

Desertification in the Sahel: Towards better accounting for ecosystem dynamics in the interpretation of remote sensing images

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ABSTRACT

To date, the interpretation of remote sensing images has not revealed wide-spread degradation of the vegetation in the Sahel. However, the interpretation of spectral information depends on a range of assumptions regarding the dynamics of the Sahelian vegetation as a function of rainfall variability and human management. Recent papers have presented diverging views on the vegetation dynamics of the Sahel and how these can be analysed with remote sensing images. We present a further analysis of the vegetation dynamics of semi-arid rangelands, in particular the Sahel, and the subsequent implications for the interpretation of remote sensing images. Specifically, the ecological processes driving the response of the Sahelian vegetation to rainfall variation are re-examined, and a regression analysis of NPP versus rainfall data is carried out. It is shown that the relation between the interannual variation in NPP and rainfall in the Sahel is non-linear and that this relation differs between sites with different average annual rainfall. It has been common practise in remote sensing studies for the Sahel to aggregate data from various Sahelian sites in order to obtain an average relation between rainfall, NPP and Rain Use Efficiency, and to assume these relations to be linear. This paper shows that this approach may lead to a bias in the interpretation of remote sensing images and that further work is required to clarify if wide-spread ecosystem degradation has occurred in the Sahel.

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1. Introduction

Semi-arid rangelands are characterised by low and highly variable rainfall. In most rangelands, livestock ranging is the most important source of income for local people. The world's largest semi-arid rangeland is the Sahel, which stretches from Senegal in the west to Sudan in the east, and harbours a population of around 70 million people (FAO, 2001). Pastoralism is the dominant form of livestock holding in the Sahel, and people tend to be food insecure in years of low rainfall (FAO, 2001). In order to enhance the livelihood of Sahelian pastoralists, and to design strategies for dealing with the impacts of climate change in the Sahel, it is essential to understand the dynamics of its vegetation.

Rain use efficiency (RUE), i.e. the amount of standing biomass produced per ha per mm of rainfall, is a central concept in

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understanding rangeland dynamics. RUE is widely used as an indicator for degradation in semi-arid rangelands (Le Houérou, 1984; Varnamkhasti et al., 1995). A range of studies have tracked changes in the RUE in the Sahel over time on the basis of remote sensing images, using NDVI (Normalized Difference Vegetation Index) values combined with rainfall data. For the Sahel, these studies tended to show stable or sometimes increasing RUE from around 1980 onwards, indicating a lack of human induced degradation (Tucker et al., 1991; Nicholson et al., 1998; Prince et al., 1998). Their findings support the non-equilibrium approach, and are summarized by Kerr (1998): “the satellite record does not show significant degradation in the Sahel”. More recent remote sensing studies show a more balanced picture for the Sahel, with zones of increasing and decreasing RUE over the last two to three decades (e.g. Heumann et al., 2007). In remote sensing studies, it is generally assumed that RUE is driven by land degradation only, and that, in the absence of degradation RUE can be assumed to be constant (e.g. Nicholson et al., 1998; Prince et al., 1998; Anyamba and Tucker, 2005; Olsson et al., 2005).

Hein & de Ridder (2006) recently proposed that, for a specific site in the Sahel, the RUE of the vegetation varies between years as a function of both ecosystem degradation and annual rainfall variation. They found that, for a certain site, the RUE tends to be low in dry years, relatively high in years with intermediate rainfall conditions, and low in years with high rainfall. Consequently, RUE cannot be assumed to be constant in the absence of degradation. The paper also indicated that the interannual variability of the RUE as a function of rainfall variability may lead to a bias in the interpretation of remote sensing images of the Sahel. Ecosystem degradation in the Sahel may have been underestimated in remote sensing studies because of an upward trend in rainfall conditions since the early 1980s, when remote sensing images for the Sahel became widely available. The paper of Hein & de Ridder (2006) evoked a critical response by Prince et al. (2007). The latter authors question the presented relationship between RUE and rainfall, the data used and the statistical test conducted. Further clarification of the variability of the RUE is therefore crucial to understand if ecosystem degradation has occurred in the Sahel, to provide input into the debate on equilibrium versus non-equilibrium approaches to understanding rangeland dynamics, to model atmosphere–biosphere interactions in regional climate models (Wang et al., 2004) and to assess the vulnerability of the Sahel to future climate change.

The aim of this paper is therefore to re-examine interannual variation in RUE as a function of rainfall variations on a given site, following up on the two earlier papers that presented diverging views on this matter, i.e. Hein & de Ridder (2006) and Prince et al. (2007). As in these papers, we focus on the herbaceous vegetation, which dominates both NPP in the Sahel and the reflection measured in remote sensing images (Bremen & de Wit, 1983). Specifically, we present (i) an updated analysis of Sahelian ecosystem dynamics on the basis of additional literature; and (ii) an improved pattern analysis, i.e. regression analysis of the relation between rainfall and NPP using new data. For the Sahel, we used additional data (1984–1993) from a long-term vegetation monitoring experiment in Mali, carried out by the International Livestock Research Institute (ILRI) and the Institut d'Economie Rurale (IER, Bamako, Mali). These data have resulted in a series of publications (e.g. Tracol et al., 2005; Hiernaux et al., 2009a), and allowed us to further examine the dynamics of Sahelian rangelands. Finally, in this paper, we re-examine the potential implications for the interpretation of remote sensing images and show that there is as yet not enough evidence from these studies to conclude that little or no degradation has occurred in the Sahel in the last three decades.

2. Methods and materials

2.1. Study area

The Sahel is conventionally defined by the zone between the 200 and 600 mm isohyets, bordering the Sahara in the north and the wetter Soudan zone in the south. The vegetation in the Sahel comprises a mix of annual grasses and forbs, with scattered trees and localised patches of perennial grasses (Bremen & de Ridder, 1991). The density of the tree cover varies throughout the Sahel, but is generally low due to low soil water availability during the dry season in combination with a high pressure on trees, which are cut for use as timber, to feed the leaves to goats, or for use as fuel wood. The contribution of the woody biomass to NPP is up to a third of NPP in some parts of the Sahel, but varies widely throughout the Sahel (Bremen and Kessler, 1995). During the last decades, there has been a gradual increase in the area of cropland in the southern part of the Sahel, driven by an increasing demand for cropland and higher rainfall conditions.

2.2. Review of processes influencing RUE and NPP

For semi-arid rangelands, the general relation between RUE, NPP and the average annual rainfall (i.e. averaged over a number of years) is generally accepted (Le Houérou et al., 1988). Note that RUE is the ratio of NPP over rainfall. For instance, in Patagonia, Paruelo et al. (1999) analyse two independent long-term datasets, one derived from field estimates and the other from remote sensing derived estimates of NPP. They find a number of factors to be responsible for annual variations in NPP and, hence, RUE of the Patagonian herbaceous vegetation, including rainfall, vegetation composition, grazing history and temperature. Paruelo et al. (1999) show that RUE typically is low at both the dry end and the wet end of the average annual precipitation gradient typical of grassland areas (200–1200 mm). They find that RUE peaks at around 475 mm, which is explained by the relatively low levels of vegetation and biogeochemical constraints at this level of water availability. At low rainfall, there are more drought resistant plant species with relatively low growth rates, and at rainfall above 400–500 mm, nutrient limitations to plant growth become increasingly important.

In this paper, we examine if and how RUE varies as a function of rainfall between years, for specific sites. In particular, we examine how RUE is influenced by annual rainfall, soil nutrient limitations, and differences in plant communities between years. The relevant processes and data are examined based on a literature review. We focus on the Sahel, but also consider studies in other semi-arid rangelands where relevant. Note that, in our analysis, we use ecosystem degradation to indicate a range of interlinked ecological processes affecting ecosystem productivity and functioning, including soil compaction, loss of soil organic matter, changes in species composition, etc (cf. Lambin et al., 2000).

2.3. Data

For this paper, we use the same dataset as Hein & de Ridder (2006), with three changes: we omit the data for Niger, we include also sites with poor and medium quality pasture in Sydenham, South Africa, and we include a new site in the Sahel: the Gourma, Mali, as described below. The sites that we maintain are (i) Sydenham, South Africa (as published in O'Connor et al., 2001); (ii) Migda, Negev Desert, Israel (Tadmor et al., 1974); (iii) Sulaihiya, Kuwait (Zaman, 1997); (iv) Ferlo, Senegal (Miehe, 1997) and (v) Chubut, Patagonia, Argentina (Jobbagy and Sala, 2000). The sampling methodologies for these datasets are described in the respective papers and not further repeated here. As pointed out in Miehe (2006), for the Ferlo, Senegal, it is assumed that biomass data represent the total NPP whereas in reality the measured NPP reflects the grazed NPP. Consequently, a bias may occur for this site (see also Miehe et al., 2010 for a comprehensive analysis of degradation in the Ferlo).

The data from Gadabedji, Niger, are replaced by additional data from Mali because the data from Niger cover only 7 years. For our analysis of the relation between rainfall and NPP, we were kindly provided a dataset for the Gourma for the years 1984–1993. These data are from a research program conducted by International Livestock Research Institute (ILRI) and the Institut d'Economie Rurale (IER), Bamako, Mali (Tracol et al., 2005; Hiernaux et al., 2009a,b). The monitored sites cover a gradient of rainfall conditions, soils and vegetation types. The data included the very dry year of 1984 as well as the wetter years of the early 1990s. Tracol et al. (2005) describe the sampling methodology followed.

For each site in the Gourma, 10 years of data were available. This time series is relatively short and we therefore selected and merged data for two nearby sites (#17 and #18). These sites have similar

ecological characteristics (including rainfall, topography, soil, and grazing history), allowing them to be merged in order to increase the number of observations in the dataset. The two sites are located in the central part of the Gourma at a distance of 7 km. They each have an average rainfall of around 350 mm, comparable grazing pressures, comparable vegetation composition and structure, and a sandy soil texture. In the two sites, runoff or run-on, which distorts the relation between rainfall and NPP, occurred only at the local scale (up to 10 s of metres), and are accounted for in the sampling methodology. The sites also had manual rain gauges on-site providing reliable estimates of annual rainfall.

The research program conducted in the Gourma monitored a range of variables expressing vegetation growth, including herbaceous and woody plants. In line with the focus of our paper, we used only the herbaceous plants for our regression analysis. Specifically, we selected the measured variable 'maximum standing mass of the herbaceous layer (weighed mean)', expressed in kg dry matter ha⁻¹ (Hiernaux and Justice, 1986). In the Gourma, this variable appeared the most accurate representation of the NPP, with the intake by grazing being not more than around 15% of the measured NPP. We are aware of the differences between standing biomass and NPP, and that the differences between the two distort the regression analysis. In the Gourma, the standing biomass measured at the end of the growing season has been corrected for grazing during growth (grazing uptake was estimated from empirical indicators of grazing and trampling density calibrated by controlled experiments). However, long-term data series are scarce for semi-arid rangelands and in particular the Sahel and standing biomass measurements are often the best information we currently have for analysing the relation between NPP and annual rainfall. The dataset that we used for the Gourma is shown in Fig. 1. Fig. 1 of Hein & de Ridder (2006) shows the dataset for the other 7 sites (for Sydenham only the medium quality pastures are shown in the figure, the full dataset for this site is shown in O'Connor et al., 2001).

2.4. Regression analysis

The regression analysis applied in Hein & de Ridder (2006) involved regression of RUE (dependent) on rainfall (independent) (cf. O'Connor et al., 2001). However, RUE is NPP divided by annual rainfall, and it is therefore not independent of rainfall. Hence, NPP rather than RUE should be regressed against rainfall (Prince et al., 2007), which is the approach taken in the current paper.

Using the NPP and the rainfall data for the various rangelands presented in Hein & de Ridder (2006) as well as for the additional

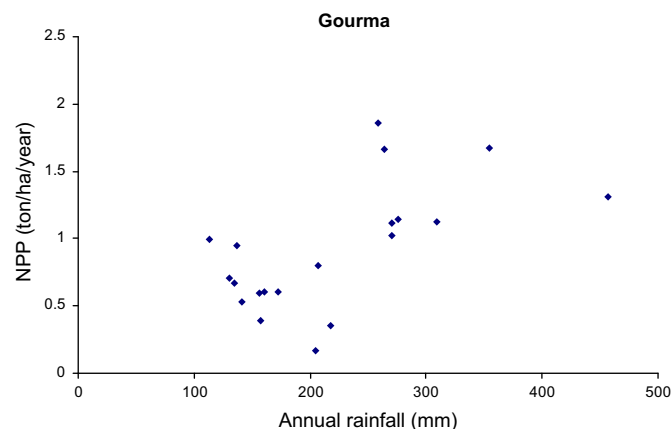


Fig. 1. Dataset for the Gourma, Mali (site 17 and 18 combined), for the years (1984–1993).

site in the Gourma, Mali, a new regression analysis was carried out. Since we were interested in revealing the relation between NPP and rainfall over the complete rainfall range for a given site, we included all rainfall points in the regression analysis.

We tested the significance of a linear, secondary and third order relation between NPP (dependent) versus rainfall (independent), assuming a normally distributed rainfall and NPP. All statistical tests were conducted in GenStat Release 10.2. In particular, we examined the R², the adjusted R², and the significance of each of the three relationships. In addition, with a normal F-test for the comparison of hierarchical models (conducted also in GenStat 10.2), it has been tested if the second order equation is significantly better than the linear equation, and if the third order is significantly better than the second order. The values for the coefficients of the regression models are also presented.

3. Results

3.1. Analysis of processes driving NPP and RUE

The ecological processes behind the relationship between annual rainfall, NPP and Rain Use Efficiency (RUE) for Sahelian vegetation dominated by annual grasses are examined below, distinguishing dry and wet years.

(i) *Dry years.* In dry years, evaporation losses and the composition of the vegetation cover play a role in explaining the low RUE. Evaporation losses depend to a large extent on the water held by the upper layer of the soil. The percolation of water to deeper layers not subject to evaporation depends on the accumulated amount of rainfall. Hence, in general, under semi-arid conditions, the relative loss of water through evaporation increases when rainfall decreases. For instance, in the Gourma (Mali), the water held in the first centimetres of the topsoil evaporates quickly after the rain event that supplied the water, with crusts reducing the evaporation rates (De Rosnay et al., 2009). In Patagonia, Paruelo et al. (2000) found that the ratio evaporation/precipitation decreased from 0.70 at the driest site, to 0.27 at the wettest extreme of a gradient ranging from 150 to 600 mm of average rainfall per year. In the Sahel, this effect is further increased because of the high proportion of annual plants. The annual grasses, and their roots, develop only after the first rain has fallen (Bremen & de Ridder, 1991). Hence, relatively more rain is evaporated before plants are able to absorb the water. Note that in addition to the general mechanism described above in the Sahel there is also a redistribution of rainwater as a function of runoff and run-on, which takes place at a more localised scale dependent on local topography (e.g. De Rosnay et al., 2009). The impact of relatively high evaporation rates in years with low rainfall could be partially mitigated if RUE was calculated on the basis of effective rainfall, i.e. the amount of rainfall that infiltrates and is available to plants, rather than total rainfall (cf. Prince et al., 2007). However, in most remote sensing studies, including Tucker et al. (1991), Nicholson et al. (1998), Prince et al. (1998), Anyamba and Tucker (2005), Olsson et al. (2005), Wessels et al. (2006) and Heumann et al. (2007), rainfall instead of effective rainfall is used to calculate the RUE.

In addition, the relative importance of C3 and C4 plants in the Sahel may play a role. In general, C3 plants have lower water use efficiency than C4 plants (Penning de Vries and Djitéye, 1982). This was also found in for instance Charleville, Australia, where the water use efficiency of the C3 plant community is only about 60% the value for the C4 community (Christie, 1978). In general,

C4 plants tend to germinate faster at the onset of the rains, and have a higher chance of failure in dry years (Penning de Vries and Djitéye, 1982). Hence, in dry years, C3 plants with generally lower RUE, tend to dominate in the Sahel (Penning de Vries and Djitéye, 1982). However, species composition and the relative contribution of C3 versus C4 at a given site also depend on a wide range of other factors. These include rainfall conditions over the past years, intensity and distribution of grazing pressure over the season, burning in the previous years - which determines the seed stock, etc. Therefore, this relation is prone to considerable variation at the local scale, and further measurements across a range of sites would be required to further substantiate the general relation between rainfall, C3 versus C4 dominated communities, and RUE.

(ii) *Wet years.* In years with high rainfall, RUE decreases because nutrients become progressively limiting to NPP (Breman & de Wit, 1983). Based on an analysis over a gradient from dry to wet conditions in the Sahel, Breman & de Wit find that NPP becomes limited by nutrients rather than soil moisture at an annual rainfall of around 300 mm y^{-1} - subject to significant variation because of differences in topography, soil, rangeland management practices, etc. Based on an elaborate review, Epstein et al. (2006) indicate that nutrient limitations in semi-arid rangelands tend to occur both at relatively high average annual rainfall, and in years with high rainfall. In the Sahel, dry years typically have a rainfall as low as 100–200 mm, and wet years may receive up to 700–800 mm depending on the latitude (Dai et al., 2004; Nicholson, 2005), which is considerably above the point where nutrients become the limiting factor.

Hence, for a given site, relatively low RUE can be expected for low and high rainfall, and relatively high RUE for intermediate levels of rainfall. This effect can be approximated by means of second order equation. The point of maximum RUE corresponds to the rainfall amount where biological and biochemical constraints are minimal, given the vegetation and soil characteristics of the site. In turn, vegetation will have developed as a function of biochemical and climatic conditions, and the peak in the RUE may also reflect adaptation of the species composition and plant community to the local rainfall pattern. Since RUE is defined as the ratio of NPP over rainfall (Le Houérou, 1984; Paruelo et al., 1999), the second order equation between rainfall and RUE implies a non-linear, second or third order equation between rainfall and NPP. Characteristic of the relation is that NPP ‘flattens off’ i.e. reaches a certain plateau or may even decrease in years with (very) high rainfall on a specific site. At low rainfall, NPP is also relatively low, with a certain minimum amount of rainfall required to support plant growth. The resulting relation between annual rainfall, RUE and NPP on a specific site, that we expect based on literature is visualised in Fig. 2. Factors that may disturb this relation, and the degree to which they may apply in the examined rangelands, are analysed in Discussion Section.

3.2. Regression analysis

The results of the regression analysis of the timeseries from the eight sites are shown in Table 1. The Table presents the overall significance of each of the three models, respectively involving a linear, quadratic and a cubic (third order) regression of NPP versus rainfall. The Table also shows the sites in which the second order equation is significantly better than the linear equation and the sites where the third order is significantly better than the second order. The values of the parameters of each regression model are also provided, based on an NPP expressed in ton ha^{-1} and rainfall expressed in mm y^{-1} . The Table demonstrates the following points.

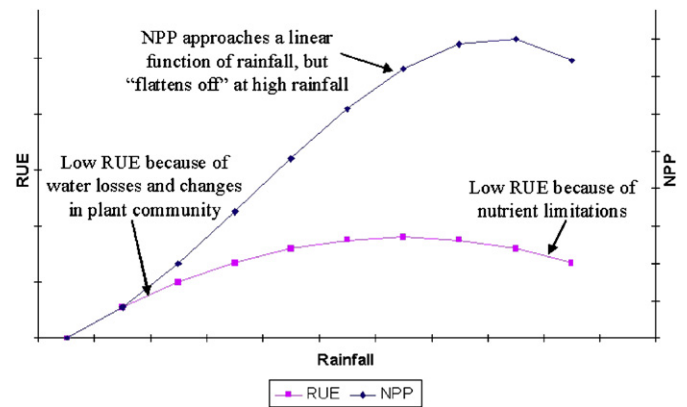


Fig. 2. Illustrative figure of RUE (squares) and NPP (rhombus) variation at a given site as a result of variation in rainfall between years.

As was to be expected, the ordinary R^2 increases when additional explanatory factors are added to the linear model to obtain the quadratic and the cubic models. The remaining, significant variability in the models is caused by, in particular, (i) inaccuracies in relating NPP to measurements of standing biomass; and (ii) inter-annual variations in the timing of the rainfall. In Sahelian vegetation, there may be rapid, significant variations in standing biomass, for instance because of grazing or because of the rapid life cycle of some of the plants. Assessing NPP based on measurements of the standing biomass therefore always leads to inaccuracies. In addition, the amount of rainfall that occurs before or after the growing season varies between years, and leads to a further disturbance of the NPP-rainfall relation when total annual rainfall is considered.

The adjusted R^2 corrects for the inclusion of additional explanatory variables and allows comparing the fit of a linear with the fit of the non-linear relations. For six of the sites, the adjusted R^2 is markedly higher for the quadratic or cubic models compared to the linear model. For Kuwait and Israel, the adjusted R^2 is approximately the same for all three models. With the exception of those two sites, the non-linear regression models have a better overall fit than the linear models. Comparison of the cubic and the quadratic models yields a more ambivalent picture. The adjusted R^2 of the cubic model is markedly better in the Gourma, and somewhat better for Patagonia and the Sydenham good and moderate pastures. For none of the datasets, the adjusted R^2 of the cubic model is markedly lower compared to the quadratic one.

The linear model is significant at $p < 0.001$ in 2 sites, at $p < 0.01$ in 4 sites, at $p < 0.05$ in 1 site and not significant in 1 site. Both the quadratic and the cubic models are significant at $p < 0.001$ in 4 sites, at $p < 0.01$ in 2 sites and at $p < 0.05$ in 2 sites. Hence, overall, the quadratic and cubic models demonstrate higher significance levels compared with the linear model. As described above, we have also tested if the quadratic model is significantly better than the linear model, and if the cubic model is significantly better than the quadratic model. It appears that, in 5 of the 8 sites, the quadratic model is significantly better than the linear model ($p < 0.05$). In two other sites (Gourma and Kuwait), moving from a linear to a quadratic model does not significantly improve the correlation, but the cubic model is significantly better ($p < 0.05$) than the quadratic model. Only in the site in the Negev desert in Israel, there is no significant difference between a linear and a non-linear model.

The vegetation dynamics of the different datasets are very different, with each of the eight different sites having a specific mix of grasses, forbs and woody plants, different pressures from grazing and burning, different soils and organic matter contents, and different temperature and rainfall characteristics. Based on these

Table 1
Regression analysis of dependent variable NPP (Mg ha^{-1}) versus independent variable rainfall (mm). The stars represent the significance level (see below). Data from O'Connor et al. (2001), ILRI-IER, Hein (2006), Tadmor et al. (1974), Zaman (1997), Jobbagy and Sala (2000).

Site (observations)	Regression models		
	Linear ($y = a + bx$)	Quadratic ($y = a + bx + cx^2$)	Cubic ($y = a + bx + cx^2 + dx^3$)
<i>S-Africa, Sydenham</i>			
Good pastures (19) (1978–1996)			
R^b	0.40	0.66	0.71
Adjusted R^b	0.36	0.62	0.66
Significance ^a	**	***	***
Significance ^b	—	**	NS
a	−0.011	−3.065	1.54
b	0.002415	0.01359	−0.0116
c	—	−0.906 E-05	3.32 E-05
d	—	—	−2.19 E-08
Moderate pastures (19) (1978–1996)			
R^b	0.51	0.64	0.72
Adjusted R^b	0.48	0.59	0.66
Significance ^a	***	***	***
Significance ^b	—	**	*
a	−0.254	−1.765	2.32
b	0.001957	0.00749	−0.0148
c	—	−0.448 E-05	3.30 E-05
d	—	—	−1.94 E-08
Poor pastures (19) (1978–1996)			
R^b	0.32	0.49	0.51
Adjusted R^b	0.28	0.43	0.41
Significance ^a	**	**	*
Significance ^b	—	**	NS
a	−0.013	−0.892	0.03
b	0.000770	0.00399	−0.00107
c	—	−0.261 E-05	0.59 E-05
d	—	—	−0.439 E-08
<i>West Africa</i>			
Mali Gourma (20)(1984–1993)			
R^b	0.37	0.55	0.57
Adjusted R^b	0.33	0.31	0.50
Significance ^a	*	*	**
Significance ^b	—	NS	*
a	0.214	−0.056	4.479
b	0.003	0.006	−0.054
c	—	−4.5 E-05	6 E-05
d	—	—	2.7 E-07
Senegal(10) (1981–1990)			
R^b	0.70	0.91	0.92
Adjusted R^b	0.66	0.88	0.88
Significance ^a	**	***	***
Significance ^b	—	**	NS
a	−0.014	−0.901	−1.554
b	0.00477	0.01672	0.0308
c	—	−3.505 E-05	−12.2 E-05
d	—	—	0.0162 E-05
<i>Latin America</i>			
Patagonia (10) (1984–1995)			
R^b	0.35	0.65	0.76
Adjusted R^b	0.30	0.63	0.68
Significance ^a	NS	*	*
Significance ^b	—	*	NS
a	0.327	−0.117	−0.548
b	0.001507	0.00754	0.01811
c	—	−1.806 E-05	−9.11 E-05
d	—	—	0.148 E-06
<i>Middle East</i>			
Kouwait (10) (1979–1988)			
R^b	0.95	0.95	0.98
Adjusted R^b	0.95	0.94	0.97
Significance ^a	***	***	***
Significance ^b	—	NS	**
a	−0.1088	−0.1251	0.262
b	0.003447	0.00393	−0.01411
c	—	−0.293 E-05	22.77 E-05
d	—	—	−0.879 E-05
Israel (11) (1962–1973)			
R^b	0.62	0.68	0.74
Adjusted R^b	0.58	0.60	0.62
Significance ^a	**	**	**

Table 1 (continued)

Site (observations)	Regression models		
	Linear ($y = a + bx$)	Quadratic ($y = a + bx + cx^2$)	Cubic ($y = a + bx + cx^2 + dx^3$)
Significance ^b	–	NS	NS
a	0.060	–0.96	0.37
b	0.00939	0.02012	–0.0134
c	–	–2.28 E-05	15.7 E-05
d	–	–	–0.0263 E-05

^a *** < 0.001; ** < 0.01; * < 0.05; NS is not significant; - means no value.

^b Significant change with regard to the former model; significance level is as indicated above.

differences between sites, three observations stand out in Table 1. First, in the Negev desert, Israel, the non-linear relation was not significantly better or worse than the linear relation. Second, the relation between rainfall and RUE in Sydenham seems disturbed in the poor quality pastures compared to the moderate or good quality pastures. Third, in Kuwait, all three models are significant. These observations are further elaborated below.

The Migda experiment in Israel comprised vegetation plots dominated by annuals, but the NPP of these plots may have been influenced by relatively high soil nutrient concentrations as the plots were established on abandoned previously fertilised cropland (Tadmor et al., 1974). High nutrient availability through the after effect of fertilisation may have resulted in higher than average biomass production particularly at higher than average rainfall causing that the tract is linearly continued at higher rainfall end (Fig. 1).

In Sydenham the significance of the quadratic and in particular the cubic relationship is lower for degraded pastures than that for moderate and high quality pastures. In these degraded sites, physical degradation of soils may cause lower infiltration of rainfall and thus lower water availability for the vegetation resulting in water-limited growth. With increasing degradation, a linear relationship will then be more applicable compared to a non-linear relationship, because overall the site may be subject to a higher level of water deficiency and a lower level of nutrient deficiency.

In Kuwait, there is no strong difference in the significance of the three models. This may be influenced by a lack of high rainfall years in the dataset as well as the characteristics of the local vegetation, which include a high share of perennial species.

In summary, the regression analysis shows that currently available data point to a non-linear relation between NPP and annual rainfall at given sites in semi-arid regions including the Sahel, with NPP 'flattening of' in years with high rainfall. However, it is less clear from the regression analysis that the cubic relation between rainfall and NPP is better than the quadratic relation. Only in three out of 8 sites the cubic relation was significantly better than the quadratic ($p < 0.05$). The next section discusses by the factors that may influence the relation between rainfall and NPP.

4. Discussion

4.1. Factors influencing the relation rainfall-NPP

In the previous section, we identified a number of ecological processes that cause RUE to vary as a function of annual rainfall, in particular relatively high evaporation losses in dry years, nutrient limitations in wet years, and differences in plant communities in years with different rainfall. However, when analysing a time series of rainfall-NPP data for a given site, the observed pattern may potentially be different from the expected pattern. The relation rainfall-NPP can be disturbed by several factors: (i) nutrient status

of the sample plots; (ii) lag effects; and (iii) differences in the relation rainfall-effective rainfall. These aspects are briefly described below.

(i) *Nutrient status of the monitored site.* As indicated by the experiment in Migda, (past) fertilisation of the site may disturb the relation between rainfall, RUE and NPP because nutrient constraints in years with high rainfall are decreased. Consequently, the non-linearity disappears and a generally linear relation between rainfall and NPP can be expected.

(ii) *Lag effects.* The relation between rainfall and NPP in semi-arid sites may be distorted by a lag in the response of vegetation to changes in rainfall, so that NPP in a specific year is partly affected by rainfall in previous years (e.g. Prince et al., 2007). A lag effect will generally not lead to a long-term trend, but may increase the interannual variability in the relation rainfall-NPP. In the Sahel, however, a retarded response to the rainfall of previous years is unlikely to be of major influence, with the exception of woody plants (Hiernaux et al., 1994). Specific for the Sahel is the dominance of annual species in the herbaceous layer. Lag effects are therefore not related to the storing of nutrients in plant biomass in favourable years. There is also no or very little carry over of water in the topsoil from one year to the next because of a long dry season with a total absence of rainfall (Penning de Vries and Djitéye, 1982). Lag effects, however, may play a more pronounced role in other semi-arid rangelands.

(iii) *Differences in the ratio rainfall - effective rainfall as a function of different runoff.* Besides losses due to evaporation, runoff can affect water availability for plant growth on sloping areas (Penning de Vries and Djitéye, 1982). Early rain showers on bare soil where annual vegetation has not been established yet are prone to runoff as are large rainfall events compared to small rainfall events. In addition, runoff increases at high-intensity rainfall events. Hence, the fraction of rainfall that is lost for plant growth due to runoff can strongly vary between years.

We now return to the criticism raised by Prince et al. (2007) on the Hein & de Ridder (2006) study. We concur with parts of the criticism raised by Prince et al. (2007), in particular that NPP not RUE should be regressed against rainfall (as we have corrected in the current paper) and regarding the availability of more sophisticated remote sensing studies that indicate zones of increasing and decreasing RUE in the Sahel. A key difference between Prince et al. (2007) and our analyses is that they exclude high rainfall years from the statistical tests. They argue that the impact of high rainfall years is irrelevant because only few years with high rainfall occurred in the Sahel since the 1980s. The purpose of our paper is, however, to come to a better understanding of rangeland dynamics and we therefore include high rainfall years. Also, because time series are

short, the omission of one or more years in each time series leads to lower significance levels.

4.2. Implications for the interpretation of remote sensing data

Remote sensing studies commonly use RUE as an indicator for degradation of the vegetation (e.g. Prince et al., 2007). The complexity of the relation between NDVI measured with remote sensing techniques as a proxy for NPP, and rainfall from rain gauges has been recognised in a range of studies. This complexity relates to establishing the physical relation between NDVI and NPP, as well as to the spatial scaling up of point measurements (NPP, rainfall) in order to relate them to remote sensing images. For instance, Wessels et al. (2006) calculate expected values for the NDVI on the basis of annual rainfall, and analyse for each pixel deviations from the expected value in order to obtain trends in degradation or rehabilitation of the vegetation in a semi-arid rangeland in South Africa.

In the Sahel, the relation between NPP and NDVI has been analysed by Milich and Weiss (2000), who conclude that “the relationship between NDVI and rainfall is fairly well established for growing season rainfall between 250 and 500 mm. In desert border zones with annual rainfall below 250 mm, this relationship becomes unpredictable”. They further propose that, in areas with rainfall below 250 mm y^{-1} , the relationship between NDVI and rainfall is non-linear, and explain part of this non-linearity through relatively high evapotranspiration losses in years with low rainfall. The complex relation between biomass, NDVI and degradation is also illustrated by Diouf and Lambin (2001), who analysed biomass and NDVI data for a range of sites in the Ferlo (Senegal), including degraded sites, during a ten-years period. They found that “for the sites which are affected by degradation, the decline in RUE is only demonstrated by the biomass-rainfall ratio, and not by the NDVI-rainfall ratio. Therefore, NDVI data are less likely to reveal trends in degradation than biomass data” (Diouf and Lambin, 2001, p142).

Heumann et al. (2007) analyse trends in various aspects of the NDVI in order to assess ecosystem degradation patterns in the Sahel. Among other factors, they examine the annual amplitude in the NDVI, the seasonally integrated NDVI, and the length of the growing season. Each of these factors provides information on the behaviour of the vegetation in a specific year. For instance, the seasonally integrated NDVI provides an indication of the total amount of green biomass present on a pixel during a year, from which vegetation net production can be estimated.

However, even if other dimensions of the NDVI are studied, such as the seasonally integrated NDVI, or the phase adjusted phenological cycle, a trend in the rainfall may still lead to a bias in the interpretation of the satellite data products. For instance, in the RESTREND method proposed in Wessels et al. (2006) both the underlying rainfall-NPP relationship and degradation impacts have to be extracted from the same time series, and the impact of a RUE that varies with annual rainfall for a given site is not factored in (as acknowledged in Wessels et al., 2006). Hence, also the recent remote sensing studies that have been deployed to examine ecosystem degradation in the Sahel to date are sensitive to a potential bias due to the impact of a trend in rainfall on the RUE.

The implications of the upward trend in rainfall in the Sahel since 1980 for the interpretation of remote sensing images are illustrated in Fig. 3. Fig. 3 shows how ecosystem degradation can potentially be masked by the rainfall variation that has occurred in the Sahel in the period 1981–2000. The figure shows two potential models for the relation rainfall and RUE, for two scenarios: with and without degradation. Rainfall patterns are conform actual, averaged rainfall patterns that occurred in the Sahel (from Dai et al., 2004). The RUE functions are specified using fictive, but potentially realistic parameter values.

Model 1 assumes RUE independent of rainfall, with an assumed value for the RUE of 5 kg $mm^{-1} ha^{-1}$ in 1981 (a typical value for Sahelian grassland, see e.g. Le Houérou, 1984). With degradation, in Model 1, the RUE gradually decreases to 4 kg $ha^{-1} mm^{-1}$ in 2000, which is a relatively strong rate of degradation (Le Houérou, 1984).

In Model 2, a quadratic relation between rainfall and RUE is assumed, with the RUE being 5 kg $mm^{-1} ha^{-1}$ (maximum) in a year with average rainfall (i.e. 250 mm), and 0 in a year with 0 mm rainfall (in line with the models presented in Hein & de Ridder, 2006). In Model 2, in the scenario with degradation, the maximum RUE gradually decreases from 5 to 4 kg $ha^{-1} mm^{-1}$ in 2000.

In the scenario *without degradation* (left hand side), RUE can be expected to be constant in case it is independent of rainfall (Model 1). If RUE is also a function of rainfall, as we propose, RUE is expected to vary, with relatively high values in years with intermediate rainfall, and relatively low values in dry or wet years (Model 2).

In the scenario *with degradation* (right hand side), we find that RUE steadily decreases if it is a function of degradation only (Model 1). If RUE is also a function of rainfall (Model 2), an interesting phenomenon occurs. Based on the actual rainfall pattern that occurred in the Sahel in the period 1981–2000, RUE increases slightly in the period 1981–2000 (trendline), in spite of the degradation that we assumed (from 5 to 4 kg $ha^{-1} mm^{-1}$). Hence, the degradation of the vegetation, expressed through a reduction in the maximum RUE of the vegetation, can be concealed by the increase in rainfall from strongly below average in the early 1980s to close to average in the second half of the 1990s.

Nicholson et al. (1998); Prince et al. (1998); Anyamba and Tucker (2005); and Olsson et al. (2005) found no significant upward or downward trend in RUE for most of the Sahel. Each of these studies assumed a linear relation between NPP and rainfall, in other words RUE independent of rainfall. As motivated above, we believe that the outcomes of these studies may be subject to a bias due to the rainfall pattern that the Sahel experienced since the early 1980s, and that it is currently not possible to make any firm conclusions on the occurrence or not of large scale degradation in the Sahel.

In order to come to a better understanding of degradation in the Sahel, the interpretation of remote sensing images would need to consider two complexities in the relation rainfall-NPP. First, the non-linearity in the relation rainfall-NPP needs to be accounted for. Second, there is a need to consider the variability in RUE between sites. This variability occurs as a function of for instance relief, soil type, runoff and run-on, plant communities, woody biomass cover, grazing and burning history, etc. The assumptions of a uniform relation between NPP and rainfall, and hence NDVI and rainfall, will lead to an overestimate of the RUE in some areas, and an underestimate of RUE in other areas.

Further analysis of remote sensing images based on enhanced modelling of the relation rainfall, RUE, NPP and NDVI is required to examine which parts of the Sahel have been subject to degradation and which parts show signs of increasing RUE. This would also facilitate reconciling the remote sensing record with the various ecological studies that point to degradation of the Sahel in specific areas, such as Lindqvist and Tengberg (1993).

4.3. Implications for the ecology of semi-arid rangelands

The effect of rainfall variation and changes in vegetation composition on RUE can be anticipated to be most significant in case of a vegetation dominated by annual species, as these species will only germinate and start developing a root system after the onset of the rains. Since the Sahel is dominated by annual plants (Penning de

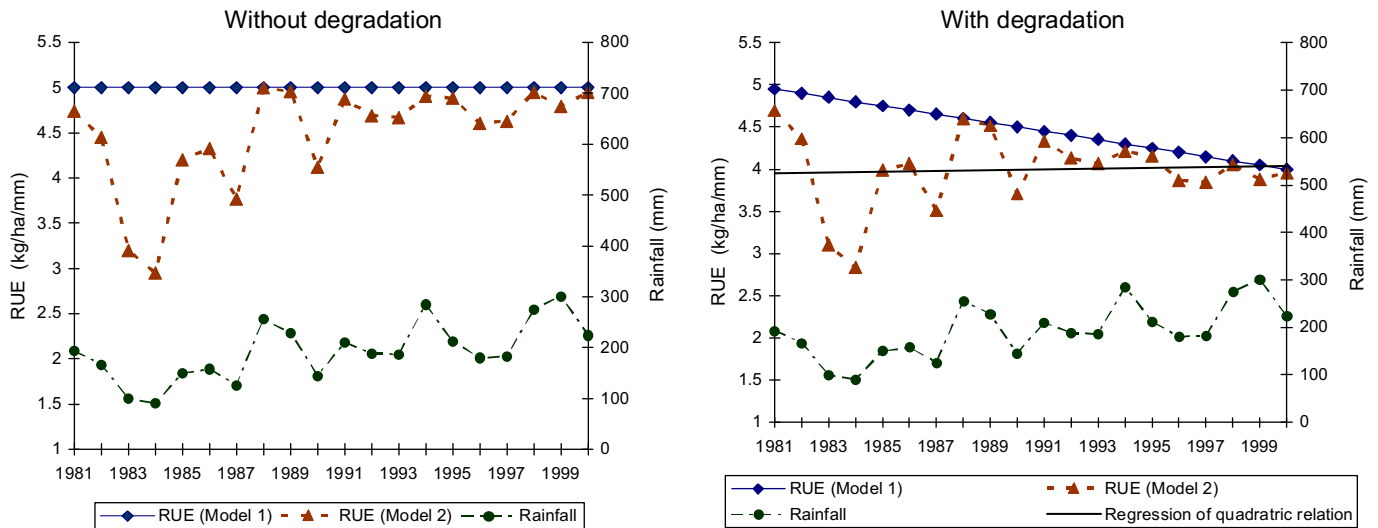


Fig. 3. The relation between rainfall, degradation and RUE, for the actual rainfall in the Sahel in the period 1981–2000. In Model 1, RUE is independent of annual rainfall, in Model 2 (quadratic relation), RUE is dependent of annual rainfall (see text above).

Vries and Djitéye, 1982), this effect may be stronger for the Sahel than for other semi-arid rangelands. Towards the southern part of the Sahel, arable farming becomes more important, and the relationship between RUE and rainfall is disturbed, as there is less change in species composition in cropland in years with different rainfall. Because nutrient limitations may be less severe, at least in fields where manure and/or inorganic fertiliser is applied, RUE and rainfall may show a different form, as discussed for the site in Israel (and see also Hiernaux et al., 2009b). The implications of interannual changes in plant communities (dominance of C3 versus C4 plants) in the Sahel need to be further examined.

Clarification of the amount of ecosystem degradation that has occurred in the Sahel in the past decades is important for the debate on equilibrium versus non-equilibrium theories, and for formulating rangeland management strategies (e.g. Vetter, 2005). A lack of degradation in the Sahel, as suggested by remote sensing analyses conducted to date, would confirm the insights of the non-equilibrium approaches to rangeland management (cf. Sullivan and Rohde, 2002). However, we question one of the assumptions underlying most remote sensing studies to date (in particular: the assumption that RUE is only influenced by degradation and is independent of interannual variation in RUE). If updated remote sensing studies detect a much higher level of degradation than currently assumed, this would point to a need for further examining the relation between grazing pressures and their impact on Sahelian rangeland dynamics and productivity.

In this case, in the Sahel, degradation in the last decades may have been concealed by an increasing rainfall trend, with relatively favourable rainfall conditions dominating throughout most of the last decade. The current relatively favourable livestock ranging conditions in the Sahel would then be a consequence of favourable rainfall conditions only (and not of a reduction in degradation or of rehabilitation of the vegetation due to better management). The impacts of a future drought on the productivity of the ecosystem may then be unexpectedly severe and the population of the Sahel would be particularly vulnerable to future droughts (cf. Schlesinger et al., 1990; Illius and O'Connor, 1999).

The results of this study are therefore also relevant for understanding the potential impacts of climate change in the Sahel. Several climate change studies indicate that there is a risk of a shift to substantial drier conditions in the Sahel in the coming decades

(e.g. Held et al., 2005, for an overview see Hein et al., 2009). For instance, Held et al. (2005) project a 14% drying for the whole Sahel region towards the 2050s. This would increase the risk of occurrence of major droughts, and point to the need to develop strategies to mitigate the impacts of droughts. In addition, increasing rainfall variability, which is expected by Held et al. (2005) may lead to a higher proportion of rain falling in high rainfall events, although the relation between rainfall variability and intensity has not yet been fully clarified (Lebel and Ali, 2009). Since high-intensity rainfall events would have a higher runoff, it would lead to a further reduction of water available to plants on slopes.

5. Conclusions

The analysis of ecosystem processes and the data regression conducted in this paper point to a non-linear rather than a linear relation between rainfall and NPP in semi-arid rangelands. The non-linearity is caused by an increasing evaporation/precipitation ratio at lower rainfall, increasing nutrient limitations in years and zones with high rainfall, and potentially by a different ratio C3/C4 plants in dry versus wet years.

These ecological findings are important for the interpretation of remote sensing studies. First, it is recommended that remote sensing studies consider the interannual variability in NPP and, consequently, RUE as a function of annual rainfall variability. Second, it is recommended that these studies account for the difference in the relation rainfall–NPP between sites. The complexity of the relation between rainfall and NPP in semi-arid rangelands, and the upward trend in rainfall that occurred in the Sahel from the early 1980s onwards need to be considered in the analysis of remote sensing images of the Sahel, before any final evaluation of the degree of ecosystem degradation in this region can be established.

Hence, further analysis of long-term ecological data and a better understanding of the relation between rainfall, degradation and RUE are required in order to interpret degradation as a function of developments of the NDVI and other spectral data. In order to improve our understanding of rangeland dynamics, there is an urgent need to combine remote sensing data with field data on vegetation structure, composition and productivity from long-term monitoring programs.

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