\rm L}$ and $S_{\rm S}$ illustrated in Fig. 3A, the sign of $\Delta S_{\rm L}$ and $\Delta S_{\rm S}$ define four potential quadrants of change in vegetation structure and cover. Positive $\Delta S_{\rm L}$ values are interpreted as suggesting increasing longterm landscape greenness, indicating increasing vegetation cover and, in particular, the presence of more woody plants. Positive $\Delta S_{\rm S}$ values indicate an increase in the ability of the landscape to respond to interannual rainfall variability, which we interpret as relating to the density of herbaceous vegetation. When $\Delta S_{\rm L}$ and $\Delta S_{\rm S}$ have similar sign (-ve or +ve), we infer that changes in both woody and herbaceous communities have similar direction (quadrants A and C). However, when ΔS_L and ΔS_S have different signs, we infer that changes in longer-lived (i.e., woody) and ephemeral (i.e., herbaceous) communities are in opposite directions (quadrants B and D). We guardedly refer to quadrants B and D as "shrub encroachment" (i.e., increasing woody plants,

with decreasing herbaceous vegetation; B) and "herb encroachment" (decreasing woody plants, with increasing herbaceous vegetation; D), recognizing that these are simplified descriptors and without any implied value judgment (because the societal value of changing woody and herbaceous vegetation are highly context-specific).

The patterns of change in $\Delta S_{\rm L}$ and $\Delta S_{\rm S}$ in our sample of Sahelian watersheds (Fig. 3B and Fig. S3) strengthen the conclusion from Fig. 1 and Table S1 that many Sahelian watersheds experienced a recovery in vegetation condition in the first decade of this century relative to the drought years of the 1980s. However, the most marked increases in RUE are concentrated in the eastern Mali study area and, to a lesser degree, in Senegal. Relatively few significant changes are observed in the Niger and western Mali regions (Fig. 3B). Overall, 78 watersheds (30%) show significant increases in long-term mean RUE (ΔS_{I}). These changes are most likely associated with the recovery of perennial vegetation between the 1983-1992 and 2003-2012 intervals, particularly in the eastern Mali study area. Given that there is no clear long-term change in herbaceous biomass [significant changes in S_S are observed only at 11 (4%) watersheds], these findings indicate that trees and shrubs are the dominant source of the improvement in vegetation condition in the Sahel between the 1980s and the 2000s. This finding is consistent with analysis of independent data from northern Senegal (Fig. S4).

Discussion

Our results show that remotely sensed vegetation greenness (i.e., NDVI) has increased across the Sahel since the droughts of the 1970s and 1980s, consistent with increasing rainfall and earlier analyses (22, 36, 41, 43). In this analysis, we are interested in the extent to which greater (or less) than expected productivity responses to rainfall (i.e., changes in S_L and S_S) have occurred and can be used to diagnose improvements in (or degradation of) vegetation condition: where vegetation condition is a function of tree and grass demographics and soil processes that jointly constrain the ability of a landscape to respond to rainfall.

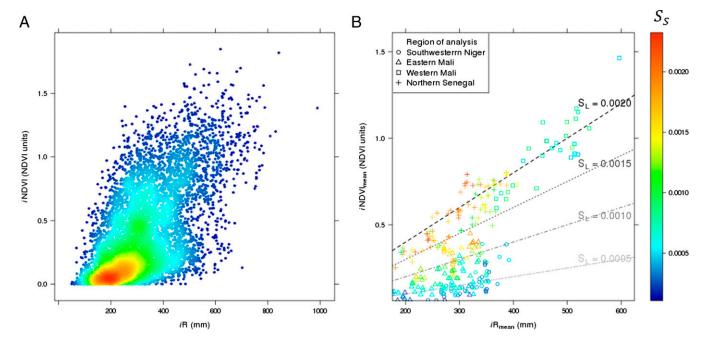


Fig. 2. Relationships between the seasonal (June–October) integrated NDVI (*i*NDVI) and the seasonal sum of rainfall (*i*R) in 260 watersheds of the Sahel for the period 1983–2012. (*A*) *i*NDVI plotted against *i*R for each watershed and each year of the study period. The density of the points varies from low (blue) to high (red). (*B*) Long-term mean *i*NDVI (*i*NDVI_{mean}) versus long-term mean *i*R (*i*R_{mean}) of all watersheds. Symbols show the four Sahelian regions, dashes show lines of equal long term sensitivity (S_L in NDVI units/mm; *i*NDVI_{mean}/*i*R_{mean}) and colors show the short-term sensitivity (S_S in NDVI units/mm; i.e., the slopes between *i*NDVI and *i*R within each watershed).

Trends in NDVI-Rainfall Relationships. The single best functional relationship in these watersheds between rainfall and integrated NDVI (our NPP proxy) is the linear model (128 or 49% of watersheds) (Fig. 1A). Examination of the log-linear, quadratic, and hyperbolic models selected for the other 132 (51%) watersheds suggests that almost all (130) exhibit a curvilinear increase and saturation of productivity with rainfall, consistent with previous studies (e.g., refs. 27 and 44). Our results run counter to the research of Hein et al. (27), who concluded that the cubic (thirdorder polynomial with four parameters) is better than the quadratic (three parameters), which in turn was better than the linear model (two parameters). However, Hein et al. (27), based their model selection simply on maximization of adjusted r^2 , without taking into account model complexity, which may have biased model selection (45). From a theoretical perspective, we might anticipate an s-shaped (e.g., logistic) functional form because, below a certain amount of rainfall, evaporative losses may reduce plant growth and thus reduce initial NPP increase with rainfall, whereas light or nutrient limitation may cause saturation at higher rainfall (25, 27). In practice, despite its theoretical support, the logistic model was never selected over the simpler models, presumably because of limited rainfall range and number of observations.

The trend-in-residuals analysis suggested that the majority (83%) of watersheds showed no significant trends through time, thus implying that increases in NDVI were proportional to increases in rainfall (Table S1). However, the great majority of those watersheds (67%) had small positive trends, suggesting modest improvements in vegetation conditions not yet emerging statistically from the measurement uncertainty. Approximately 17% of watersheds showed significant increases in RUE, whereas less than 1% showed significant declines. The primary conclusion of this component of our research is that the functional form (linear, asymptotic, and so forth) of the rainfall–NPP relationship had no impact on the conclusions of a trend-in-residuals analysis across Sahelian watersheds (Fig. 1*B*).

Trend Assessments Using Changes in Decadal and Interannual Rainfall Sensitivity (S_1 and S_5). The existence and nature of Sahelian regreening following the 1980s drought has been greatly debated, with considerable polarization between camps arguing the desertification and recovery narratives (20-22, 25-29). A few studies have examined the specific role of long-term changes in woody and herbaceous components (e.g., refs. 28, 29, 41, 46, and 47) but their numbers are low because of the limited number of long-term vegetation surveys in the Sahel. Although the meaning of changing rainfall sensitivity shown in Fig. 3A may be debated (48-50), we argue that changes in short- and long-term rainfall sensitivity may allow broad inference of trends in long-lived (woody) and ephemeral (herbaceous) vegetation. We recognize that interannual rainfall variability and seasonality may also be changing through time, and that such changes may independently impact the NDVI-rainfall relationships. These effects are, however, likely smaller in magnitude than the first-order effects of annual rainfall totals on long-term rain-use efficiency and sensitivity related to woody and herbaceous demographic loss and recovery.

Our results indicate that the greening phenomenon observed in the more northerly Sahelian regions of eastern Mali and Senegal may be mainly the result of tree population recovery, as found in the recent study of Brandt et al. (41) in Senegal and Dardel et al. (22) in eastern Mali. This is particularly marked in the eastern Mali region, where most watersheds show strong (significant) increases in S_L and, to a somewhat lesser degree, in the watersheds of Senegal. The western Mali and Niger study regions show less clear long-term recovery (increases in $S_{\rm L}$ and $S_{\rm S}$) postdrought. In the Niger study area, postdrought recovery of vegetation may be prevented by intense human utilization in the areas near the capital city, Niamey. In contrast, in western Mali (the wettest of our four study regions) drought-related declines may have been less severe than in the more northerly Sahel, thus recovery postdrought is less marked. That is, vegetation recovery (i.e., increasing RUE) implies and requires an earlier degradation event. Only a very small fraction of watersheds, two in western Mali and two in Niger, show significant long-term declines

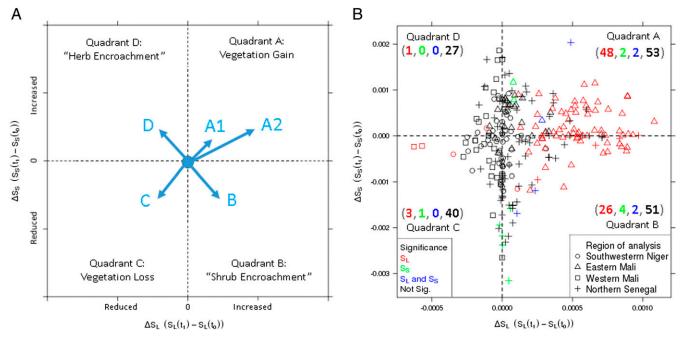


Fig. 3. Long-term trends in the state (vegetation structure and cover) of watersheds. (*A*) Conceptual representation of temporal shifts in the state of a watershed. The direction of change reflects changes in long-term rainfall response (ΔS_L ; i.e., temporal change in S_L of Fig. 2*B*) and changes in interannual sensitivity (ΔS_S) in four quadrants. When ΔS_L and ΔS_S have similar signs we infer similar changes in both woody and herbaceous communities (quadrants A and C). However, when ΔS_L and ΔS_S have different signs we infer that changes in longer-lived (i.e., woody) and ephemeral (i.e., herbaceous) communities are in opposite directions (quadrants B and D). The magnitude of the vector indicates the magnitude of the changes through time. For example, A1 and A2 indicate movements in the same direction (vegetation gain) but with different magnitude. (*B*) Vegetation structure and cover changes in watersheds of the schede the tirts (1983–1992) and last (2003–2012) decade of the study period. Symbols show the four Sahelian regions, colors show the significance of the change in S_L or S_S , and numbers indicate the count of significant watersheds of each quadrant.

in decadal-scale RUE (S_L). These watersheds may merit a more detailed analysis of the nature and causes of their recent trends.

Relatively few watersheds show significant changes in shortterm rainfall sensitivity (S_S), with approximately equal numbers of watersheds showing positive and negative ΔS_S (both significant and nonsignificant). Only four watersheds show significant trends in both S_L and S_S . Thus, overall we conclude that there are no consistent temporal trends in herbaceous RUE across the Sahel, contrary to the study by Dardel et al. (22), who found increases in herbaceous biomass in eastern Mali and decreases in Niger.

Although our results point to the important role of postdrought tree population recovery and, in some areas, active tree planting in the regreening of the Sahel, such changes in tree cover may be associated with changes in tree species diversity not detected in our remote sensing data (28, 29, 51, 52). Higher primary production is not necessarily associated with a higher biodiversity and the decline in populations of economically and culturally important trees and shrubs—despite the increase in woody cover—may explain the negative perception of vegetation condition among some local populations (51, 52).

Although anthropogenic pressures undoubtedly contribute to and maintain degradation at local scales in the Sahel (e.g., local to population centers), our results suggest that vegetation condition—at the watershed scale in the majority of our samples in Senegal, Mali, and Niger—is stable or improving since the droughts of the 1970s and 1980s. The drier, more northerly, Sahelian watersheds in Senegal and eastern Mali appear to have stronger reforestation trends than the more mesic region of western Mali and the high human population area near Niamey, Niger.

Materials and Methods

Hydroclimatic Data. A total of 260 endhoreic (i.e., internally draining) watersheds were sampled from four regions of analysis shown in Fig. S1, representing between 12% and 35% of the total number of watersheds in each region, with watershed sizes ranging from 0.1 to 2,920 km². The selected

regions include areas of semidesert [Sahelian 200 \leq mean annual rainfall (MAR) < 400 mm], dry savanna (Soudano-Sahelian: 400 \leq MAR < 600 mm), and dry subhumid savanna (Soudanien 600 \leq MAR < 900 mm). ASTER 30 \times 30-m digital elevation model (DEM) v2 (53) was used to delineate watershed boundaries, with flow pathways toward identified water bodies (89% being pehemeral; 11% being perennial). The watersheds were delineated using the Hydrology toolbox available in ARCGIS software program (54).

African Rainfall Climatology v2 (ARC2) data at $0.1^{\circ} \times 1^{\circ}$ grid size and 1-d sampling frequency for the 1983-2012 period (38) were used in this study. Daily rainfall from June to October were summed to produce the annual integral of rainfall (iR). Monthly composite MODIS NDVI data (Collection 5) at a spatial resolution of 5.6 km for the 2000-2012 period (39) and monthly composite AVHRR GIMMS NDVI data at a spatial resolution of 8 km for 1983–1999 (40) were combined for this analysis. The AVHRR time series was adjusted to be consistent with the MODIS data using a simple linear adjustment calculated during their period of overlap (i.e., 2000-2006). The 15-d AVHRR-NDVI composites were aggregated to monthly scale using a maximum value composite approach and spatially resampled using the nearest-neighbor approach to match the pixel resolution of the MODIS data. Monthly NDVI values acquired between June and October and greater than zero were summed to produce seasonal integrals of NDVI (iNDVI) used as proxy of NPP. Because NDVI does not necessarily reach zero during the dry season because of the effects of reflectance properties of soils and dead vegetation, the NDVI of the dry season-computed as average dry-season NDVI between January and May-was subtracted from each monthly NDVI of the growing season when calculating the seasonal integral *i*NDVI.

Analytical Methods. For each watershed, the seasonal integrals of rainfall (*i*R) and (*i*NDVI) during the growing season obtained at 5.6-km resolution (see *Hydroclimatic Data*) were extracted and averaged for the watershed. In response to earlier controversy (20, 21, 25–27), we first examine the shape of the rainfall–productivity relationship in the Sahel with four curve-forms commonly used in ecological growth analyses (Table 1). The goodness of fit of *i*NDVI against *i*R was assessed using the corrected cAIC for small sample sizes (45). Trend analysis of the residuals (i.e., the difference between the observed and predicted *i*NDVI), also known as the trends in residual approach (ResTrend

approach) (36, 37), was used to assess the nonclimatic drivers of trends in vegetation condition through time. The nonparametric Kendall test (55) was used to detect any consistent temporal trends at the 5% significance level.

For every watershed, the "long-term rainfall sensitivity" (S_L), defined as the ratio of the mean *i*NDVI (*i*NDVI_{mean}) by mean *i*R (*i*R_{mean}), and the "shortterm rainfall sensitivity" (S_S), or interannual sensitivity, defined as the slope of the regression of *i*NDVI against *i*R, were computed to investigate the ecosystem sensitivity to rainfall variability. Long-term changes (decadalscale) in these indices (statistically quantified using a *t* test for differences between means in S_L values and an ANCOVA for differences in S_S slopes,

- 1. Le Houérou HN (1980) The rangelands of the Sahel. J Range Manage 33(1):41-46.
- Bégué A, Vintrou E, Ruelland D, Claden M, Dessay N (2011) Can a 25-year trend in Soudano-Sahelian vegetation dynamics be interpreted in terms of land use change? A remote sensing approach. *Glob Environ Change* 21(2):413–420.
- Pedersen J, Benjaminsen TA (2008) One leg or two? Food security and pastoralism in the Northern Sahel. *Hum Ecol* 36(1):43–57.
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408(6809):184–187.
- Running SW (2008) Climate change. Ecosystem disturbance, carbon, and climate. Science 321(5889):652–653.
- Weltzin JK, et al. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53(10):941–952.
- Knapp AK, et al. (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience* 58(9):811–821.
- Stebbing JE (1935) The encroaching Sahara: The treat to the West African Colonies. Geogr J 85(6):506–519.
- 9. Harding G (1968) The tragedy of the commons. Science 162(3859):1243-1248.
- Charney JG (1975) Dynamics of deserts and drought in the Sahel. Q J R Meteorol Soc 101(428):193–202.
- UNCOD (1977) Desertification, Its Causes and Consequences, Compiled and Edited by the Secretariat of the U.N. Conference on Desertification (Pergamon Press, Oxford).
- 12. Synclair ARE, Fryxell JM (1985) The Sahel of Africa: Ecology of a disaster. Can J Zool 63(5):987–994.
- Thomas DSG, Middleton NJ (1994) Desertification: Exploding the Myth (John Wiley, Chichester, UK).
- Leach M, Mearns N (1996) Environmental change and policy. The Lie of the Land: Challenging Received Wisdom on the African Environment, eds Leach M, Mearns R (The International African Institute, Oxford), pp 1–33.
- Swift J (1996) Desertification: Narratives, winners and losers. The Lie of the Land: Challenging Received Wisdom on the African Environment, eds Leach M, Mearns R (The International African Institute, Oxford), pp 73–90.
- Ostrom E (1990) Governing the Commons: The Evolution of Institutions for Collective Action (Cambridge Univ Press, New York), p 280.
- 17. Nicholson SE (1993) An overview of African rainfall fluctuations of the last decade. J Clim 6(7):1463–1466.
- Tucker CJ, Nicholson SE (1999) Variations in the size of the Sahara Desert from 1980 to 1997. Ambio 28(7):587–591.
- Reynolds JF, Stafford Smith DM (2002) Do humans cause deserts? *Global Desertification:* Do Humans Cause Deserts, eds Reynolds JF, Stafford Smith DM (Dahlem Univ Press, Berlin), pp 1–21.
- Prince SD, Brown de Colstoun E, Kravitz LL (1998) Evidence from rain-use efficiency does not indicate extensive Sahelian desertification. Glob Change Biol 4(4):359–374.
- 21. Prince SD, Wessels KJ, Tucker CJ, Nicholson SE (2007) Desertification in the Sahel: A reinterpretation of a reinterpretation. *Glob Change Biol* 13(7):1308–1313.
- Dardel C, et al. (2014) Re-greening Sahel: 30 years of remote sensing data and field observations (Mali, Niger). *Remote Sens Environ* 140:350–364.
- Reij C, Tappan GG, Smale M (2009) Agroenvironmental transformation in the Sahel— Another kind of "Green Revolution." IFPRI Discussion Paper, No. 914, 52 pp. Available at ebrary.ifpri.org/cdm/ref/collection/p15738coll2/id/15847. Accessed August 27, 2015.
- Haglund E, Ndjeunga J, Snook L, Pasternak D (2011) Dry land tree management for improved household livelihoods: Farmer managed natural regeneration in Niger. *J Environ Manage* 92(7):1696–1705.
- Hein L, de Ridder N (2006) Desertification in the Sahel: A reinterpretation. Glob Change Biol 12(5):751–758.
- Miehe S, Kluge J, Von Wehrden H, Retzer V (2010) Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. J Appl Ecol 47(3):692–700.
- 27. Hein L, et al. (2011) Desertification in the Sahel: Towards accounting for ecosystem dynamics in the interpretation of remote images. J Arid Environ 75(11):1164–1172.
- 28. Gonzalez P, Tucker CJ, Sy H (2012) Tree density and species decline in the African Sahel attributable to climate. *J Arid Environ* 78:55–64.
- Hermann SM, Tappan GG (2013) Vegetation impoverishment despite greening: A case study from central Senegal. J Arid Environ 90:55–66.

both at a 5% significance level) were used to infer trends in greening/degradation of the watersheds and to assess the potential role of woody and herbaceous vegetation in those temporal trends. All statistical analyses were performed within the R environment (56).

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- Brown L (2006) The Earth Is Shrinking: Advancing Deserts and Rising Seas Squeezing Civilization (Earth Policy Institute, Washington, DC). Available at www.earth-policy.org/ plan_b_updates/2006/Update61. Accessed August 27, 2015.
- Shoumatoff A (2006) Forecast: Dry and brutal. OnEarth Magazine Winter 2006:28–37.
 UNEP (2012) Sahel Atlas of Changing Landscapes: Tracing Trends and Variations in
- OVEP (2012) Same Atlas of Changing Landscapes: Tracing Tends and Variations in Vegetation Cover and Soil Condition (United Nations Environment Programme, Nairobi), 104 pp.
- Sala OE, Parton WJ, Joyce LA, Lauernroth WK (1988) Primary production of the Central grassland region of the United States. *Ecology* 69(1):40–45.
- Huxman TE, et al. (2004) Convergence across biomes to a common rain-use efficiency. Nature 429(6992):651–654.
- Ponce Campos GE, et al. (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494(7437):349–352.
- Hermann SM, Anyamba A, Tucker CJ (2005) Recent trends in vegetation dynamics in the African Sahel and their relationship to climate. *Glob Environ Change* 15(4): 394–404.
- Wessels KJ, van den Bergh F, Scholes RJ (2012) Limits to detectability of land degradation by trend analysis of vegetation index data. *Remote Sens Environ* 125:10–22.
- Novella NS, Thiaw WM (2013) African Rainfall Climatology Version 2 for early warning systems. J Appl Meteorol Climatol 52(3):588–606.
- Huete A, et al. (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens Environ* 83(1-2):195–213.
- Tucker CJ, et al. (2005) An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. Int J Remote Sens 26(20):4485–4498.
- Brandt M, et al. (2015) Ground- and satellite-based evidence of the biophysical mechanisms behind the greening Sahel. Glob Change Biol 21(4):1610–1620.
- Leblanc MJ, et al. (2008) Land clearance and hydrological change in the Sahel: SW Niger. Global Planet Change 61(3-4):135–150.
- Nicholson S (2005) On the question of the "recovery" of the rains in the West African Sahel. J Arid Environ 63(3):615–641.
- Hsu JS, Powell J, Adler PB (2012) Sensitivity of mean annual primary production to precipitation. Glob Change Biol 18(7):2246–2255.
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19(2):101–108.
- Hiernaux P, et al. (2009) Woody plant population dynamics in response to climate changes from 1984 to 2006 in the Sahel (Gourma, Mali). J Hydrol (Amst) 375(1-2): 103–113.
- Hiernaux P, et al. (2009) Sahelian rangeland response to changes in rainfall over two decades in the Gourma region, Mali. J Hydrol (Amst) 375(1-2):114–127.
- Caylor KK, Dowty PR, Shugart HH, Ringrose S (2004) Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa. *Glob Change Biol* 10(3):374–382.
- Huxman TE, et al. (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141(2):254–268.
- Emmerich WE (2007) Ecosystem water use efficiency in a semiarid shrubland and grassland community. Rangeland Ecol Manag 60(5):464–470.
- Brandt M, Romankiewicz C, Spiekermann R, Samini C (2014) Environmental changes in time series—An interdisciplinary study in the Sahel of Mali and Senegal. J Arid Environ 105:52–63.
- Hermann SM, Sall I, Sy O (2014) People and pixels in the Sahel: A study linking coarseresolution remote sensing observations to land users' perception of their changing environment in Senegal. *Ecol Soc* 19(3):29.
- Abrams M, Bailey B, Tsu H, Hato M (2010) The ASTER global DEM. Photogramm Eng Remote Sensing 76:344–348.
- ESRI (2011) ArcGIS Desktop: Release 10 (Environmental Systems Research Institute, Redlands, CA).
- 55. Kendall MG (1975) Rank Correlation Methods (Oxford Univ Press, New York).
- R Development Core Team (2011) R: A Language and Environment for Statistical Computing. (R Foundation for Statistical Computing, Vienna, Austria). Available at www.R-project.org/. Accessed December 15, 2014.