

# Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal

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## Summary

1. Sustainable management of rangelands will become increasingly important as the climate changes, yet rangeland dynamics are still a challenge to dryland ecologists because degradation patterns are difficult to sample and interpret. There are contradictions between remote sensing-based studies and field-based analyses, for which long-term data are almost non-existent. In the rangelands of North Senegal, remote sensing studies have not revealed any extensive degradation during the past three decades. The present study used a 27-year series of field data from the area to assess the impact of grazing on rangeland degradability.

2. Rainfall, standing crop and floristic data from North Senegal were analysed to quantify the effects of rainfall patterns and grazing on plant composition and the overall rain use efficiency. Monitoring plots of 1 ha comprised five ungrazed and 19 grazed plots with two different grazing treatments. Standing crop was sampled annually at the peak of biomass development. Data were analysed with mixed effect models.

3. Changes in herbaceous production were mainly caused by fluctuations in rainfall, whereas the grazing intensity had a long-term effect, interacting with precipitation dynamics. During the first and drier phase, the rainfall variability masked the grazing influence, whereas during the second phase with above-average rainfall, grazing treatments differed significantly, indicating rangeland degradation.

4. The patterns of productivity and floristic composition followed predominant non-equilibrium dynamics during the first phase (rainfall variability 40%), whereas gradual changes especially in species composition represented characteristics of equilibrium systems during the second phase (rainfall variability 23%). Thus, the study supports the existence of shifts between periods of non-equilibrium conditions and those more typical of equilibrium systems.

5. *Synthesis and applications.* Our 27 years field study, carried out with the aim of assessing the non-degradability of Sahelian rangelands, revealed long-term degradation trends linked to grazing intensity. Longer observation periods provide an increasing probability of including 'equilibrium phases' that allow the identification of long-term degradation processes. Consequently, both rangeland research and management policies demand monitoring periods that are long enough to account for long-term trends. The grazing experiment in this study has shown that degradation processes are reversible, but long-term enclosure and ranching with fixed stocking rates are less suitable for rangeland amelioration than moderate, production-adjusted grazing regimes mimicking traditional nomadic systems.

**Key-words:** degradation assessment, grazing enclosure, non-equilibrium debate, NPP, pastoralism, rain use efficiency, species composition

## Introduction

Assessing degradation in arid lands with stochastic rainfall regimes is widely recognized as a challenge (Verón, Paruelo

& Oesterheld 2006), as the distinction between climate-driven and human-induced vegetation dynamics is difficult (Prince, De Colstoun & Kravitz 1998; Herrmann, Anyamba & Tucker 2005; Wessels *et al.* 2007). In the African Sahel, indicators of aridification and pasture degradation through overgrazing are broadly equivalent, i.e. reduction of plant cover

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and production of biomass, an increasing dominance of annual species (Penning De Vries & Djiteye 1982; Coughenour 1985; Skarpe 1992). Widespread degradation was reported during the great Sahel droughts in the 1970s and the beginning of the 1980s (e.g. Sinclair & Fryxell 1985; Le Houerou 1989). Rainfall, and thus productivity, increased in the second half of the 1980s. This coincided with the development of the non-equilibrium concept of range ecology, which states that drylands cannot degrade under variable conditions because grazing resources, mainly determined by the rainfall conditions, control the number of herbivores (Wiens 1984; Ellis & Swift 1988; Westoby, Walker & Noy-Meir 1989; Behnke, Scoones & Kerven 1993). This theory, however, remained controversial (e.g. Briske, Fuhlendorf & Smeins 2003; Vetter 2005):

Most recent studies of the production dynamics in the Sahel are large-scale assessments based on satellite data (e.g. Prince *et al.* 1998, 2007; Anayamba & Tucker 2005; Herrmann *et al.* 2005; Olsson, Eklundh & Ardo 2005), which have revealed a 'greening' trend. Hickler *et al.* (2005) showed that precipitation was the primary driver of production dynamics between 1982 and 1998, as did Retzer (2006). Nicholson, Tucker & Ba (1998) and Prince *et al.* (1998) did not find any significant decrease in rain use efficiency (RUE) between 1982 and 1990/1994, thus no indication of Sahel-wide degradation was revealed by remote sensing data. Seaquist *et al.* (2009) reported a positive correlation between a process-based production model and satellite-derived greenness with grazing intensity (using census data), and concluded that pastoralism does not affect vegetation dynamics at the Sahel-wide level. Whereas all these regional studies support the non-equilibrium theory, several field studies report grazing-induced rangeland degradation in the Sahel (e.g. Penning De Vries & Djiteye 1982; Hiernaux & Turner 1996; Hiernaux 1998; Turner 1999; Hérault & Hiernaux 2004). However, these studies only cover periods of a few years; hence, the degradation phenomena may be regarded as a short-term effect of climatic fluctuations.

This study evaluated a data set spanning 27 years of vegetation monitoring from the central Sahel. The moni-

toring period (1981–2007) included two major droughts and the recent 15 years of relatively stable climatic conditions, so grazing effects could be tracked under medium-term climatic oscillations. Contrary to previous rangeland monitoring undertaken in northern Senegal (e.g. Hanan *et al.* 1991; Diouf & Lambin 2001), this study compared different variants in grazing intensity, including grazing enclosures, to allow climatic and grazing-induced effects to be separated.

The aim of the study was to check the long-term non-degradability of a Sahelian rangeland. The main hypotheses tested were:

- (1) The precipitation regime governs the dynamics of the herbaceous vegetation, and the grazing intensity only modifies it;
- (2) Degradation is a short-term phenomenon of drought periods.

The hypotheses were tested by evaluating herbaceous biomass and species composition field data. RUE (see Le Houerou 1984), defined as the quotient between annual production and precipitation, was used as a measure of productivity. The results are discussed in the context of the non-equilibrium debate, and recommendations for research and management are given.

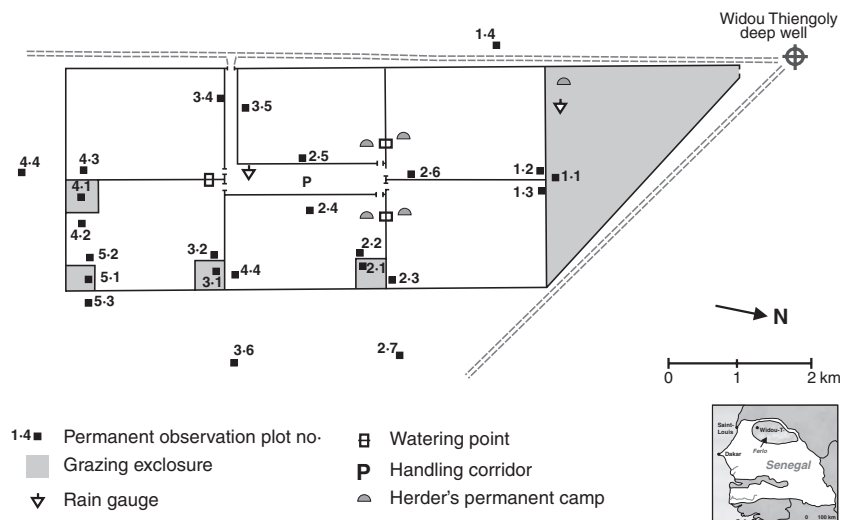
## Materials and methods

### LOCATION, ENVIRONMENT AND CLIMATIC DYNAMICS OF THE STUDY AREA

The study area is located in the central part of the sandy Ferlo region in northern Senegal, south of the deep well Widou Thiengoly (15°59'N, 15°19'W; Fig. 1; for details and bibliography on the Ferlo environment see Le Houerou 1989). Average precipitation is 296 mm year<sup>-1</sup>, with rainfall being widely restricted to the summer months (mainly July to September). The long-term variability of rainfall is 28% (Table S1, Supporting information).

The vegetation consists of tree and shrub savannas with the woody strata, restricted by the topography, covering on average <5% of the ground. The herbaceous layer consists almost exclusively of annuals, and is usually dominated by grasses (species list: Table S2,

**Fig. 1.** Location of the study area and sketch of the experimental setting in Widou Thiengoly. The 'controlled grazing' experiment took place on six fenced paddocks. The grey framed areas in the corners of the paddocks and the triangle between the tracks are grazing enclosures ('no grazing'). The fenced area is surrounded by the communal pasture ('free grazing'). The black squares symbolize the permanent observation plots of 1 ha.



Supporting information). The frequency of forbs shows strong inter-annual and spatial fluctuations.

#### LAND USE

Prior to the installation of a network of deep wells in the 1950s, the study area was used as a wet-season pasture with cattle, sheep and goats managed by nomadic herders. The installation of a permanent water supply led to a fivefold increase in livestock numbers, with 87% of cattle becoming more or less sedentary (Le Houerou 1989). The great Sahel drought in the 1970s led to the involvement of external agencies and encouragement to adopt pastoral systems with lower stocking rates more suited to the environment.

#### EXPERIMENTAL DESIGN

In 1981, a grazing trial was set up in Widou Thiengoly by a Senegalo-German cooperation. The experiment was undertaken on six fenced paddocks each of 200 ha (Fig. 1). Each paddock had its own watering point, herders' camp and a mixed herd of cattle, sheep and goats (ratio 1:1:0.5). Stocking densities were kept constant between 0.10 and 0.12 Tropical Livestock Unit (TLU) per ha ('controlled grazing'). This area could not maintain the herds during the most severe drought years, making migration or supplementary feeding necessary. Therefore, constant stocking rates were abandoned from the 1990–1992 drought onwards, leaving management decisions to each herder. Consequently, the herd size was approximately doubled, utilizing communal pasture during the rainy season and the paddocks in the dry season. Animal numbers on the communal pasture ('free grazing') were only estimated (Table S3, Supporting information), with stocking densities varying around 0.2 TLU ha<sup>-1</sup> (Ancy *et al.* 2008).

The vegetation was monitored on 14 permanent plots of 1 ha scattered among the paddocks ('controlled grazing', Fig. 1). For comparison, the surrounding communal pasture was recorded on five plots ('free grazing'). Within the paddock area, five plots were fenced off as non-grazed control plots. The position of the grazed plots was deliberately chosen in order to resemble the topography of the 'no grazing' areas. A gradient of increasing productivity with increasing distance from the deep well, as reported by Turner (1999), could not be detected in the present study.

Preliminary results from the grazing trial were documented in unpublished project reports (see Appendix S1, Supporting information). Results focusing on pastoralism were published by Thébaud, Grell & Miede (1995), André (2001), Hein (2006) and Hein & De Ridder (2006), the latter two using only a subsample of the data set.

#### DATA COLLECTION AND ANALYSIS

Daily rainfall was measured in two rain gauges (Fig. 1). The standing crop of the herb layer, serving as a measure for the net primary production (NPP), was harvested annually at the time of maximum vegetation development at the end of the growing season. Plants were clipped close to the soil surface on 25 subplots of 1 m<sup>2</sup>, which were systematically distributed across each of the 24 1-ha observation plots (in total 600 subplots). Repeated clipping on the same spot was avoided by rotating around the reference point in the sample grid from 1 year to the next, in order to reduce disturbance effects. The clipped plants from all subplots were air-dried and weighed. To account for the residual water content we oven-dried the biomass of three subplots randomly chosen from the 25 subplots per hectare; the mean value was extrapolated to obtain the dry matter biomass of each hectare-plot. The composition of the herb layer was assessed annually

from 1992 to 2007 (except 1994 and 1996), using the line transect method according to Daget & Poissonnet (1971). A metal pin was placed vertically on the ground at 100 collection points along the SE–NW diagonal of each 1-ha plot. Every species touching the metal pin was counted once at each point. The number of individuals of each species across all 100 collection points was taken as a measure of the absolute frequency of the species.

Effective rainfall was calculated after Boudet (1981) as follows: (i) From total daily rainfall, half of the potential evapotranspiration (PET) was subtracted. Values for PET/2 in the Sahel (mm): June (3.5), July and October (3.0), August (2.5), September (2.2). (ii) In cases where the daily rainfall exceeded the fivefold PET, the respective amount was subtracted from the sum. (iii) If there was no effective rainfall in a period of at least 3 weeks, all precipitation accumulated during the whole rainy season before that date was ignored. The mean values from both rainfall stations were used in the statistical analyses (see Table S1 and Fig. S1, Supporting information, for details). The possible effects of topography on the standing crop were non-significant within a mixed effects model, and were therefore not considered in this study. Temporal trends were analysed by linear regression models. Initial analyses of the biomass based on a regression tree suggested a division of the study period into two parts (1981–1995/1996–2007). We used a linear mixed model to test the differences in effective RUE between these two phases, where the treatments were implemented as a random factor, and temporal autocorrelation was reduced by using the years as a random intercept. A *post-hoc* test (Tukey) was used to test the difference between the three grazing treatments. All statistical analyses were calculated with the R-software platform (R Development Core Team 2008).

## Results

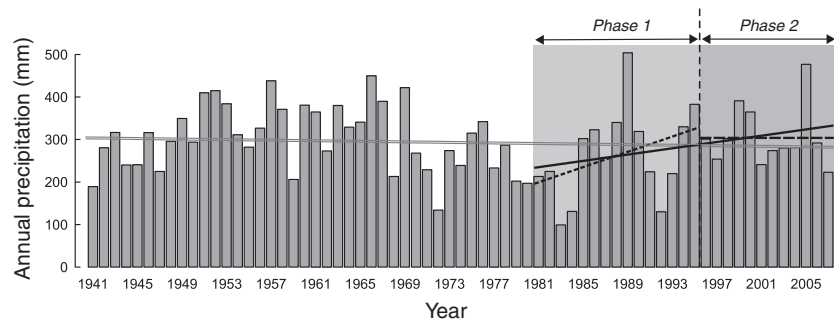
#### PRECIPITATION DYNAMICS

The trends in annual and effective precipitation between 1981 and 2007 are non-significant, but the two phases differed significantly based on the linear mixed model ( $P < 0.001$ ), especially in rainfall variability (phase 1: 40.1%; phase 2: 23.3%; Fig. 2; Table S1 and S4, Supporting information). Two severe droughts occurred during the first phase, followed by a period of higher rainfall. The second phase (1996–2007) included some years with unusual rainfall patterns (intra-annual droughts) and showed a weaker relationship between effective and total precipitation (Fig. S1, Supporting information), as well as between the number of rainfall days and the accumulated precipitation of the rainy season (Fig. S2, Supporting information).

#### THE RELATIONSHIP BETWEEN STANDING CROP AND PRECIPITATION

This is best explained by nonlinear functions (Fig. 3). The first phase of the study period showed a saturation of the production curve at higher rainfall, whereas the second phase showed a reversed unimodal relationship. The communal pasture ('free grazing') generally showed the strongest relationship between standing crop and precipitation, especially in the first phase.

**Fig. 2.** Long-term pattern of annual rainfall totals for Widou Thiengoly (after Akpo, Grouzis & Gaston 1993 and records of the present project from 1981 onwards; rain gauge stations see Fig. 1). Neither the long-term trend (grey line), nor those of the entire study period (black line) and its two phases (hatched lines) are significant, which is partly due to the high inter-annual variability (Table S1, Supporting information).



#### DYNAMICS IN RAIN USE EFFICIENCY

Rain use efficiency differed significantly between the grazing treatments in relation to the two phases (1981–1995/1996–2007) ( $P < 0.001$ ; Fig. 4). There was an overall slight but significant, decrease in the RUE (1981–2007) in the ‘controlled grazing’ treatment ( $R^2 = 0.06$ ;  $P < 0.001$ ), a hardly significant decrease ( $R^2 = 0.02$ ;  $P = 0.057$ ) under ‘free grazing’, but no trend under ‘no grazing’. The RUE of both grazed treatments was significantly lower than that of the ‘no grazing’ treatment, which is due to the differences during the second phase ( $P < 0.001$ ). The differences between the two grazed treatments are non-significant. Treatments alone were non-significant in the linear mixed model; however, in interaction with phase they became highly significant ( $P < 0.001$ ). All other interactions were non-significant and therefore not included in the linear mixed model.

#### DYNAMICS IN SPECIES COMPOSITION

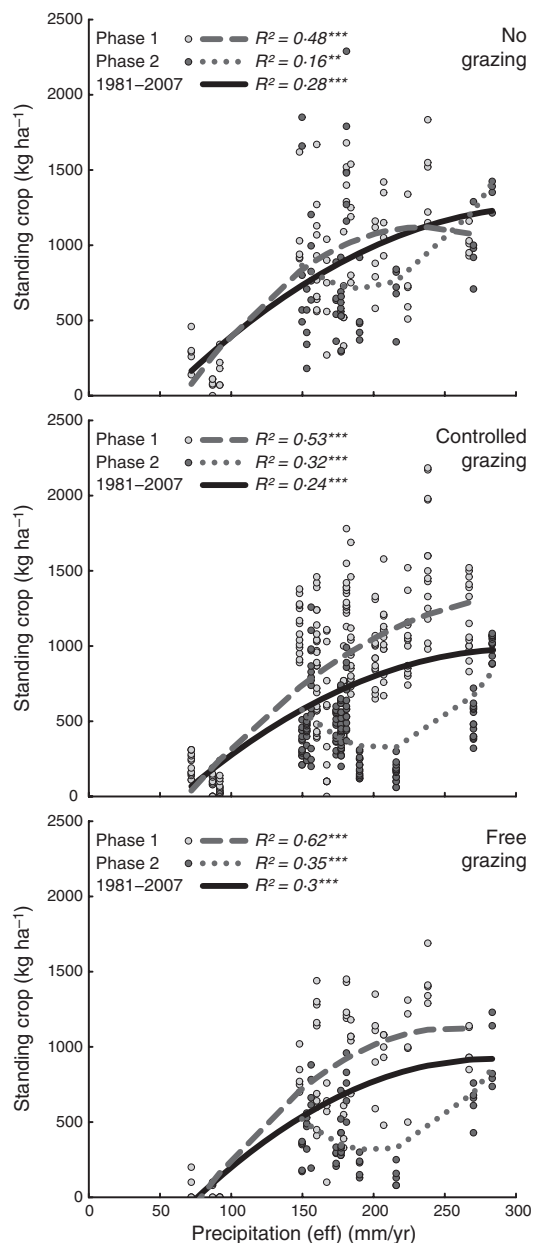
After 10 years of the grazing experiment, the herbaceous plant composition of the ungrazed plots started to deviate markedly from those of the grazed treatments, and an almost complete separation along DCA 1 was apparent after 1997 (Fig. S3, Supporting information). Figure 5 shows that on enclosure plots (‘no grazing’) there was a significant increase in the magnitude of non-graminoid herbs and high-quality forage species since 1992 (end of the last drought). In contrast, there was a significant augmentation in the frequency of aridity-indicating species, of grasses in general, and of low-quality fodder species in the grazed treatments. *Aristida mutabilis* Trin. & Rupr. dominated all three species groups, with significantly increasing frequencies since 1992 ( $R^2 = 0.71$ – $0.83$ ,  $P < 0.001$ ).

## Discussion

#### HYPOTHESIS 1: THE PRECIPITATION REGIME GOVERNS THE DYNAMICS OF THE HERBACEOUS VEGETATION, AND THE GRAZING INTENSITY ONLY MODIFIES IT

The grazing intensity had a significant influence on RUE, yet only in interaction with the second phase of the monitoring period. During the first phase the high variability in rainfall largely masked other influences on productivity, lending support

to hypothesis 1. Nonetheless, grazing had a modifying (but not significant) effect on the short-term vegetation dynamics: During the first drought the minimum RUE values (in 1984) were lowest under the strongest grazing pressure and highest on the enclosure plots. Based on this, Hein (2006) concluded that strong grazing pressure enhances degradation in dry years, which confirms findings from other regions (Penning De Vries & Djiteye 1982; Le Houerou 1989; Illius & O’Connor 1999). On the other hand, all treatments showed pronounced peaks in RUE in the years following a drought, with highest values on the communal pasture in the first year (1985, 1993, Fig. 4). This contradicts the hypothesis that lag effects reduce pasture productivity after droughts, based on previous studies (Prince *et al.* 1998, 2007; Diouf & Lambin 2001). Yet, RUE regularly decreases over the course of several years with above average rainfall in all treatments (see periods with rising rainfall 1987–1989 and 1993–1995 in Fig. 4). This again suggests that rainfall-induced effects add to the grazing impact on the production, causing the hump-shaped relationship between RUE and rainfall (Fig. S4, Supporting information). The inversion of this relationship during the second phase of the study period – comparable with the standing crop pattern in Fig. 3 – occurred for all grazing treatments, and was therefore caused by environmental factors other than grazing. Intra-annual drought periods were prominent during the second phase of the study and might have had a strong influence on production. If the herb layer dries up completely in such mid-season droughts and then re-establishes through re-germination (e.g. in 1999 and 2000), the biomass sampling at the end of the whole rainy season would not represent complete annual production accurately, and the productivity would be much lower than suggested by the standing crop/rainfall relationship in average years. As a measure, effective rainfall does not control for the effects of these anomalies on biomass production, because the pattern is similar when the standing crop is plotted against the total rainfall (not shown, but see Fig. S1, Supporting information, for correlation between total and effective rainfall). The weaker correlation between total annual precipitation and the number of rainfall days in the second phase of the study also points to dissimilar rainfall conditions (Fig. S2, Supporting information). More sophisticated analyses of the rainfall patterns would probably result in a better understanding of the NPP relationship, but detailed environmental data was not available in this study (e.g. Penning De Vries & Djiteye 1982; Mougin *et al.* 1995; Tracol *et al.* 2006; Hiernaux *et al.* 2009a).



**Fig. 3.** Relationship between standing crop [as a measure of the net primary production (NPP)] and effective rainfall during the entire study period and the two phases distinguished, for the three grazing treatments. Each dot symbolizes the mean standing crop of an individual 1 ha-plot, obtained from 25 sample sites of 1 m<sup>2</sup>. The lines indicate best fitting functions. To describe the trend, we used a quadratic model which had throughout a higher fit compared with a linear one. Phase 1: 1981–1995; phase 2: 1996–2007. The complex inter-annual variability in the production of annual grasslands is reflected by the weak correlation between standing crop and rainfall. The asymptotic levelling of the production curve above 400 mm total (not shown) and 250 mm effective annual rainfall, as occurred in the first phase, is a well-known pattern (e.g. Diouf & Lambin 2001; Huxman *et al.* 2004; Prince *et al.* 2007). This is in contradiction to the U-shaped functions in the second phase, with lowest production values at rainfall totals around the long-term mean.

Our results support hypothesis 1 in demonstrating that rainfall governs vegetation dynamics, especially during the first phase of the study when there were strong fluctuations in rain-

fall. Grazing was found to be a subordinate factor with regard to the inter-annual changes of herbaceous productivity.

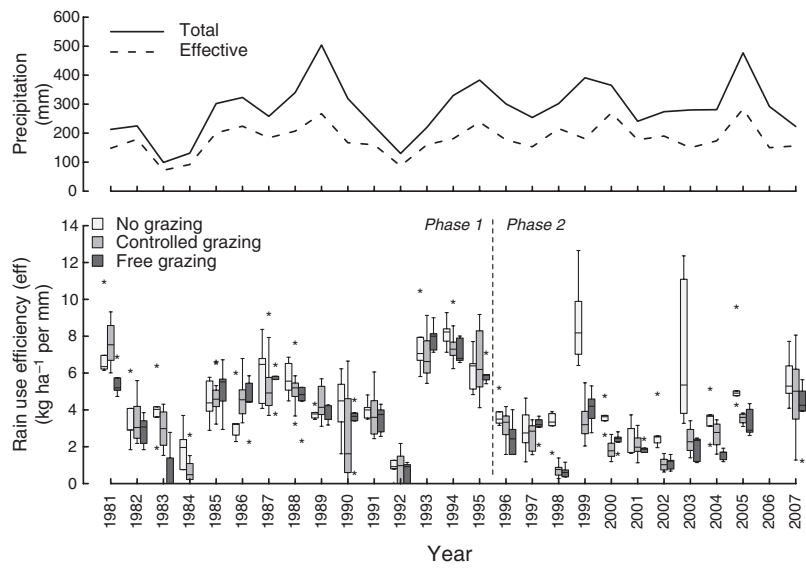
#### HYPOTHESIS 2: DEGRADATION IS A SHORT-TERM PHENOMENON OF DROUGHT PERIODS

The regression of RUE over the whole study period revealed significant declines on the grazed plots, in contrast to the treatment 'no grazing' and to the improving rainfall conditions (Fig. 4, Table S4, Supporting information). Decreasing RUE is commonly taken as an indicator of rangeland degradation (Le Houerou 1984; Verón *et al.* 2006). Higher ratios between the variability of the standing crop and that of rainfall (Table S1, Supporting information) indicate a lower stability, i.e., a weaker resilience to rainfall fluctuations, of the grazed production systems (Le Houerou, Bingham & Skerbek 1988). Furthermore, the change in plant composition in the grazed herb layer reflects the same dynamics (Fig. 5): The gradual increase in grasses, in species of low fodder value as well as in aridity-indicating species since 1992 can be interpreted as a medium-term result of persistent high grazing pressure. The non-grazed plots support this interpretation: Here, the significant augmentation of herbs is in accordance with the improving rainfall conditions.

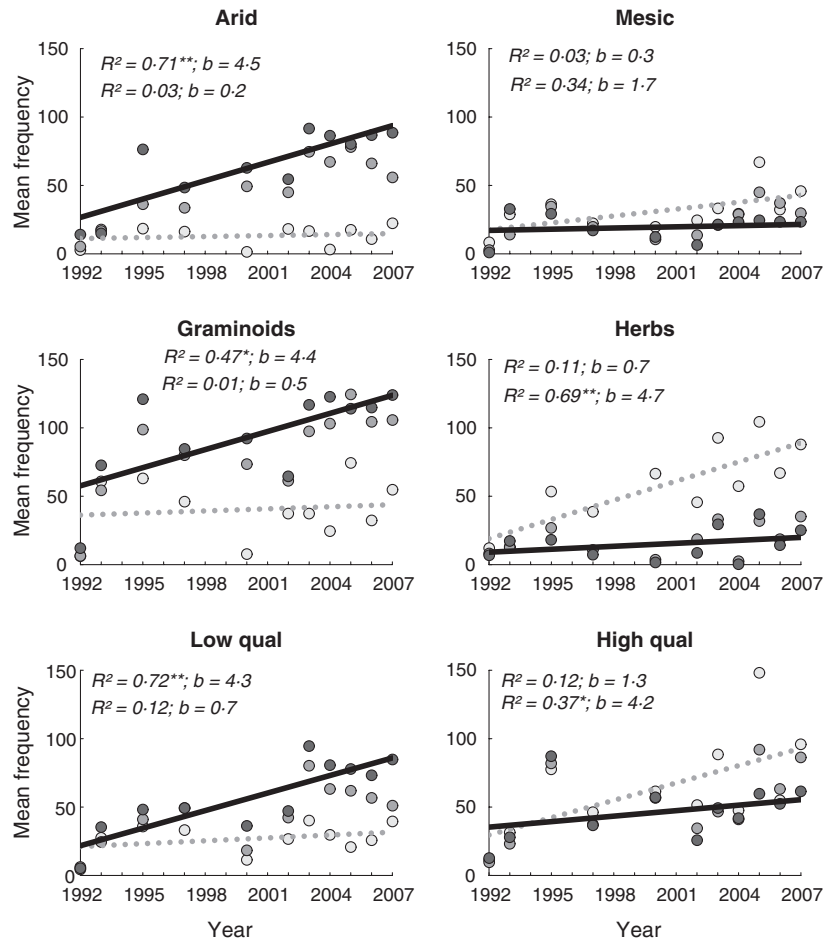
The decrease in productivity on the pastures might also be explained by medium- or long-term depletion of soil nutrients (Penning De Vries & Djiteye 1982; Hiernaux & Turner 1996; Hiernaux *et al.* 1999; Turner 1999). Reporting on studies covering a wide climatic gradient in Mali, Penning De Vries & Djiteye (1982) and Breman & De Wit (1983) concluded that in areas with annual rainfalls above 300 mm year<sup>-1</sup> the soil nutrients might become the limiting factor for production. Furthermore, Turner (1998a,b) has proven the long-term effect of the reduction in soil nutrients with increasing grazing intensity around permanent watering places in Mali (450 mm year<sup>-1</sup>). This might contribute to the drop in RUE in periods of rising rainfall found in this study, which also occurred on non-grazed plots (Fig. S4, Supporting information), but which is obviously reinforced by high grazing intensities. The sandy soils in our study area are generally low in N and P (Le Houerou 1989). If the herb layer is grazed off completely, 50% of nitrogen from the biomass is lost (Penning De Vries & Djiteye 1982). Soil analysis on 'no grazing' plots and those of the adjacent communal pasture undertaken, in 2006, in our experimental area revealed comparably higher nutrient contents in the exclosures (C, N, P, K; L. Möller, Unpublished data). Despite lacking statistical proof due to insufficient sample sizes, these results may either indicate a restoration of the soil conditions in the exclosures, a silent degradation of the communal pastures or a combination of both processes.

The long-term degradation demonstrated in this case study leads to the rejection of hypothesis 2 and corroborates the conclusions from short-term experiments investigating the mechanisms of pasture deterioration. However, the degradation trends found at our study site are not shown by the numerous

**Fig. 4.** Trend of rain use efficiency (RUE) over time derived from the effective rainfall. The cumulative total and effective rainfall are shown in the upper diagram; the overall trend of both parameters is not significant (Table S4, Supporting information). Maximum values of RUE regularly develop in the second or third season after a drought, in contrast to the more gradual increase of the standing crop (Fig. S5, Supporting information). These peaks reach about double the mean values (in accordance with Diouf & Lambin 2001). Overall trends are best shown by linear functions, whereas the dynamics in the two phases are better reflected by quadratic ones (statistics: Table S4, Supporting information). Phase 1: 1981–1995; phase 2: 1996–2007.



**Fig. 5.** Trend in the frequency of ecological indicator species (mean values of absolute frequencies for each treatment) over time. Regression lines only shown for the grazing extremes, i.e. the communal pasture ('free grazing'; solid line, upper line of statistical information) and the enclosures ('no grazing', hatched, lower line of statistics). Explanation of species groups (species listed on Table S2, Supporting information): 'arid' = aridity indicators (species of the northern Sahel with short life cycles, after Penning De Vries & Djiteye 1982), 'mesic' = more humidity-demanding species (central to southern Sahel, op. cit.), 'graminoids' = grasses (Gramineae), Cyperaceae and other grass-like monocotyledons, 'herbs' = dicotyledons (forbs = non-graminoid herbs), 'low qual'/'high qual' = species of low/high fodder quality (mainly after Boudet 1984). Species composing the pastures are still present on the enclosure plots. The fact that the frequencies of the species groups show clear gradients from 'no grazing' through 'controlled grazing' to 'free grazing' in most years, supports the premise that the enclosure plots still fit in a series of graduated grazing intensity in the local savanna.



remote sensing studies covering the study area and time period (e.g. Prince *et al.* 1998; Herrmann *et al.* 2005; with updated maps kindly made available by the first authors). Discrepancy between field production data and a remote sensing-derived productivity index (normalized difference vegetation index, NDVI) was also found by Diouf & Lambin (2001) in North

Senegal. Either the degradation processes are spatially very restricted (max. extent of experimental area 7 km), and thus the resolution of the existing sensors would be not sufficient (U. Herrmann and S. Prince, pers. comm.; Hanan *et al.* 1991); or the degradation is not yet pronounced enough to be discernible by remote sensing (Prince *et al.* 2007). Degradation might

be more severe in SW Niger, where the results of field data evaluation (Hiernaux *et al.* 2009a) agree with remote sensing data.

#### EVALUATION OF THE RESULTS IN THE CONTEXT OF THE NON-EQUILIBRIUM DEBATE

The present long-term study revealed degradation processes in the herb layer of the grazed plots which contradict the non-equilibrium theory. Yet, the non-degradability of non-equilibrium systems is based on the natural regulation of consumers by the NPP (Behnke *et al.* 1993). This precondition is increasingly ruled out in the study area (permanent presence of livestock, increasing amounts of bought-in fodder). Under these conditions, degradation of non-equilibrium systems is admitted (Illius & O'Connor 1999; Briske *et al.* 2003; Vetter 2005).

Both the grazed and the non-grazed treatments showed more characteristics of equilibrium systems in the second phase of the trial, when the rainfall variability amounted to 23%, than during the first phase (coefficient of variation (CV) = 40%). According to Ellis, Coughenour & Swift (1993), semi-arid ecosystems tend to have more equilibrium properties where the CV of annual rainfall is below 33%. In our study, the CV of 23% corresponds with average annual rainfall totals above 300 mm, conditions under which soil nutrients are expected to become a limiting production factor (Penning De Vries & Djiteye 1982). Thus, the Widou results provide evidence for shifts between periods of predominant non-equilibrium events and those more typical of equilibrium systems. Hence, the separation between these systems can be regarded as a matter of dominating effects in dependence of both temporal and spatial scales (Fernandez-Gimenez & Allen-Diaz 1999; Illius & O'Connor 1999; Briske *et al.* 2003; Vetter 2005). Therefore, our study offers an explanation for the contradictory results reported from earlier research projects in the investigation area: The findings of ecological analyses depend heavily on the climatic conditions during the study period, which may show both equilibrium and non-equilibrium dynamics on a long-term scale. If there are any trends, they largely depend on which temporal segment of the rainfall oscillations was measured. Consequently, it is unsurprising that Diouf & Lambin (2001), analysing the period 1987–1997, did not report any degradation processes in Widou Thiengoly, which is supported by our data for the respective time span (Table S4, Supporting information). Thus, longer observation periods increase the probability of including 'equilibrium phases' in the study that allow the identification of long-term degradation processes.

#### CONCLUDING RECOMMENDATIONS FOR RANGELAND RESEARCH AND MANAGEMENT

Our study clearly underlines the importance of sufficiently long observation periods for field studies within drylands, ideally a minimum of 15 years. Unfortunately, due to logistics and funding, the majority of studies are restricted to < 5 years. Due to the fact that our study was undertaken in

an overlap area between equilibrium and non-equilibrium conditions, the occurrence of effects and dynamics characterizing both regimes could be expected (Fernandez-Gimenez & Allen-Diaz 1999).

Remote sensing techniques are valid tools for long-term studies; however, field-based studies have the advantage in permitting vegetation parameters to be monitored that may indicate long-term changes (O'Connor & Roux 1995; Hiernaux *et al.* 2009b). Pasture deterioration as assessed by the plant composition need not necessarily relate to a reduction in productivity; the latter may even rise in areas with higher rainfall (Hiernaux *et al.* 2009b). Thus, the greening of the Sahel does not necessarily mean an improvement in the pasture (Herrmann *et al.* 2005; Verón *et al.* 2006). Monitoring periods covering long time frames and climatic gradients under different land use regimes are therefore a precondition to understanding rangeland fluctuations and the ecological and managerial consequences.

The Widou experience shows that opportunistic rangeland policies developed during a climatic 'non-equilibrium phase' need to be applied with caution, especially in areas where nomads became sedentary. The medium-term degradation of the pastures, shown in the present study, provide support for the warnings of a degradation risk for the Widou pastures given by Akpo, Grouzis & Gaston (1993) and Hein (2006). The persistence of a species- and nutrient-poor grassland throughout dry and wet periods not only keep production at a low level but also affect the nutritional status of livestock (Illius & O'Connor 1999). The shortage of legumes on the communal pasture during the last phase of the study period may even have limited sheep raising (Thébaud *et al.* 1995).

The Widou example shows that the persistence of drought-tolerant species during wet periods is a characteristic feature of Sahelian pastures and the main reason for their high resilience at the onset of drought periods; however, beyond a critical stocking density this resilience is gained at the price of a lower production level and pasture quality.

On the sandy soils of the study area, degradation was found to be reversible, as proven by the regeneration on the enclosure plots. Yet, the grazing experiment has also shown that neither long-term enclosure nor ranching with fixed moderate stocking rates are practical regeneration measures in this habitat, if the focus is not on biodiversity preservation but on rangeland amelioration (Thébaud *et al.* 1995; André 2001). Moderate grazing regimes imitating traditional nomadic systems are more likely to improve pasture quality and stability, but this regeneration measure will require decades of careful management.

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## References

- Akpo, L.E., Grouzis, M. & Gaston, A. (1993) Pluviosité et productivité des herbages de l'aire pastorale de Widou Thiengoli au Ferlo (Nord Sénégal). Une estimation des charges fréquentielles. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux*, **46**, 675–681.
- Anayamba, A. & Tucker, C.J. (2005) Analysis of Sahelian vegetation dynamics using NOAA-AVHRR NDVI data from 1981–2003. *Journal of Arid Environments*, **63**, 596–614.
- Ancey, V., Wane, A., Müller, A., André, D. & Leclerc, G. (2008) Payer l'eau au Ferlo. Stratégies pastorales de gestion communautaire de l'eau. *Autrepart*, **46**, 51–66.
- André, D. (2001) Dix sept ans de suivi de la végétation ligneuse et herbacée dans le périmètre expérimental de Widou-tiengholy (Ferlo, nord-Sénégal). *Élevage et Gestion de Parcours au Sahel, Implications Pour le Développement* (eds A. Tielkes, E. Schlecht & P. Hiernaux), pp. 35–48. Verlag Ulrich E. Gauer, Beuren/Stuttgart.
- Behnke, R.H., Scoones, I. & Kerven, C. (1993) *Range Ecology at Disequilibrium. New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London.
- Boudet, G. (1981) *Systèmes de Production d'Élevage au Sénégal; Étude du Couvert Herbacé (2ième Campagne)*. IEMVT, Maisons-Alfort.
- Boudet, G. (1984) *Manuel sur les Pâturages Tropicaux et les Cultures Fourragères*. 2 edn. IEMVT, Maisons-Alfort.
- Breman, H. & De Wit, C.T. (1983) Rangeland productivity and exploitation in the Sahel. *Science*, **221**, 1341–1347.
- Briske, D.D., Fuhlendorf, S.D. & Smeins, F.E. (2003) Vegetation dynamics on rangelands: a critique of the current paradigms. *Journal of Applied Ecology*, **40**, 601–614.
- Coughenour, M.B. (1985) Graminoid response to grazing by large herbivores: adaptation, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden*, **72**, 852–863.
- Daget, P. & Poissonnet, J. (1971) Une méthode d'analyse phytologique des prairies. Critères d'application. *Annales Agronomiques*, **22**, 5–41.
- Diouf, A. & Lambin, E.F. (2001) Monitoring land-cover changes in semi-arid regions: remote sensing data and field observations in the Ferlo, Senegal. *Journal of Arid Environments*, **48**, 129–148.
- Ellis, J.E. & Swift, D.M. (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management*, **41**, 450–459.
- Ellis, J.E., Coughenour, M.B. & Swift, D.M. (1993) Climate variability, ecosystem stability, and the implications for range and livestock development. *Range ecology at disequilibrium. New Models of Natural Variability and Pastoral Adaptation in African Savannas* (eds R.H. Behnke, I. Scoones & C. Kerven), pp. 31–41. Overseas Development Institute, London.
- Fernandez-Gimenez, M.E. & Allen-Diaz, B. (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, **36**, 871–885.
- Hanan, N.P., Prevost, Y., Diouf, A. & Diallo, O. (1991) Assessment of desertification around deep wells in the Sahel using satellite imagery. *Journal of Applied Ecology*, **28**, 173–186.
- Hein, L. (2006) The impacts of grazing and rainfall variability on the dynamics of a sahelian rangeland. *Journal of Arid Environments*, **64**, 488–504.
- Hein, L. & De Ridder, N. (2006) Desertification in the Sahel: a reinterpretation. *Global Change Biology*, **12**, 751–758.
- Hérault, B. & Hiernaux, P. (2004) Soil seed bank and vegetation dynamics in Sahelian fallows; the impact of past cropping and current grazing treatments. *Journal of Tropical Ecology*, **20**, 683–691.
- Herrmann, S.M., Anyamba, A. & Tucker, C.J. (2005) Recent trends in vegetation dynamics in the African Sahel and their relationship to climate. *Global Environmental Change – Human and Policy Dimensions*, **15**, 394–404.
- Hickler, T., Eklundh, L., Seaquist, J.W., Smith, B., Ardö, J., Olsson, L., Sykes, M.T. & Sjöström, M. (2005) Precipitation controls Sahel greening trend. *Geophysical Research Letters*, **32**, L21415, doi: 10.1029/2005GL024370, 2005.
- Hiernaux, P. (1998) Effects of grazing on plant species composition and spatial distribution in rangelands of the Sahel. *Plant Ecology*, **138**, 191–202.
- Hiernaux, P. & Turner, M.D. (1996) The effect of clipping on growth and nutrient uptake of Sahelian annual rangelands. *Journal of Applied Ecology*, **33**, 387–399.
- Hiernaux, P., Biélers, C.L., Valentin, C., Bationo, A. & Fernandez-Rivera, S. (1999) Effects of livestock grazing on physical and chemical properties of sandy soil in sahelian rangelands. *Journal of Arid Environments*, **41**, 231–245.
- Hiernaux, P., Ayantunde, A., Kaliou, A., Mougin, E., Gérard, B., Baup, F., Grippa, M. & Djaby, B. (2009a) Trends in productivity of crops, fallow and rangelands in Southwest Niger: impact of land use, management and variable rainfall. *Journal of Hydrology*, **375**, 65–77.
- Hiernaux, P., Mougin, E., Diarra, L., Soumaguel, N., Lavenu, F., Tracol, Y. & Diawara, M. (2009b) Sahelian rangeland response to changes in rainfall over two decades in the Gourma region, Mali. *Journal of Hydrology*, **375**, 114–127.
- Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E. & Williams, D.G. (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, **429**, 651–654.
- Illius, A.W. & O'Connor, T.G. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813.
- Le Houerou, H.N. (1984) Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments*, **7**, 213–247.
- Le Houerou, H.N. (1989) *The Grazing Land Ecosystems of the African Sahel*. Ecological Studies, 75, Springer, Berlin-New York.
- Le Houerou, H.N., Bingham, R.L. & Skerbek, W. (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments*, **15**, 1–18.
- Mougin, E., Lo Seen, D., Rambal, S., Gaston, A. & Hiernaux, P. (1995) A regional Sahelian grassland model to be coupled with multispectral satellite data. 1: validation. *Remote Sensing of Environment*, **52**, 181–193.
- Nicholson, S.E., Tucker, C.J. & Ba, M.B. (1998) Desertification, drought, and surface vegetation: an example from the West African Sahel. *Bulletin of the American Meteorological Society*, **79**, 1–15.
- O'Connor, T.G. & Roux, P.W. (1995) Vegetation changes (1949–71) in a semi-arid, grassy dwarf-shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology*, **32**, 612–626.
- Olsson, L., Eklundh, L. & Ardo, J. (2005) A recent greening of the Sahel – trends, patterns and potential causes. *Journal of Arid Environments*, **63**, 556–566.
- Penning De Vries, F.W.T. & Djiteye, M.A. (1982) *La Productivité des Pâturages Sahéliens. Une Étude des Sols, des Végétations et de L'exploitation de Cette Ressource Naturelle*. Agricultural Research Reports, 918, Pudoc, Wageningen.
- Prince, S.D., De Colstoun, E.B. & Kravitz, L.L. (1998) Evidence from rain-use efficiencies does not indicate extensive Sahelian desertification. *Global Change Biology*, **4**, 359–374.
- Prince, S.D., Wessels, K.J., Tucker, C.J. & Nicholson, S.E. (2007) Desertification in the Sahel: a reinterpretation of a reinterpretation. *Global Change Biology*, **13**, 1308–1313.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at: <http://www.R-project.org>.
- Retzer, V. (2006) Impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland revisited (Hein, 2006) – new insights from old data. *Journal of Arid Environments*, **67**, 157–164.
- Seaquist, J.W., Hickler, T., Eklundh, L., Ardö, J. & Heumann, B.W. (2009) Disentangling the effects of climate and people on Sahel vegetation dynamics. *Biogeosciences*, **6**, 469–477.
- Sinclair, A.R. & Fryxell, J.M. (1985) The Sahel of Africa: ecology of a disaster. *Canadian Journal of Zoology*, **63**, 987–994.
- Skarpe, C. (1992) Dynamics of savanna ecosystems. *Journal of Vegetation Science*, **3**, 293–300.
- Thébaud, B., Grell, H. & Mische, S. (1995) *Vers une Reconnaissance de L'efficacité Pastorale Traditionnelle : Les Leçons D'une Expérience de Pâturage Contrôlé Dans le Nord du Sénégal. (Recognising the Effectiveness of Traditional Pastoral Practices: Lessons From a Controlled Grazing Experiment in Northern Senegal)*. IIED Drylands Programme, Issue Paper, 55, IIED, London.
- Tracol, Y., Mougin, E., Jarlan, L. & Hiernaux, P. (2006) Testing a sahelian grassland functioning model against herbage mass measurements. *Ecological Modelling*, **193**, 437–446.
- Turner, M.D. (1998a) Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 1. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography*, **25**, 669–682.
- Turner, M.D. (1998b) Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 2. Effects of a phosphorus gradient on



- spatial patterns of annual grassland production. *Journal of Biogeography*, **25**, 683–694.
- Turner, M.D. (1999) Spatial and temporal scaling of grazing impact on the species composition and productivity of Sahelian annual grasslands. *Journal of Arid Environments*, **41**, 277–297.
- Verón, S.R., Paruelo, J.M. & Oesterheld, M. (2006) Assessing desertification. *Journal of Arid Environments*, **66**, 751–763.
- Vetter, S. (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments*, **62**, 321–341.
- Wessels, K.J., Prince, S.D., Malherbe, J., Small, J., Frost, P.E. & VanZyl, D. (2007) Can human-induced land degradation be distinguished from the effects of rainfall variability? A case study in South Africa. *Journal of Arid Environments*, **68**, 271–297.
- Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.
- Wiens, J.A. (1984) On understanding a nonequilibrium world: myth and reality in community patterns and processes. *Ecological Communities: Conceptual Issues and the Evidence* (eds D.R. Strong, D. Simberloff, L. Abele & A.B. Thistle), pp. 439–458. Princeton University, Princeton, NJ.

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## Supporting Information

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

**Appendix S1** Supplementary references.

**Table S1** Statistical information on rainfall and production

**Table S2** Species list/ecological groups

**Table S3** Animal numbers in Widou Thiengoly

**Table S4** Trends in rainfall, standing crop and rain use efficiency (RUE)

**Table S5** Results of the linear mixed model

**Figure S1** Relation between total and effective rainfall.

**Figure S2** Correlation between the number of rain days and rainfall totals per season.

**Figure S3** Dynamics in species composition (DCAs).

**Figure S4** Relation between rain use efficiency (RUE) and effective rainfall.

**Figure S5** Temporal trend of the standing crop.

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